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The conservation status of Hutton's shearwater (*Puffinus huttoni*) at Shearwater Stream, Kaikōura, New Zealand: a small population at risk?

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Abstract: Hutton's shearwater (*Puffinus huttoni*) is a burrowing petrel endemic to the alpine zone of the Seaward Kaikōura Ranges, New Zealand. In November 2019, we accessed an understudied breeding colony at Shearwater Stream in the Puhi Peaks Nature Reserve for the first time since a M_w 7.8 earthquake struck the region in 2016. We measured population parameters and carried out a geomorphological assessment. We estimate that the Shearwater Stream colony supports approximately 3,000 breeding pairs. Ground deformation attributed to the 2016 earthquake did not explain the discrepancy between this estimate and the commonly cited (pre-quake) population estimate of ~8,000 pairs. We highlight the limitations of extrapolated population parameters and of using vegetation cover as a coarse proxy for colony area. We discuss how low burrow occupancy and long-term reductions in the availability of suitable habitat indicate a population at risk of decline. We highlight how stable long-term data for burrow density and breeding success may not be reliable indicators of population health at Shearwater Stream.

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INTRODUCTION

The effective conservation management for species with limited breeding range and fragmented conservation units requires the assessment of species health at the population level (Wilcox & Murphy 1985). For example, the adverse effects of predator-prey dynamics, in combination with demographic, genetic and environmental stochasticity, on the long-term viability of small populations are often disproportionately high (Shaffer 1981; Lyver *et al.* 1999). Conservation managers must implement mitigation measures to address progressive habitat fragmentation and insularity caused by anthropogenic factors and/or natural perturbation, at the population level. Such considerations have motivated the present study of a relict population of Hutton's shearwater (*Puffinus huttoni*) (Matthews 1912).

Hutton's shearwater is a burrowing petrel limited to two localities on the east coast of South Island New Zealand (Marchant & Higgins 1990; BirdLife International 2019), where breeding is confined to the alpine zone (1,200–1,800 m a.s.l.) of the Seaward Kaikōura Ranges. The two colonies comprise 94% and 6% of the total remaining population (Cuthbert 2019), in addition to one recently established lowland artificial colony of about 75 birds on the Kaikōura Peninsula (Rowe 2014, 2018; Rowe & Howard 2023). Historic range contractions for Hutton's shearwaters are primarily credited to habitat destruction by feral pigs (*Sus scrofa*) (Cuthbert 2002). Other factors considered to be involved include interannual declines in the seasonal availability of pelagic Euphausiid krill and Clupeid fish prey (Sherley 1992; Bennet *et al.* 2019), the destruction of burrows by browsing red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), and wild goats (*Capra hircus*) (Sherley 1992; Cuthbert 2002), and to a lesser degree predation by invasive stoats (*Mustela erminea*) (Cuthbert & Davis 2002a).

The smaller of the two remaining alpine colonies is located at Shearwater Stream in the Wharekiri Valley (42.10°S, 173.40°E), within the Puhi Peaks Nature Reserve. The terrain across the Shearwater Stream colony catchment consists of steep rock and scree slopes, which are difficult to access and traverse. The current classification (Endangered) of the species on the IUCN Red List, including the population trend (stable) (BirdLife International 2019) has been largely informed by long-term monitoring studies conducted at the larger and more accessible Kowhai Valley colony (42.16°S, 173.36°E) (Sommer *et al.* 2009), and supported by regional-scale population estimates derived from colour-mark-recapture studies of individuals foraging at sea (Rowe *et al.* 2018).

In November 2016, a shallow M_w 7.8 earthquake with a depth of about 14 km struck near Waiau, north-east Canterbury, propagating northwards towards Kaikōura. The Shearwater Stream colony is situated about 1.3 km from the Jordan Thrust, which underwent surface rupture during the earthquake (Litchfield *et al.* 2018) and was therefore within the high-shaking and high-damage zone surrounding the fault (Massey *et al.* 2018, 2020). Ground shaking in the area was modelled with peak ground acceleration (PGA) values exceeding 1 (gravity is overcome at $PGA > 1$) over large parts of the region (Kaiser *et al.* 2017). In December 2017, an assessment of both the Shearwater Stream and Kowhai Valley colonies was commissioned by Fisheries New Zealand to assess the extent of habitat loss attributable to the earthquake (Cuthbert 2019). However, access on foot was not permitted at the Shearwater Stream colony due to the instability of the terrain at the time (Cuthbert 2019).

Prior to this study, the colony boundaries at Shearwater Stream were mapped once, in 1988, providing a planimetric colony area of 2.5 ha with a population estimate of 9,800 breeding pairs (Sherley 1992). Following the implementation of the burrowscope and standardized methodology for determining burrow occupancy in the late 1990s, the population at Shearwater Stream was thought to be more in the region of 7,750 breeding pairs (Cuthbert & Davis 2002b). The calculation used an average rate of burrow occupancy as measured over a ten-year period in the larger Kowhai Valley colony (Cuthbert & Davis 2002b), applied to the colony area as determined at Shearwater Stream the previous decade (Sherley 1992). The revised population estimate was never verified in the field. However, numerous studies, species assessments, and literature reviews have since reported the Shearwater Stream population of Hutton's shearwaters to be about 8,000 pairs (Cuthbert & Davis 2002a, 2002c; Sommer *et al.* 2009; Waugh *et al.* 2013; Rowe *et al.* 2018; BirdLife International 2019).

Up-to-date, site-specific population parameters are required to determine the conservation status of the smaller Hutton's shearwater colony and to inform appropriate management. The objectives of this study were, 1) to provide revised estimates of mean burrow density, mean burrow occupancy, breeding success, colony area, and population size for Hutton's shearwater at Shearwater Stream, and 2) to assess the underlying geomorphology of the colony catchment in order to better understand the extent of any damage to breeding habitat sustained during the 2016 earthquake. The current and long-term conservation status of the colony was inferred using longitudinal data derived from an in-depth review of primary and grey literature.

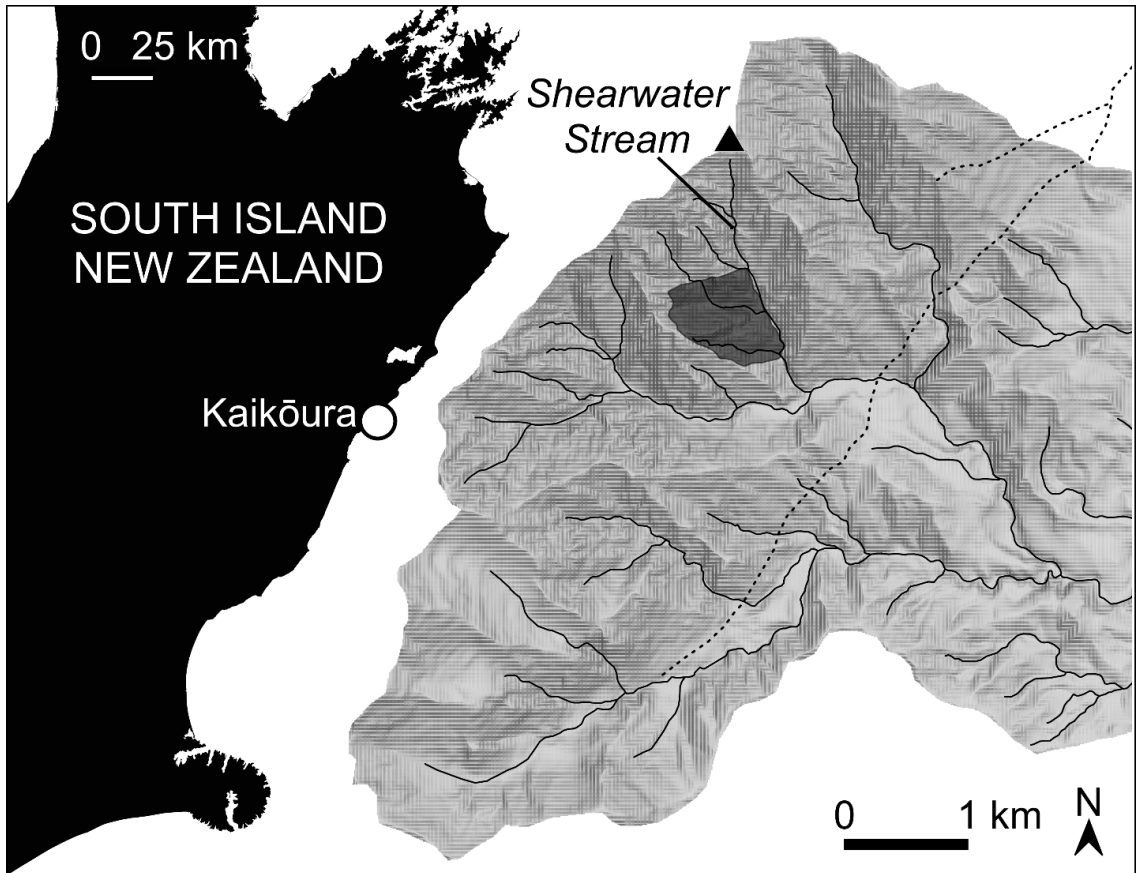


Figure 1. Location of the Hutton's shearwater (*Puffinus huttoni*) colony, darker shaded region south of Tarahaka Peak (2,283 m above mean sea level, black triangle), at Shearwater Stream in the Wharekiri catchment (white region to the north of the Kaikōura township) in the Seaward Kaikōura Ranges, New Zealand (42.2°S, 173.8°E), in relation to the local elevation (LINZ 2014), its nominal tributary of the Wharekiri watercourse (solid black lines, LINZ 2011a) and the Jordan Thrust (dashed black lines), which ruptured during the 2016 Kaikōura earthquake. Base map of New Zealand sourced from LINZ 2011b

MATERIALS AND METHODS

Study site

The rock substrate of the site of the Hutton's shearwater colony at Shearwater Stream (Fig. 1) is a mixture of argillite and sandstone dominated sequences of Torlesse (Pahau) terrane 'greywacke' (Rattenbury *et al.* 2006). The headwaters of the catchment drain from the main divide of the Seaward Kaikōura Ranges, from an unnamed peak (2,414 m) and Tarahaka (2,283 m), before joining with the larger Wharekiri Stream at 1,050 m elevation (Fig. 1).

The terrain is steep, with local relief >1,300 m, and comprises rocky slopes facing all directions. Chutes of shingle scree and thick colluvium (a mixture of grain sizes from clay to boulders

indicative of down-slope movement and deposition of debris) separate the rock faces. Shearwaters burrow in areas of deeper soil associated with *Chionochloa* snow tussock (Cuthbert & Davis 2002c), in numerous small sub-colonies (Fig. 2). We were able to access sub-colonies 1, 2a and 5a in the 2019/20 and 2020/21 breeding seasons. Sub-colonies 2b-2d, 3a, 3b, 4 and 5b-5e were deemed inaccessible due to safety concerns.

Population parameters of the Hutton's shearwater

Measuring burrow density and burrow occupancy

The mean number of burrows per square metre, hereafter referred to as 'burrow density', was calculated using a plot sampling approach within sub-colony 1, sub-colony 2a, and sub-colony 5a

(sub-colonies labelled as per Fig. 2 in Sherley 1992). Sub-colonies were visited over two days 21–22 November 2019. Circular plots of 20 m² were constructed by describing a circle of radius (*r*) 2.52 m around a central aluminium pole using a length of rope with a marker at 2.52 m. The location of each non-overlapping plot was determined by sighting a plot centre at random, working uphill through each sub-colony in a zig-zag motion. One person walked the rope in an anti-clockwise direction beginning and ending at an azimuth of 270°. The same person counted all burrow entrances within the plot where $\sim 1.26 \text{ m} < r < 2.52 \text{ m}$. A second person walking behind the rope counted all burrow entrances located on the inside of the circle ($0 \text{ m} < r \leq \sim 1.26 \text{ m}$). The rope was kept taut and lifted over tussock where required. Where it could be determined, a burrow with two or more entrances was recorded as a single burrow. Burrows at the edge of a plot were excluded where more than 50% of its entrance was beyond the 2.52 m marker. Burrows were counted by calling aloud consecutive numbers (starting at '1' with each new plot) and staking all entrances with 15 cm long, white pegs immediately after detection. The mean burrow density for each sub-colony was calculated as the sum of the burrow densities measured for each plot, divided by the total number of plots scored for burrow density within that sub-colony.

The rate of burrow occupancy (the proportion of burrows containing a nest chamber with both an egg and incubating bird at the time of detection) was determined for a subset (due to time limitations) of plots sampled for burrow density. A burrowscope (Sextant Technology Ltd, model "Taupe") was used to determine the contents of all tunnels and chambers within each burrow. Observers either had previous experience burrowscoping for Hutton's shearwater at Shearwater Stream (NRM, MM, MB, J. Kilgour) or were trained *in situ*. To reduce false negatives due to observer fatigue, observers were swapped out every 30 minutes from a team of five. Empty burrows were double-checked by a second observer. Occupied burrows were checked once. Observer initials were recorded against each burrow. Nesting material can be retained within burrows for consecutive years following a breeding attempt (A. Davis in Sherley 1992), therefore the sole presence of nesting material was not considered as adequate evidence of an occupied burrow. To prevent duplications, white pegs placed when scoring burrow density were removed immediately after scoping. In cases where the end of the burrow could not be located the burrow was excluded from further analysis. Burrows were first visited an average of 22 days after peak egg laying (around the second week of November, see Cuthbert & Davis 2002c). The mean burrow occupancy for each sub-colony was calculated as the sum of the burrow

occupancies measured for each plot, divided by the total number of plots scored for burrow occupancy within that sub-colony.

Measuring breeding success

Breeding success, here defined as the proportion of chicks reared to late nestling or about 84 days old (Cuthbert & Davis 2002c), from a sample of incubating birds, was calculated for both the 2019/20 and 2020/21 breeding seasons. A subset of occupied burrows from sub-colony 5a were marked by inserting an upright metal pole of 1 m in length into the ground near the entrance of each burrow. These burrows were then checked for the presence of a live chick during the late chick-rearing stage (Table 1).

Table 1. Visit dates and sample sizes used to measure breeding success of Hutton's shearwater in sub-colony 5a at Shearwater Stream (see Fig. 1).

Season	1 st visit	2 nd visit	Difference	Number burrows
2019/20	24 November 2019	10 February 2020	79 days	60
2020/21	4 December 2020	22 February 2021	81 days	50

Burrowscopes are a reliable method for monitoring breeding success where occupancy can be confirmed (Cuthbert & Davis 2002c). The presence of down at the second check was not considered as sufficient evidence of a successful breeding attempt, as shed down feathers have been known to remain for at least one successive year in an unused burrow (A. Davis in Sherley 1992). All tunnels and chambers of 'failed' burrows were checked independently by two observers to prevent false negatives.

Delineating colony area

The boundaries of all known areas of burrowed ground at sub-colonies 1, 2a and 5a were recorded on foot using a hand-held GPS unit on 10 February 2020. The boundaries of inaccessible sub-colonies 2b–2d, 3a, 3b, 4, and 5b–5e were drawn by MM on 0.5 m resolution aerial photographs captured by drone on 10 February 2020. MM was able to assess the entire colony catchment by helicopter on 10 February 2020 and has considerable experience working within all sub-colonies both pre- and post- the 2016 earthquake.

Statistical and spatial analyses

ASSESSING SPATIAL HETEROGENEITY IN BURROW DENSITY AND BURROW OCCUPANCY

The following statistical analyses were carried out using the statistical software R v4.0.2 (R Core

Team 2020). Statistical significance was assumed at the 95% level where $\alpha = 0.05$. Factorial regression with Analysis of Variance (ANOVA) was first used to test for between-sub-colony variation in burrow density. Burrow density data were square root transformed to adjust for a positive skew in the observed distribution. Burrow occupancy was analysed as a function of sub-colony using binomial regression within a Bernoulli Generalized Linear Model (GLM), with a complementary-log-log link function to account for asymmetry in counts of successes and failures (occupied and unoccupied burrows). Models were sequentially relevelled and rerun to test for differences in burrow density and burrow occupancy against differing sub-colony baselines. A Pearson's chi-squared test was used to test the independence of count data between observer and sampling location, and a 5-sample two-sided test for equality of proportions was used to test for observer bias in determining burrow occupancy. Model assumptions and goodness of fit were verified by examining the distribution of either the standardised residuals (burrow density ANOVA) or the range of the deviance residuals (burrow occupancy GLM), by checking for unduly influential data points, and by plotting the residuals versus the fitted values and versus the covariates specified in the model.

ESTIMATING COLONY AREA AND POPULATION SIZE

The boundaries of all occupied areas were manually digitized in QGIS v3.10.11 (QGIS Development Team 2020) using a New Zealand Transverse Mercator 2000 (NZTM2000) projection (LINZ 2008). Sub-colony areas were overlaid against aerial photographs captured February 2020 (0.5 m² resolution) to identify and remove areas of scree and bare rock. The boundary polygons representing each sub-colony were buffered by the hypotenuse of the raster resolution prior to further analysis to mitigate for edge effect negative bias during surface area calculations (see Jenness 2004). The total 3D surface area of the colony was estimated from post-2016 raster elevation data (digital surface model, 1 m resolution (Aerial Surveys 2017) using the tool *r.surf.area* (Brown *et al.* 1994–2011) available in the Geographic Resources Analysis Support System v7.8 plugin (GRASS Development Team 2020). This tool estimates the 3D surface area of a region by employing the following method: for every cell within a polygon, eight three-dimensional triangles were generated connecting the cell centrepoint with the centrepoint of the eight surrounding cells, and the areas of the portions of each triangle that lay within each cell-boundary were calculated and summed.

Population size, given in breeding pairs, was calculated as the summed product of colony area,

burrow density, and burrow occupancy using sub-colony specific parameters. Appropriate values for burrow density and burrow occupancy were assigned to unvisited sub-colonies based on detailed descriptions provided by MM following both aerial assessment and a qualitative comparison of these sites to those where burrow density was measured (see RESULTS). A 95% confidence interval (CI) around the population estimate was calculated using the lower and upper 95% confidence intervals around the mean values for burrow density and rate of burrow occupancy calculated in R using a nonparametric bootstrap with replacement over 100,000 simulations.

Literature review

Longitudinal data for population parameters specific to the Shearwater Stream colony were sourced from all available primary and grey literature. Where required, raw data values were sourced from archived material provided by the Hutton's Shearwater Charitable Trust, formerly the Hutton's Shearwater Recovery Group, and the New Zealand Department of Conservation. Long-term averages and 95% confidence intervals around the mean were calculated where appropriate.

Quantifying habitat loss attributed to the 2016 Kaikōura earthquake

A detailed survey of the colony catchment was carried out on 10 February 2020. Cracks, faults, damage, and joint defects observed in sub-colonies 1, 2a, and 5a were recorded and measured *in situ*, and the general stability of the landscape was assessed across the catchment. Aerial photographs of all sub-colonies were taken the same day using a drone. See Townsend & Morgenstern (*In prep.*) for detailed methodology and full results of the geomorphological assessment conducted across the Shearwater Stream catchment.

RESULTS

Population parameters

Burrow density and burrow occupancy

Burrow density ranged from 0.15 to 1.5 burrows m⁻², with a colony mean of 0.565 burrows m⁻² (number of plots = 39, 0.476–0.661 95% CI; Table 2). The rate of burrow occupancy ranged from 0% to 88% per plot, with a colony mean of 33.8% (number of burrows = 225, 22.8–45.4 95% CI; Table 2). Burrow density was significantly lower in sub-colony 1 compared to sub-colony 5a (ANOVA, $df = 36$, $t = -2.623$, $P = 0.0127$).

For the purpose of estimating population size, sub-colonies inaccessible on the ground were pooled into categories for burrow density according

to common visual descriptions provided during an aerial survey of the colony catchment. Inaccessible sites that were observed to have a relatively good cover of burrows were assigned the mean burrow density value measured at neighbouring colonies with similar slope angle, soil type, and underlying rock type. Where this was not possible, inaccessible sub-colonies were divided between two categories. The categories were 'good' or 'mostly destroyed' and were assigned a value for burrow density that was either equal to the colony average, or a lower, fixed value of five burrows per 20 m² plot, respectively (Table 2). The colony mean for burrow occupancy was assigned to all inaccessible sub-colonies (Table 2). Whilst burrow occupancy in the sub-colonies visited was found to be lower in sub-colonies with lower burrow density, and *vice versa*, we felt that this observation alone did not justify lowering the rate of burrow occupancy for unvisited sites. Overall, the summed area of the inaccessible sub-colonies accounted for 20% of the total colony area.

Each observer sampled a mean of 43.8 ± 25.3 *sd* burrows for burrow occupancy. Observers were correlated with sub-colony (Pearson's Chi-squared test, $df = 8$, $\chi^2 = 111.74$, $P < 2.2 \cdot 10^{-16}$), and spatially auto-correlated with sampling plot (Pearson's Chi-squared test, $df = 80$, $\chi^2 = 335.08$, $P < 0.001$). However, no observer recorded any more or less occupied burrows than expected under an assumption of equal detection probability (5-Sample Two-Sided Test for Equality of Proportions, $\chi^2 = 7.56$, $df = 4$, $P = 0.109$).

Breeding success

Breeding success for the 2019/20 and 2020/21 breeding seasons was 0.53 (number of burrows monitored = 60) and 0.50 ($n = 50$), respectively. Observations of note recorded at failed burrows included single, intact eggs within the nest chambers of three separate burrows, one depredated chick found at a burrow entrance, and one burrow containing four eggs.

Table 2. Summary of parameters for the Shearwater Stream sub-colonies of Hutton's shearwater. Sub-colonies, denoted 'Site', are grouped by the method of assessment (either estimates obtained in the field or by aerial survey in February 2020) and then, for inaccessible sites, by qualitative score. A cross † denotes where specific values for burrow density ('Density') and burrow occupancy ('Occupancy') were assigned to inaccessible sub-colonies based on qualitative assessment. 'Samples' refers to the total number of plots or burrows scored for burrow density and burrow occupancy in the following format, 'plots for burrow density: plots for burrow occupancy, total burrows for burrow occupancy'. Areas given are three-dimensional values calculated for each sub-colony or set thereof (summed where appropriate). Corresponding population estimates are given in terms of breeding pairs ('Pairs'). Asterisks * mark the pair of sub-colonies for which the difference in burrow density between sub-colonies was statistically significant ($P < 0.05$). Boot-strapped 95% confidence intervals are given in parentheses where appropriate.

Site	Samples	Density (m ⁻²)	Occupancy (%)	Area (ha)	Pairs
1	12:6, 57	0.43* (0.33–0.53)	24.4 (11.2–36.7)	0.40	410 (150–770)
2a–b	13:7, 74	0.52 (0.41–0.65)	35.3 (17.4–45.0)	0.34	620 (240–1,190)
2c–d, 3a–b, 5b	-	0.25†	33.8 (22.8–45.2)†	0.19	150 (99–196)
4	-	0.57 (0.48–0.66)†	33.8 (22.8–45.2)†	0.17	320 (180–510)
5a–e	14:8, 94	0.73* (0.54–0.92)	39.6 (19.1–60.8)	0.53	1,530 (540–2,980)
Total				1.62	3,030 (1,210–5,640)

Colony area and population estimate

The total occupied area across the entire Shearwater Stream catchment was calculated to be 1.62 ha (Table 2), supporting an estimated 3,030 breeding pairs (1,210–5,640 95% CI, Table 2). Colony areas were sited on moderate slope angles (30–60°). There were many slopes similar in both angle and aspect that did not have nesting sites and burrowed ground across the colony was considerably fragmented (Fig. 2). Sub-colonies 1 and 2a comprised the largest continuous regions of utilised habitat and many burrowed areas comprised isolated patches of less than 0.1 ha.

Long-term colony status

Longitudinal data for population parameters specific to the Shearwater Stream shearwater colony were scarce. We observed negligible long-term change in burrow density (Fig. 3a). Mean burrow occupancy appears to have decreased, although the long-term trend was not statistically significant (Fig. 3b). Breeding success was punctuated by years with low or near-total breeding failure. Breeding success was lower post-quake than in previous years, but was generally as expected for the species at this location (Fig. 3c).

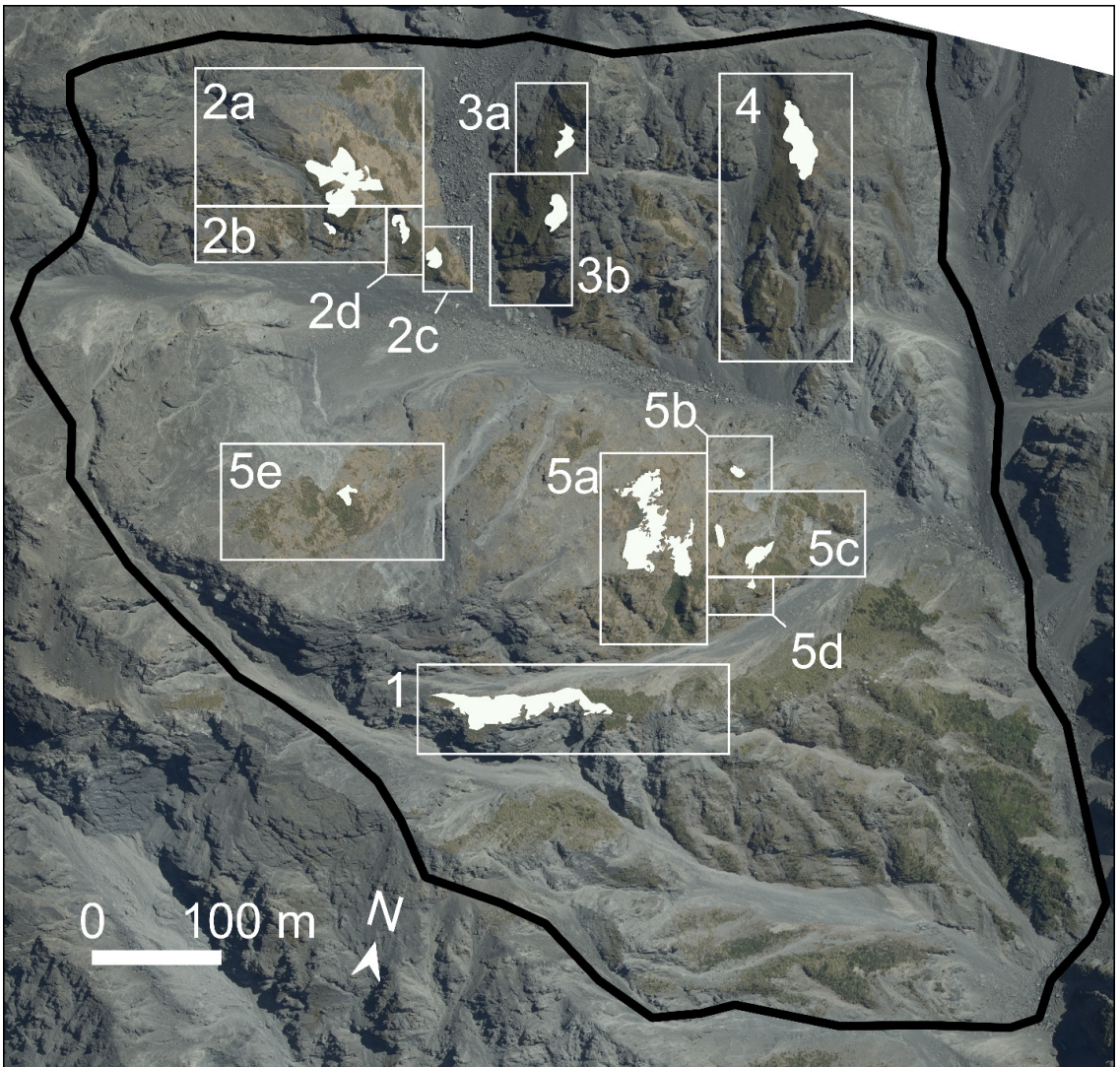


Figure 2. Hutton’s shearwaters breed in numerous small sub-colonies associated with *Chionochloa* snow tussock (vegetated areas) at scattered sites across the Shearwater Stream colony catchment (delineated here by the solid black line; shown as the darker shaded region south of Tarahaka Peak in Fig. 1) in the Wharekiri Valley, Puhī Peaks Nature Reserve. The general locations of the sub-colonies (white boxes) are delineated and labelled as per Sherley 1992 for consistency. Areas occupied by Hutton’s shearwaters across the Shearwater Stream colony catchment in November 2019 are indicated by the solid white polygons. Total occupied area: 1.62 ha. Aerial photograph captured by RM in February 2020.

Habitat loss attributed to the 2016 Kaikōura earthquake

Burrowed ground in sub-colony 1 was intersected by three cracks, the largest of which was associated with >2 m of southwards displacement. We also noted evidence of minor ravelling or toppling of the cliff edge at the southern edge of the sub-colony. A 1 m approximate scarp and an approximate 15 m wide area of shallow slumping was noted on the

north face of the sub-colony where a large boulder and the surrounding soil has pulled away from the ridge. A collapse was also recorded cutting into an area of vegetated ground to the west of sub-colony 5a. Deformation within the sub-colony proper was limited to minor cracking (about 20 cm vertical) and disruption and jostling of *in situ* blocks or boulders along the ridgeline to the southeast at the colony edge. Evidence of fresh rockfalls sourced from the

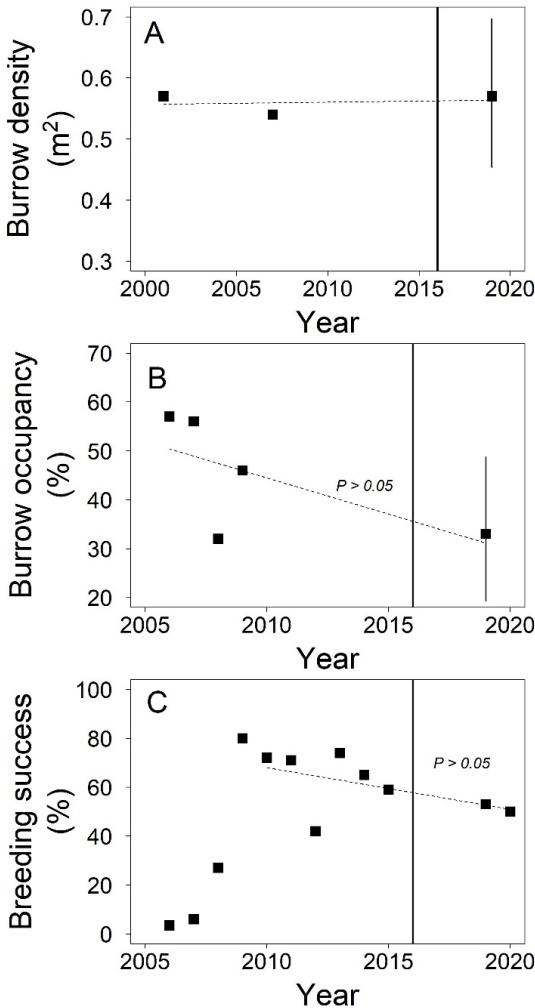


Figure 3. Colony-level means for burrow density (A), burrow occupancy (B) and breeding success (C) for the Hutton's shearwater at Shearwater Stream. Dashed lines indicate the direction of the long-term trends. Note that these were not statistically significant ($P > 0.05$). Linear regression models for burrow density and occupancy were informed by all available and comparable data, whereas we provide a decadal trend for breeding success. Error bars in panels A and B represent 95% confidence intervals around the mean for data collected over the 2019/20 breeding season. Data for burrow occupancy and breeding success prior to the 2005/06 breeding season were not included due to positive bias incurred from the field methods used. Vertical lines indicate the 2016 earthquake event. Data sourced from this study, Bell (2007 *unpubl. data*, 2008 *unpubl. data*), Sommer *et al.* (2009), Cuthbert (2019) and the New Zealand Department of Conservation.

cliff faces above were observed in two gullies within sub-colony 5a. Only minor damage was observed in sub-colony 2a, limited to fresh and unweathered minor cracks (about 5 cm) on a structure parallel to the slope. No cracking or soil separation was observed at the base of the exposed rock faces at the upper edges of either sub-colony 5a or sub-colony 2a, as would be expected if there had been shallow sliding of the soil and vegetation (e.g. Massey *et al.* 2018).

DISCUSSION

The current population of Hutton's shearwaters at Shearwater Stream is estimated to be about 3,000 breeding pairs. This figure is substantially lower than both the 1988 population estimate of 9,800 pairs (Sherley 1992) and the commonly cited 2002 recalculation (~8,000 pairs) (Cuthbert & Davis 2002a, 2002b, 2002c; Sommer *et al.* 2009; Waugh *et al.* 2013; Rowe *et al.* 2018; BirdLife International 2019). We did not find evidence to suggest that this difference was attributable to damage incurred during, nor in the aftermath of, the 2016 earthquake. Instead, the current population status of the Shearwater Stream colony is a likely consequence of, 1) improved methodology for measuring colony area, 2) lower burrow occupancy than expected for the species, and 3) long-term declines in the availability of suitable habitat. We address these in turn.

This study reports the first time that the colony boundaries have been mapped in the field for over three decades. We found the colony considerably fragmented, nested within larger areas of tussock-covered ground and only occupying a total of 1.62 ha (three-dimensional surface area). In 1988, the total colony area was estimated at 2.65 ha (planimetric) (Sherley 1992). In 2002, the corresponding population estimate was revised using the same estimate of colony area, despite this figure being over a decade old (Cuthbert & Davis 2002b). More recently, in 2019, the groundcover of snow tussock (*Chionochloa* sp.) was used as a proxy for estimating the area of burrowed ground at Shearwater Stream from aerial photographs (Cuthbert 2019). We suggest that the use of snow tussock cover as a proxy for burrowed ground is not an appropriate method in terrain with high heterogeneity of topography, soil structure, and tussock development, such as occurs across the Shearwater Stream catchment. We observed that the best soil development (up to 80 cm thick in gullies) appeared to coincide with patches of snow tussock and spear grass (*Aciphylla* sp.) on moderately dipping, relatively stable slopes. These were also the densest areas of shearwater burrows, which concurs with records from the Kowhai Valley colony (Cuthbert & Davis 2002c). Other areas, however, had smaller tussock and generally

thinner soils (<20 cm), which did not contain as many burrows. Burrow diameters of about 10–15 cm were noted, therefore there must be a minimum soil thickness to enable burrowing. Whatever the threshold, it is clear that not all areas of tussock-covered ground comprise suitable habitat at the Shearwater Stream colony. Unfortunately, it is not possible to retrospectively measure the sub-colony boundaries from the preceding decades, nor is it appropriate to recalculate the 1988 area estimate using contemporary methods (digital surface models). Nevertheless, we highlight the potential for previous estimates of colony area and population size to be inflated.

The rate of burrow occupancy used to estimate the population size at the Shearwater Stream colony has been assumed to be equal to that measured over ten years at the larger Kowhai Valley colony: 70.5% (61.8–77.4% CI, Cuthbert & Davis 2002b). In contrast, burrow occupancy measured in the 2019/20 breeding season at the Shearwater Stream colony was 33.8% (22.8–45.4% CI). Burrowscopes are not infallible and require some experience to use effectively. We took steps to prevent false negatives by training and swapping-out observers, and by double-checking all burrows initially recorded as empty. It is likely that, compared to the Kowhai Valley colony, the rate of burrow occupancy is generally lower at Shearwater Stream; the maximum rate of burrow occupancy measured at the Shearwater Stream colony prior to this study was 57% (Sommer *et al.* 2009). Further, the rate of occupied burrows also appears to be lower than expected for the species at this location (Fig. 3). We discuss predation by stoats as a possible driver.

Predation by stoats is not considered to be responsible for population decline in an otherwise “healthy” colony (Cuthbert & Davis 2002a). However, it is not a novel suggestion that the Shearwater Stream sub-colonies are likely to be disproportionately affected due to their relatively small sizes (see Sommer *et al.* 2009), and the propensity of the stoat to systematically destroy all accessible prey beyond their immediate needs for sustenance (King *et al.* 2021). Cuthbert’s previous assertion in relation to stoat predation is relevant: ‘there will be a threshold colony size beyond which the impact of predation is less than the [Hutton’s] shearwaters’ population growth rate, and predation therefore becomes non-regulatory. Below this threshold, predator control is needed if the population is not to decline to extinction’ (Cuthbert 2002, p.75).

Prior to the 2016 earthquake, baited trap lines were regularly maintained throughout the Shearwater Stream catchment and likely played an important role in reducing predation pressure on the colony. No predator control was implemented

during the three years following the earthquake and preceding this study. Upon accessing the colony, we observed one live stoat above ground in sub-colony 5a (November 2019), in addition to a stoat cache (see King *et al.* 2021) of shearwater eggs and a predated chick at a burrow entrance (February 2021). However, we note that the long-term trend for breeding success at Shearwater Stream appears relatively stable (Fig. 3), an observation which seems contrary to that expected within a colony hypothesised to be experiencing an increase in predation pressure. We suggest the following explanation: Stoats with ‘ermine’ (mainly white) winter coats have historically been seen in the snow-covered Shearwater Stream sub-colonies during the early breeding season (GS, September 1987). The stoat is an opportunistic, voracious predator with the ability to efficiently kill large animals relative to its size (King *et al.* 2021). At Shearwater Stream, stoats likely predate and cache adult shearwaters during courting and burrow clearing, and before eggs and chicks become available. Such behaviour has been well documented in the Kowhai Valley colony, where incidence of egg predation by stoats was rare, and of chicks, low (12% of study burrows) (Cuthbert & Davis 2002a).

An important consideration for the long-term viability of the Shearwater Stream colony is the deterioration of the remaining habitat. Reports of progressive loss of vegetation in the colony catchment and the negative impacts of ungulates on the colony date from January 2003 (Hutton’s Shearwater Charitable Trust, *unpubl. data*). ‘Considerable numbers of deer and chamois’ were observed in the colony during the 2008/09 season, ‘with some evidence of damage to burrows and certainly to vegetation’ (Sommer *et al.* 2009, p.149). Deer tracks and live deer and chamois were also observed throughout the colony catchment in both 2019/20 and 2020/21 (this study). Feral pigs were not able to access the colony prior to the 2016 earthquake, however, important physical barriers were destroyed during the 2016 earthquake (NRM, MM, & J. Kilgour *pers. obs.*) and the species is considered an important factor in the contraction of the Hutton’s shearwater’s historic breeding range (Cuthbert 2002).

Ground deformation attributed to the 2016 earthquake was mainly surface deformation and slumping of the shallow soil and regolith, in addition to rockfalls, shallow slides, toppling, and a few large block failures in greywacke. The Torlesse greywacke comprises variably bedded sandstone and mudstone (or argillite) and is highly deformed. The argillite sequences are inherently dominated by small-scale fractures (cleavage), whereas the sandstone is dominated by widely spaced fractures that define large blocks. The different rock types

responded differently to shaking during the earthquake: the largest failures seated in sandstone were likely influenced by the pre-existing structure and defects and were consistent with the styles of slope failure observed throughout the wider region (Massey *et al.* 2018; Townsend & Morgenstern *In prep.*). The main geological hazards to the colony at Shearwater Stream are rock fall or inundation from above, and cliff collapse or retreat from below, triggered by earthquake shaking, intense or long-duration rainfall, and freeze-thaw processes (Townsend & Morgenstern *In prep.*). A gully in sub-colony 2a had a collapsed soil-pipe/tunnel gully structure, open to the rock surface below for about 1 m, which was related to ongoing erosion of the soil rather than earthquake damage. In many places there was very little soil, possibly having been stripped off in previous landslide/avalanche events. Thick deposits of colluvium in the 'chute' that separates sub-colony 1 from the main hillslope also indicate that there is a history of inundation by debris in this area.

Burrow density is often cited as a useful indicator of fluctuations in population size and/or habitat availability in seabirds (Rodway & Lemon 2011; Sutherland & Dann 2012). The fine, sandy aeolian soil in which the shearwaters burrow is extremely friable and vulnerable to collapse, thus population decline is expected to be reflected by decreasing burrow density over time (Sommer *et al.* 2009). This reasoning can be applied at the sub-colony level within the Shearwater Stream colony: Here, slumping and shallow sliding of the vegetation and soil attributable to the 2016 earthquake occurred within sub-colony 1. Mean burrow density in sub-colony 1 was found to be lower than sub-colony 2, and significantly lower compared to sub-colony 5 (Table 2). This did not influence mean burrow density at the population level because the loss of suitable habitat in sub-colony 1 was offset by an increase in burrow density in sub-colony 5, which was markedly higher than the long-term mean recorded for the species at this colony. The results of this study concur with Sommer *et al.* (2009), who identified negligible change in population-level burrow density at the Shearwater Stream colony over the last forty years. However, we reject the corresponding hypothesis of long-term population stability and suggest that the small population of Hutton's shearwaters occupying this catchment is at high risk of, if not already undergoing, long-term decline. We note that this hypothesis contrasts with the conclusion of Sommer *et al.* and offer the following explanation: Inferences using longitudinal burrow density data require the use of consistent methodology including sampling effort which should be equal and unbiased over time. The use of fixed plots across years has been a feasible

method at the Kowhai Valley colony (Sommer *et al.* 2009), whilst the sampling approach at the Shearwater Stream colony has been less structured, with no fixed reference plots retained between breeding seasons (see Sommer *et al.* 2009). Although plots were sampled at random across sub-colonies (Sommer *et al.* 2009; this study), the boundaries of the sub-colonies at Shearwater Stream are not marked in the field, save for the natural separation of tussock by scree slopes (all authors *pers. obs.*). The definition of 'sub-colony' therefore equates to 'an area of tussock seen to contain burrows'. Estimates of burrow density cannot be indicative of population trends if the areas sampled are targeted because of the presence of burrows. Rather, the estimates will be positively biased. We recommend that all previous burrow density data available for the Shearwater Stream colony are treated with extreme caution if used to infer a population trend.

Populations of a long-lived species are highly sensitive to the loss of breeding adults from a population, either by mortality, reduced recruitment, or emigration (Sæther & Bakke 2000). Both the Shearwater Stream and Kowhai Valley colonies suffered highly reduced breeding success, and therefore downstream recruitment to the breeding population, in the 2007/06 and 2007/08 breeding seasons. This was attributed to poor at-sea feeding conditions (Sommer *et al.* 2009). Sommer *et al.* (2009) also suggested that fluctuations in natal recruitment at the Shearwater Stream colony might be offset by the immigration of birds from the larger Kowhai Valley colony. Alternatively, the Kowhai catchment may act as a net sink, drawing birds prospecting for breeding sites and/or partners away from Shearwater Stream because they are attracted by the larger numbers of established birds (Brown & Rannala 1995), their calls (Major & Jones 2011; Oro *et al.* 2011), and public information such as breeding success (e.g. Danchin *et al.* 1998). This scenario is consistent with the finding of Hale *et al.* (2015), who reported no genetic differentiation between colonies, indicating some level of long-term connectivity. Thus, while recognizing the limitations of comparing demographic parameters between the two populations due to differences in methodologies, the possible drift of Hutton's shearwaters from the Shearwater Stream colony to the Kowhai Valley colony could be a factor in population depensation at Shearwater Stream and a contributor to the stable/increasing population trend reported for the Kowhai Valley prior to the 2016 earthquake (Sommer *et al.* 2009).

If a population of a long-lived species is made small enough through a series of additive or interacting events, such as habitat loss, breeding failure, predation, and low recruitment, it loses the ability to recover from the adverse effects

of, for example, environmental variation and demographic stochasticity (Gilpin & Soule 1986). It is a priority that throughout at least the next decade, standardized monitoring methodology using fixed plots is carried out on an annual basis at the Shearwater Stream Hutton's Shearwater colony. This will enable a robust assessment of the long-term population trend and colony viability once sufficient data become available. A clear priority is also to review the impact of stoats. We recommend fencing any points that might provide access into the colony for feral pigs, and a review of the methods employed to control ungulates in the catchment. Serious consideration should be given towards establishing a new colony or facilitating the recolonization of a former alpine colony within the flight path. Alpine catchments with similar environmental characteristics to existing colonies are preferable to lowland areas because the comparatively low agricultural value of the surrounding land provides space for colony establishment and expansion. Proposals to establish a new alpine colony should certainly consider in detail the underlying geomorphology, including rock type, soil structure, and pre-existing faults.

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