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Aspects of breeding by Hutton's shearwaters (*Puffinus huttoni*) at a recently established colony at Te Rae o Atiu, Kaikōura Peninsula, New Zealand

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Abstract: A colony of the Nationally Vulnerable Hutton's shearwater (*Puffinus huttoni*) was established by translocations to Te Rae o Atiu, Kaikōura Peninsula from 2005. Weekly observer visits to the wooden nestboxes, and records from passive integrated transponder readers, provided detailed records of breeding activity. Birds visited many nestboxes in a season, with up to 29 birds recorded at one nestbox, and one bird recorded at 23 nestboxes. Breeding started at 4 years for males and 5 years for females. The pre-laying exodus by females averaged 11.8 days; however, there were instances of birds making up to three brief visits back to the colony. Egg laying was usually on the night of arrival back from the pre-laying exodus, and was asynchronous — average 6 November, but as late as 25 December. There were seven instances of two eggs being found in a nestbox in one season, with evidence of relaying in at least one case. The average hatching date was 13 December, incubation averaged 52 days, with a mean hatching success of 58%. Fledgling period was 87 days on average, with a mean success of 88%, resulting in mean productivity of 52%. Chicks left nestboxes on average 8 nights before fledging, before their first migration to Australian waters. Adults stopped visiting the nestboxes on average 17 days before their chicks fledged for females and 8 days for males. Fledging mass averaged 415 g, 75% of the mean peak mass of 550 g. Single parents successfully fledged a chick when the mate was lost or ceased visiting for up to 71 days before fledging, and a light mass chick (310 g) returned to Te Rae o Atiu and paired up. Divorce occurred in 36% of pairings that did not end with the loss of a partner; 87% of birds had at least one divorce, and one bird lost one mate and divorced six times in 13 years. Nestbox fidelity showed changes by many pairs, especially if there has been a change of partner.

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INTRODUCTION

Hutton's shearwater (*Puffinus huttoni*) is a small black-and-white shearwater (length 36–38 cm; mass 365 g; Marchant & Higgins 1990) that is classified as Endangered (BirdLife International 2021), and Threatened – Nationally Vulnerable under the New Zealand Threat Classification system (Robertson *et al.* 2021). Hutton's shearwater is considered to be one of a group of eight small, closely related shearwaters comprising the Manx shearwater (*P. puffinus*) group; the others being the fluttering shearwater (*P. gavia*) in New Zealand, Newell's shearwater (*P. newelli)* in the Hawaiian Islands, Townsend's shearwater (*P. auricularis*)

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in the Revillagigedo Islands off the west coast of Mexico, Balearic shearwater (*P. mauretanicus*) and Yelkouan shearwater (*P. yelkouan*) in the Mediterranean Sea, and black-vented shearwater (*P. opisthomelas*) off Baja California (Brooke 1990; Warham 1990).

In 1965, following up on anecdotal reports from high-country farmers, hunters and others of "muttonbird" burrows high in the Seaward Kaikōura Range, Hutton's shearwater breeding grounds were found in the headwaters of the Kōwhai River (42.261°S, 173.603°E) at altitudes between 1,200 and 1,800 m a.s.l. by Geoff Harrow (1965). Hutton's shearwaters breed at the highest altitudes of the Manx group of shearwaters, with Newell's shearwater breeding close to 1,200 m (BirdLife International 2021) and Townsend's shearwater above 800 m (Martinez-Gomez & Jacobsen 2004). In autumn, Hutton's shearwaters migrate to Australian waters before returning in spring (Imber & Crockett 1970; Halse 1981; Warham 1981; Rowe & Taylor 2020).

There are only two known natural Hutton's shearwater colonies remaining today – in the Kōwhai River and at Shearwater Stream (42.167°S, 173.727°E) (Marchant & Higgins 1990; Cuthbert 2001; Sommer *et al.* 2009). Major threats to these colonies are pigs (*Sus scrofa*) (Cuthbert 2002) and earthquakes. The 7.8 magnitude Kaikōura earthquake on 14 November 2016 resulted in about 12% of the colony area being lost through landslides and a reduction in burrow density of about 29% in the surviving colonies; a minimum of 40,000 breeding Hutton's shearwaters were lost in landslides and potentially another 80,000 from burrow collapse (Cuthbert 2019; and see Cargill *et al*. 2023).

The Department of Conservation (DOC) identified the Hutton's shearwater as a threatened species requiring medium term action for its recovery (Molloy & Davis 1992). It was recommended that a third, lowland colony be established (Paton & Davis 1997; Cuthbert 2001). An agreement was reached in 2005 between DOC and Whale Watch Kaikōura for a new colony (now called Te Rae o Atiu) to be established on Whale Watch land on the Kaikōura Peninsula (42.429°S, 173.703°E). The first translocation of chicks was in 2005, and a further five translocations were undertaken up to 2013. Rowe & Howard (2023) report on the first 16 years' progress of the new colony and described some of the pitfalls encountered when establishing a new colony without a predator-proof fence in place for the first five years. This paper reports on aspects of the breeding of Hutton's shearwaters at Te Rae o Atiu after birds returned from their migrations to Australian waters.

METHODS

The initial area selected was 0.3 ha of farmland enclosed by a standard farm fence; this was extended to 2 ha in 2010 when the predator-proof fence was erected (Rowe 2014; Rowe & Howard 2023). All observations reported here are of birds breeding in 108 artificial burrows (wooden nestboxes), the details of which and the translocation programme can be found in Rowe & Howard (2023).

In total, 493 chicks translocated from the Kōwhai River colonies to Te Rae o Atiu were banded with unique numbered leg-bands. Monitoring of the new colony was usually carried out during visits in the morning at approximately weekly intervals. In the early years, the Hutton's Shearwater Charitable Trust (HSCT) site protocols restricted night visits as we did not want to disturb any returning birds unduly; it was considered that birds seen and/or handled during the day would have settled by nightfall. Band numbers of birds found in nestboxes were recorded and, up until 2010, white correction fluid (Twink™) was applied to their heads to reduce handling. A line running from above the bill to the back of the head was applied to the first bird found in a nestbox and a line across the head was applied to the second bird assumed to be its mate. However, this simple system proved not to be foolproof as some birds seen together in a nestbox very early in the season and marked were later found to be breeding in other nestboxes with different partners, and sometimes both members of the new pair had the same marking.

Chicks from the 2012 and 2013 cohorts also had passive integrated transponders (PIT-tags) inserted in the back of their necks after translocation to Te Rae o Atiu. PIT-tag reader systems similar to those used by Taylor *et al*. (2012) were placed on frequented nestboxes to log when birds passed through the antennae coils placed around the outlet tunnels, 20 cm up from the entrance (Rowe 2014; Rowe & Howard 2023). From 2012-13, birds from the earlier translocations that returned as adults were PIT-tagged when captured in nestboxes. Some of the earlier birds were not tagged, or not tagged for several seasons, as they were not found in nestboxes during the weekly checks, although they may have been present at night. Movement of a set of three pins at the external entrance to the tunnel indicated which nestboxes may have been used since the last visit and that needed PIT-tag readers installed. Movements of another set of pins at the nest chamber entrance indicated which nestboxes were used since the last monitoring visit. Many PIT-tag readers were not attached to nestboxes until the internal pins had been moved, and so there may be some bias in recording the dates of

first returns to a given nestbox. Incomplete records were occasionally caused by operator error, battery failure, and antennae detuning through moisture ingress into the coils (Taylor *et al*. 2012). Because the PIT-tag reader can record several times per second and therefore fill the memory in a short time, the recorder was programmed to record each PIT-tag once per minute.

The pre-laying exodus in petrels is defined as the period which a female was absent from the colony immediately before laying (Warham 1990; Bull 2005). For statistical purposes, the egg laying date was defined as the middle of the date of first sighting of the egg and the previous date that the female was determined to be present, provided the interval was <= 8 days, otherwise it was considered indeterminate; the date was refined by the return date of the female to the nestbox after an exodus. Chick hatching date was determined as the middle of monitoring visits but was refined where there was evidence of egg pipping, wet chicks, and from chick size using growth rates from Cuthbert & Davis (2002). Chick fledging date was determined as the middle of the last date seen and the first date absent, or the last date the chick was present according to PIT-tag records.

Eggs were measured using digital calipers to 0.1 mm. Digital scales were used to obtain egg mass to 0.1 g and chick mass to 1 g. Sexes were determined from feather samples using DNA analysis (Griffiths *et al.* 1998; undertaken by the Equine Parentage and Animal Genetic Service Centre, Massey University or Zoology Department, University of Canterbury). Birds that were not DNA-sexed were inferred to be the opposite sex to their mates. It was not possible to infer sexes in some instances. In most cases, birds sitting on eggs or with chicks are assumed to be the parents of the egg and/or chick; however, there were some instances where the link could not be confirmed.

A bird arriving back in its n^{th} year after hatching is considered to be n-years-old as it will pass its n^{th} birthday in late December/early January (Brooke 1990). With the exception of some late fledging birds, laying through to fledging occurs within New Zealand Daylight Saving Time (NZDST). The PIT-tag readers were programmed in NZDST to reduce the possibility of errors in setup. All times given here are in NZDST.

Data presented are from the 2005-06 translocation up until 2022-23; data from 2021-22 are limited because a case of avian pox was detected and visits to the colony and bird handling were reduced as a precaution against disease spread. Calculated averages are given with 95% confidence intervals. Other statistics and tests performed used routines in Freese (1967) or Sokal & Rolfe (1981). The values of t, r, F and χ^2 are compared to tabulated values at the 95% significance level; calculated test statistics < tabulated values are not significant and *vice versa*.

RESULTS

Annual return from Australia

Hutton's shearwaters undertake an autumn migration to Australian waters and arrive back to the New Zealand breeding grounds from late-August. Very few birds were seen in nestboxes during daytime before egg laying. Therefore, reliable data on the dates of first returns are only available for PIT-tagged birds. These show that on average, the earliest birds were back each year on 30 August (range 22 August to 10 September). Birds aged 2–6 years-old tended to arrive back later in the year than older birds that arrived back from late August (Fig. 1). There was no significant difference between the first recorded dates back each year for each female and each male over the years 2017–2022 (female average 14 September; male average 16 September; unpaired sample t test: $t = 0.17 < t_{P=0.05} = 1.97$, df = 169).

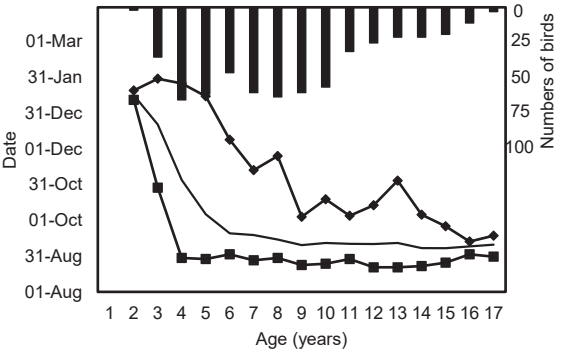

Figure 1. The date PIT-tagged Hutton's shearwaters first returned to Te Rae o Atiu by age. Data are from 2013-14 (when the 2006 translocation chicks were already in their 8^{th} year) through to 2022-23. ■ = earliest date; line only = average date; ♦ = latest date.

Age of first return from Australia

Hutton's shearwaters returning to the colonies for the first time generally make landfall in their 3^{rd} (males) or 4^{th} year (females); however, the difference was not significant ($\chi^2 = 7.56 < \chi^2_{P=0.05} = 7.81$, df = 3; Fig. 2). Three of 139 birds were recorded back first in their 2^{nd} year and others were as late as 11-years-old. It is probable that some birds were back at Te Rae o Atiu earlier than noted, as we know from PIT-tag records that not

all recorded birds were seen by human observers. For example, only 35% of 4-year-old birds recorded back at Te Rae o Atiu from PIT-tag records from the 2012 and 2013 transactions and Te Rae o Atiu bred chicks were physically seen, and birds from the 2006 to 2008 translocations were not PIT-tagged until into their 5th year or later.

Nestbox visitations

Over the course of a season, adult Hutton's shearwaters often visited a number of nestboxes apart from that in which they bred. Up to 29 birds visited a given nestbox in one season, e.g., nestbox 58 in 2017-18 (Fig. 3). X20909 was the only male with an extended presence over the season and was the probable male incumbent. These records do not show an obvious female presence; however, an egg was laid between 18 and 28 November.

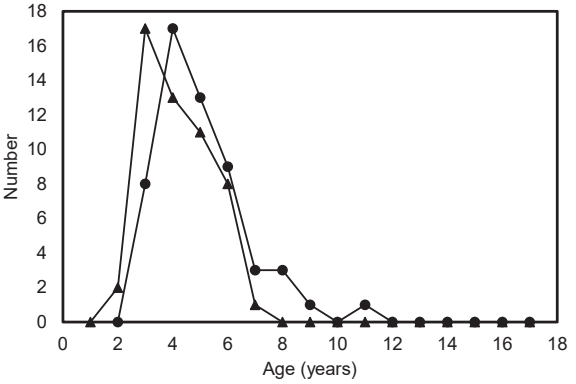

Figure 2. Age at which Hutton's shearwaters were known to return to Te Rae o Atiu for the first time. Key: ▲ males; ● females.

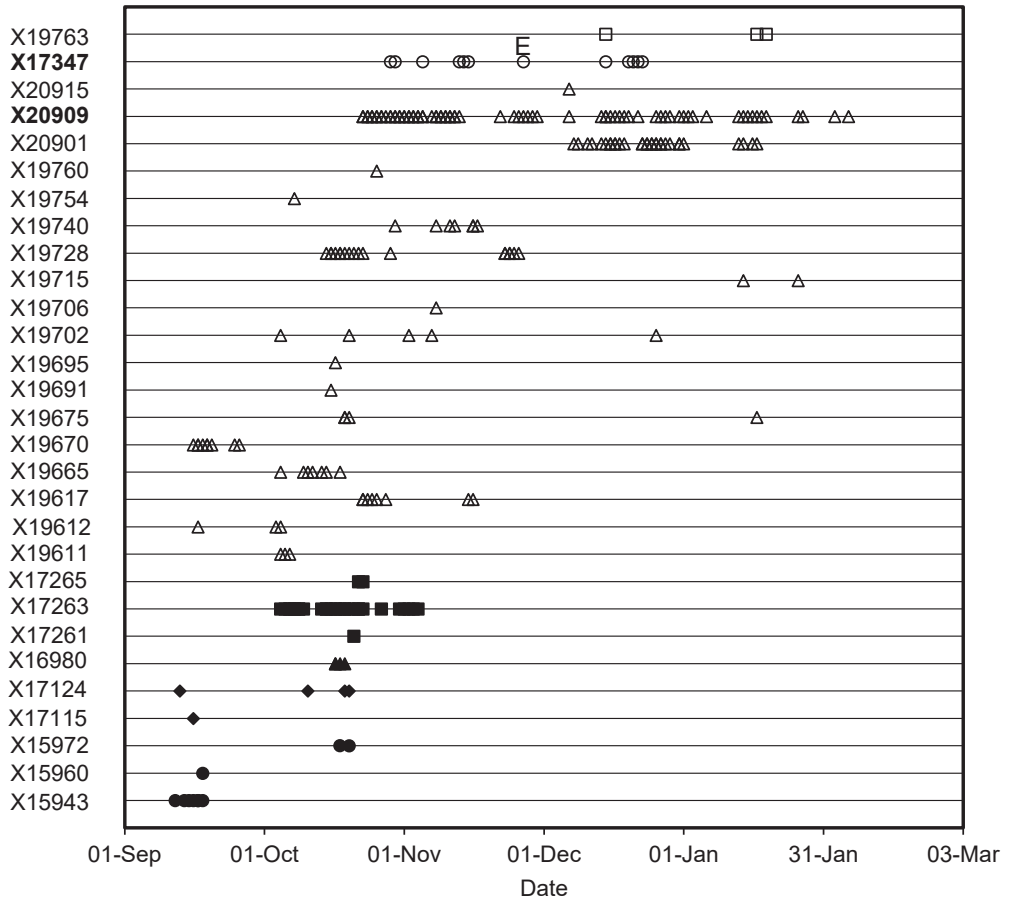

Figure 3. Timelines when 29 Hutton's shearwaters triggered the PIT-tag reader at Te Rae o Atiu nestbox 58, 2017–18. X20909 (bold) is the probable male incumbent at this nestbox and X17347 (bold) was likely to have laid an egg on 27 November (point E). Each marker type represents birds from one cohort, the oldest being at the bottom: ● = 2006; ♦ = 2007; ▲ = 2008; ■ = 2012; Δ = 2013; ○ = bird first banded as adult; □ = 2014-15 Te Rae o Atiu bred chick.

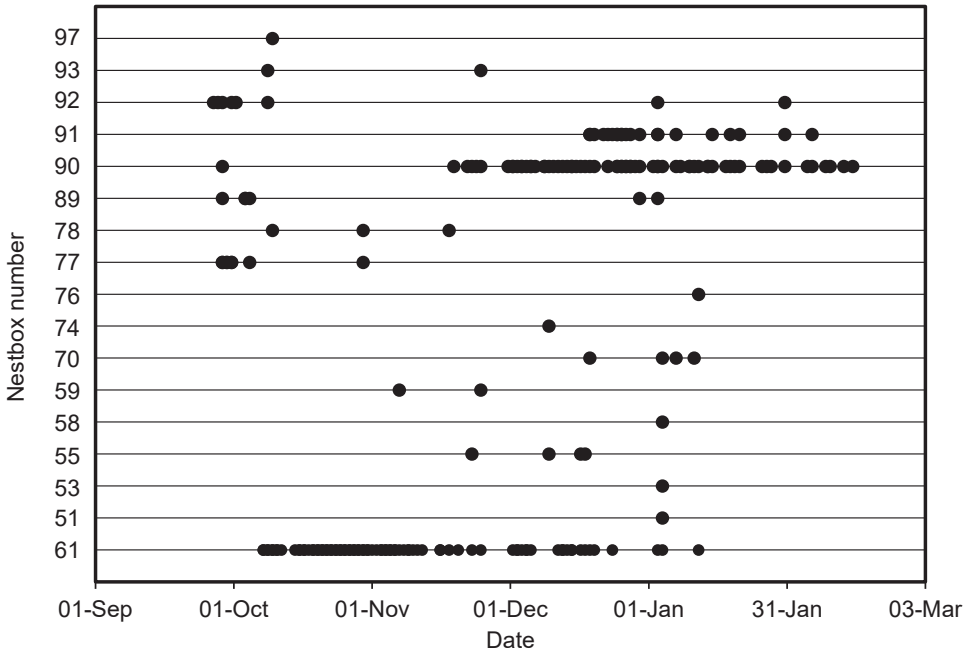

Figure 4. Timelines for Hutton's shearwater X19728 triggering the PIT-tag readers at 17 Te Rae o Atiu nestboxes in 2018-19. Note his home nestbox was #61; however, there were significant concurrent visits to nestbox 90 until mid-December, and then at nestboxes 90 and 91 until February.

The only female seen in nestbox 58 during that interval was X17347 on 27 November, and it is probable that she laid the egg after returning from a 12-day pre-laying exodus beginning 15 November. Some of the visits to nestbox 58 were by younger birds, e.g., 5-year-olds from the 2013 translocation, that visited the colony later in the season.

Individual birds visited up to 23 nestboxes in a season. For example, male X19728 from nestbox 61 in 2018–19 visited 17 nestboxes (Fig. 4). In addition to nestbox 61, this bird was a frequent visitor to nestbox 90 from mid-November then to nestboxes 90 and 91 from mid-December. The number of visits may have been related to age (he visited more nestboxes as a 5- and 6-year-old than when older), or whether or not he was caring for a chick (Table 1).

Table 1. Number of nest boxes visited by a male Hutton's shearwater, other than his home nestbox.

Year	Age (years)	Number of nestboxes	Egg hatched
2017-2018	5	11	No
2018-2019	6	17	No
2019-2020	7	4	Yes
2020-2021	8	3	Yes
2021-2022	9	3	Yes
2022-2023	10	5	No

Pre-laying exodus

Before laying, females were absent from the colony for several days on pre-laying exoduses. The lengths of 203 absences from the colony were determined from PIT-tag records (Fig. 5). These absences averaged 11.8 days (sd = 3.3 days, CI = ± 0.5 days, n = 203), and ranged from 5 to 22 days. Absences for individual birds varied widely (Fig. 6). For example, X15997 was recorded as being away for 6 days in 2014, 20 days in 2018, and averaged 12.1 days (sd = 4.4 days, CI = ± 2.7 days, n = 10).

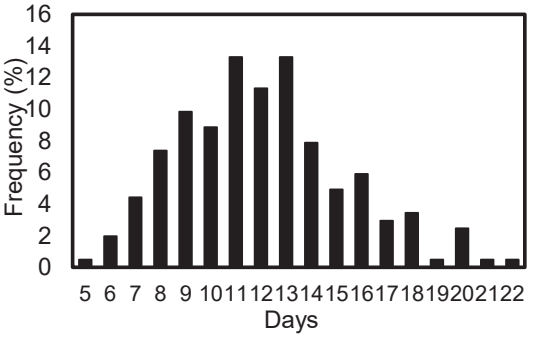

Figure 5. Frequency of the length of pre-laying exoduses of Hutton's shearwaters at Te Rae o Atiu 2012-2022.

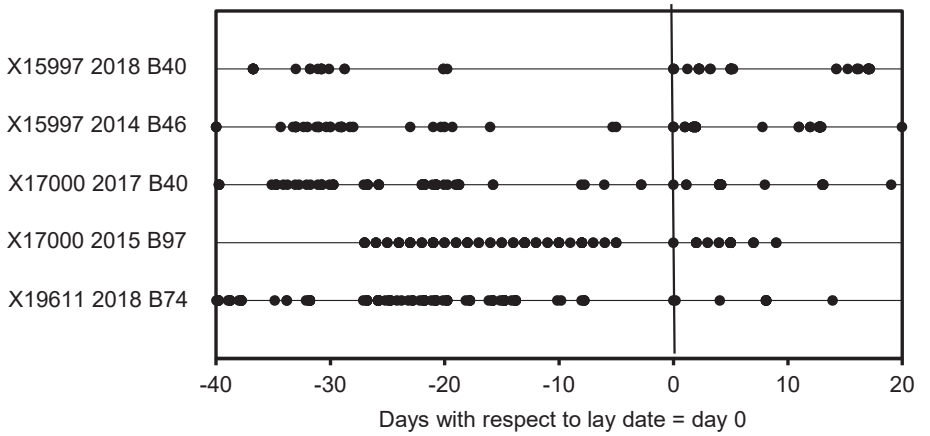

Figure 6. Examples of timelines for breeding female Hutton's shearwaters triggering the PIT-tag readers at Te Rae o Atiu nestboxes before and after egg laying (day 0) showing the variation in absences during pre-laying exoduses.

On the basis that many shearwater species have an exodus of 14 days or more (Warham 1990; Bull 2005), 57 instances of exoduses <10 days were re-examined. Twenty-six of these had another gap >4 days long before a brief visit to the colony. If that visit was ignored, the exoduses of these 26 birds were extended by an average of 8 days; the balance did not show evidence of significant gaps prior to the exodus determined previously. As an example, X15997 in 2014 had an 11-day gap prior to the short visit 6 days before the lay-date which, if ignored, extended the determined exodus to 17 days (Fig. 6). X17000 in 2015 had a 5-day absence with no earlier gaps, whereas during 2017 she was absent for only 43 hours before laying; the exodus could be considered extending to 16 days with three brief visits back to Te Rae o Atiu during that time. The trace for X19611 suggests there were two visits during an exodus of 14 days.

The 2021 PIT records were examined for 28 of 36 layings when both parents had records. Of these, 27 showed that the male was present for the majority of the time that the female was away as, e.g., in Fig. 7. In only one instance was the male away for a significant amount of the time the female was absent – an 8-day break by X17265 at the end of the 16-day exodus for X17000.

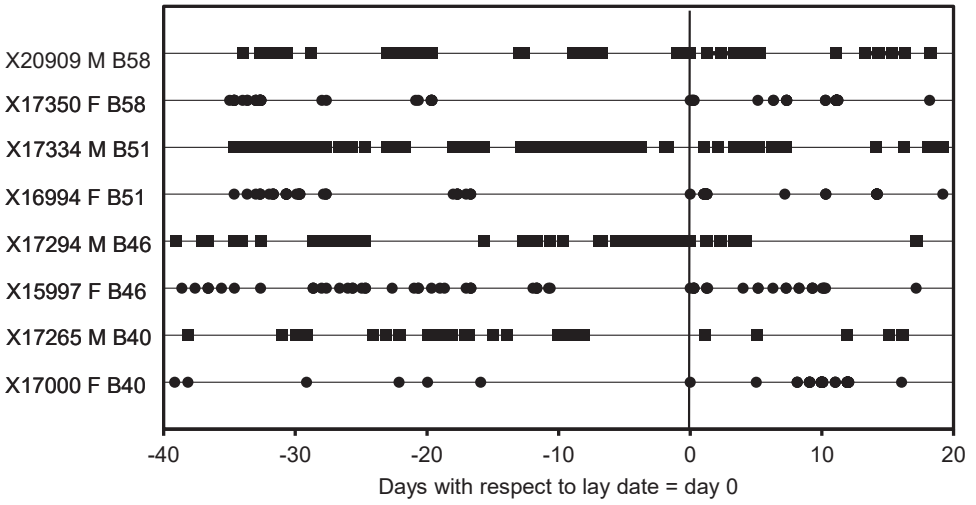

Figure 7. Timelines for selected breeding pairs of Hutton's shearwaters triggering PIT-tag readers at Te Rae o Atiu during 2021 before and after egg laying (day 0) showing the variation in male attendance during the female pre-laying exodus. ■ males, ● females.

Egg-laying and eggs

By the end of 2022-23 season, 279 eggs had been laid at Te Rae o Atiu. Two eggs were laid in one nestbox in one season seven times.

The age at which Hutton's shearwaters at Te Rae o Atiu were first recorded with eggs was significantly different between the sexes (χ^2 = 21.87 > $\chi^2_{tab,P=0.05}$ = 9.49, df = 4, Table 2). Two females are known to have successfully laid eggs at 4 years old, while 18 (38%) of 47 individuals laid first at 5 years old. A higher proportion of males started breeding at 4 years old; 14 (29%) of 49 males that age were in pairs that produced eggs.

Table 2. Ages at which Hutton's shearwaters were first observed with an egg at Te Rae o Atiu.

Age (years)	4	5	6	7	>7	Total
Male	14	22	11	2	0	49
Female	2	18	10	9	8	47
Total	16	40	21	11	8	96

Laying was asynchronous, occurring between 20 October and 25 December (a spread of 66 days), with an average lay date of 6 November (Table 3); 90% of eggs were laid within a 4-week period (Fig. 8). On an annual basis for 2012 to 2022, the average laying date varied from 2 to 12 November (SD=2 days, CL=±1 day, n=11). Apart from 2010 (the two eggs that year were laid on 20 & 23 November), the first eggs in any year were laid from 20 October to 2 November, average 27 October. There were seven eggs (2.7%) laid as late as December: second eggs that were laid in nestboxes on 3 Dec 2017, 3 Dec 2021, 7 Dec 2012, 11 Dec 2015, and single eggs that were laid on 2 Dec 2021, 6 Dec 2021, and 25 Dec 2012.

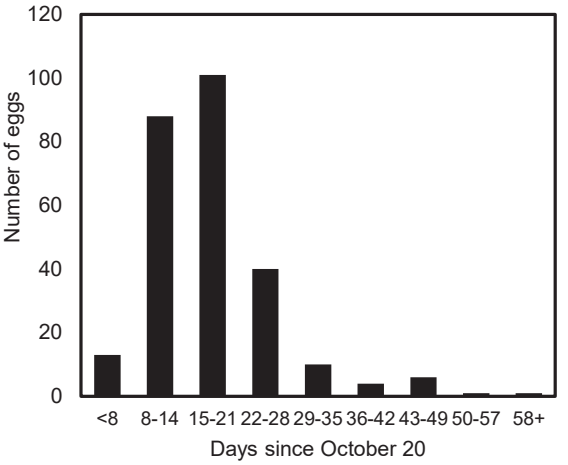

Figure 8. Numbers of Hutton's shearwater eggs laid at Te Rae o Atiu, 2010–2022 in seven–day intervals from the earliest recorded date, 20 October.

Observers visiting Te Rae o Atiu noted the period when an egg was laid in a nestbox, and PIT-tag readers have the time when the female arrived back from the pre-laying exodus, hence, allowing laying dates to be refined. Records show females arrived at nestboxes from their exoduses shortly after sunset (about 2015 h) through to 0200 h, with 89% arriving between 2000 h and 2300 h. Most females (73%) left nestboxes 2–8 hours after arrival and after laying their egg; 85% departed between 0200 h and 0500 h. The rest left after one or more days, having begun to incubate the egg. Males were present at least 66% of nights that eggs were laid. Where clear records were available, on the first day of incubation, 36% of nestboxes were occupied by males, 22% by females, and 42% of eggs were unattended.

Table 3. Breeding data for Hutton's shearwaters at Te Rae o Atiu, Kaikōura, 2010–2022.

	Laying date	Hatching date	Incubation duration (days)	Fledgling date	Fledging duration (days)
Number	279	163	163	145	145
Earliest	20 Oct	13 Dec	45	13 Mar	78
Average	6 Nov	27 Dec	52	23 Mar	87
Latest	25 Dec	25 Jan	63	19 Apr	97
sd (days)	8.6	7.6	3.2	7.1	3.8
95% CI (days)	± 1.0	± 1.3	± 0.6	± 1.2	± 0.8
Hatching success (%)		58.4			
Fledging success (%)				89.0	
Productivity (%)				52.0	

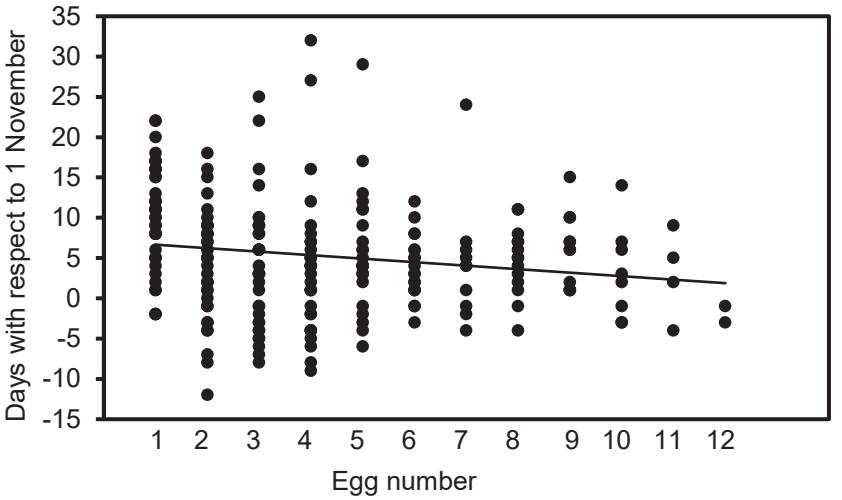

Figure 9. Relationship between the date of laying with respect to 1 November and the number of the egg known to have been laid by an individual female (one egg per annum).

Females tended to lay earlier as they become more experienced (Fig. 9). The relationship 'lay date = 7 November – 0.43 x egg number' is significant ($F = 6.93 > F_{0.95} = 3.89$, $r^2 = 0.029$, n = 235); however, this only explains 2.9% of the variation in the data. A similar relationship with female age, 'lay date = 9 November – 0.41 x age years' was also significant ($F = 6.97 > F_{0.95} = 3.89$, $r^2 = 0.029$, n = 233).

Measurements of 90 eggs laid from 2010 to 2016 are summarised in Table 4. There was no significant relationship between the length and breadth of these eggs, breadth mm = 41.2 - 0.023 x length mm ($r = 0.048 < r_{P=0.05} = 0.207$, $r^2 = 0.0023$, df = 88) with only 0.2% of the variance in the data being explained. However, there was a significant relationship showing an increase in egg mass with the age of the female parent: mass = 45.7 + 0.72 x years ($r = 0.330 > r_{P=0.05} = 0.210$, $r^2 = 0.109$, df = 86) (Fig. 10); however, the relationship explained only 11% of the variance in the data.

Table 4. Measurements of Hutton's shearwater eggs laid at Te Rae o Atiu, Kaikōura, from 2010 to 2016.

	Length (mm)	Breadth (mm)	Mass (g)
Number	90	90	88
Average	59.9	39.9	51.2
Maximum	66.0	42.6	60.9
Minimum	51.7	35.8	41.2
SD	2.6	1.3	3.8
95% CL	± 0.5	± 0.3	± 0.8

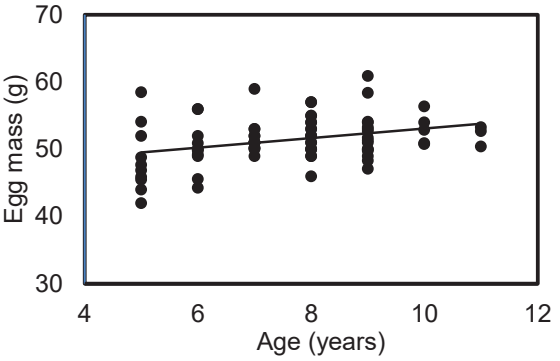

Figure 10. The relationship between the mass of Hutton's shearwater eggs and the age of the female parent.

Incubation and hatching

Of the 279 eggs laid at Te Rae o Atiu between 2010 and 2022, 163 (58%) hatched (Table 3). Hatching was spread over a period of 43 days (13 December to 25 January); none of the eggs laid after 6 December hatched. The egg laying period to 6 December spanned 47 days, similar to the hatching period. Seventy-five % of eggs hatched within ±8 days of the average date, 27 December. The incubation period averaged 52 days (Table 3) and 88% hatched within ±4 days of that. There was a tendency for eggs laid later in the season to have lower hatching rates (Table 5).

As birds have become older and more experienced at breeding, their hatching success improved (Fig. 11). From 257 layings grouped into female age-classes, there was a significant

Table 5. Hatching percentages of Hutton's shearwater eggs laid with respect to 1 November (Day 1)

Date range	Number of eggs laid	Number of eggs hatched	% of eggs hatched
< 1	55	40	72.7
1 – 7	109	74	67.9
8 – 14	61	31	50.8
15 – 22	20	6	30.0
23 – 28	8	4	50.0
> 29	9	2	22.2
Total	262	157	59.9

relationship that explained 61% of the variance in the data: hatching success (%) = 23.9 + 4.1 x age class (years) ($r = 0.78 > r_{P=0.05} = 0.553$, $r^2 = 0.61$, df = 12).

PIT-tag records indicated that there were instances when no birds were on eggs the day following laying. Visits to nestboxes from 2011 to 2022 also found eggs not being incubated and that subsequently hatched. Discounting the immediate days after laying, for eggs that hatched, there were 36 (2.5% of 1448) unattended eggs <21 days after laying, and 13 (0.9%) unattended eggs >=21 days after laying, including three in the last 10 days before hatching. Nine eggs were unattended twice, and one egg three times. There was an average of 9.3 observations/nestbox/season which equates to each nest being checked every 5.6 days, suggesting that the number of occurrences of eggs being left unattended may have been 5-6 times higher than observed.

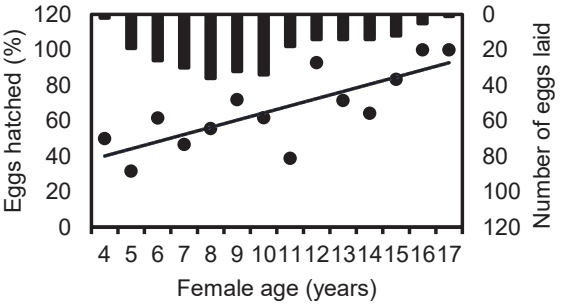

Figure 11. The relationship between the age-class of female Hutton's shearwaters at Te Rae o Atiu and hatching success over the period 2010-2022: ● = eggs hatched/egg laid (%); solid bars = number of eggs laid in that age class.

Chick growth and fledging

Of the 163 eggs that hatched, 145 chicks fledged (89%), resulting in a breeding success (= productivity = fledglings/egg laid) over the study of 52% (Table 3). Most of the 18 chicks that died did so in the first ten days after hatching. However, three chicks died in the last week before fledging: two of unknown natural causes; the third chick became caught in the exit tunnel, was extracted, but subsequently died. From available records, all chicks that died over 20 days old had weights that were comparable to the Kowhai River average (Cuthbert & Davis 2002) and were being visited by both parents through to the time they died, i.e. none appeared to have been abandoned.

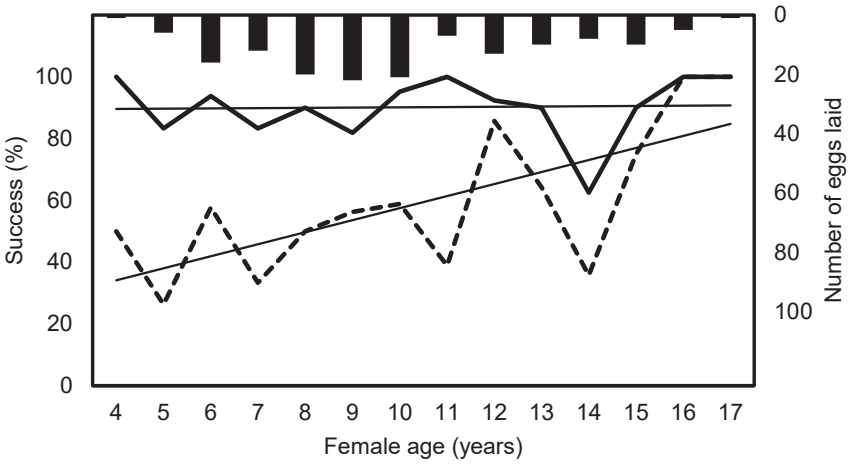

Figure 12. Relationships between fledging success (solid line = fledglings/egg hatched) and productivity (dashed line = fledglings/egg laid) with the age of the female parent. Bars are the number of eggs laid by parents in that age group.

The time from hatching to fledging averaged 87 days (range 78–97) and 85% of chicks fledged within 6 days of that time. Where fledging dates could be estimated, the average date was 23 March (range 13 March to 19 April; Table 3); 80% of chicks fledged within 7 days of 23 March.

With the exception of the 14 year-old age class, the fledging success (fledglings/egg hatched %) was 82% or better for all female age groups (Fig. 12). However, the relationship between fledging success and female parent age was not significant, success (%) = 89.2 + 0.088 x age (years), and explained only 0.1% of the variance in the data ($r = 0.04 < r_{P=0.05} = 0.53$, $r^2 = 0.001$, df = 12). Productivity averaged 52.0% and the relationship with female age (Fig. 12) was significant, explaining 48% of the variance in the data: success (%) = 19.3 + 3.8 x age ($r = 0.69 > r_{P=0.05} = 0.53$, $r^2 = 0.48$, df = 12).

Chick growth was highly variable. Fledgling mass averaged 415 g (range 267–565 g, sd = 47 g, CI = 9 g, n = 112 birds), 75% of the average peak mass of 550 g (range 377–693 g, sd = 70 g, CI = 12 g, n = 111). Fig. 13 shows variation in growth curves for 12 chicks that fledged in 2017. In addition to the differences in peak mass and fledging mass, the variability between measurements also reflected the frequency of feeds, and the length of time since the last feed before the measurements. At fledging, the average wing length was 226 mm (range 208–237 mm, sd = 7 mm, CI = 2 mm, n = 81); the degree of variability is demonstrated in Fig. 14 for 12 2016-17 fledglings.

Adults generally ceased returning to the colony to feed chicks several days before their chicks fledged. Considering only birds that returned the following season, i.e. confirmed to be alive when their chicks fledged, females stopped visiting nests an average of 17 days before fledging (range = –54–0 days, SD = 11 days, CI = 2 days, n = 92) whereas male parents were last recorded at nests on average 8 days before the chick departed (range = -44–7 days, SD = 8 days, CI = 2 days, n = 96). The difference between departure dates of the sexes (unpaired sample t-test: $t = 7.08 > t_{P=0.05} = 1.97$, df = 186) was revealed as significantly different frequency distributions ($\chi^2 = 50.4 > \chi^2_{P=0.05} = 11.1$, df = 5, Fig. 15). The last time either parent visited the nest averaged 6 days before the chick fledged (range -24–7 days, SD = 6 days, CI = 1 day, n = 103). Fifteen % of males and no females were recorded at nests up to 7 days after chicks had departed.

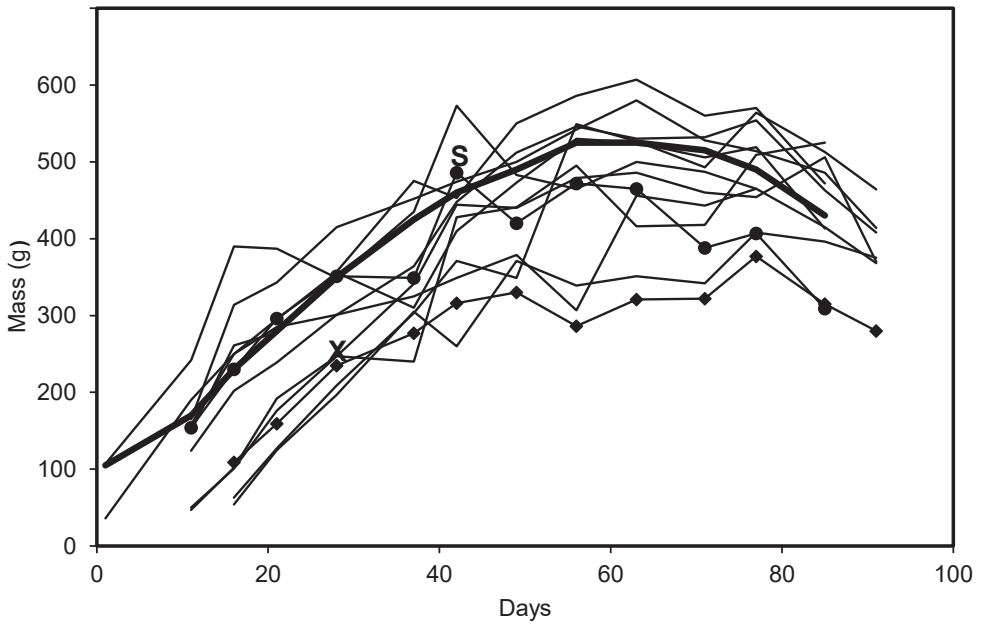

Figure 13. The variability of growth curves for 12 Hutton's shearwater chicks at Te Rae o Atiu in 2016–17. The first chick measurements were made on 19 December 2016 (day 1) and the final measurements were made on 20 March 2017 (day 91) just prior to the last chicks fledging. The heavy line is the average growth curve for chicks at the Kōwhai River colonies (extracted from Fig. 1d in Cuthbert & Davis 2002). ♦ = X21226 growth pattern after the loss of male X19745 at point X; ● = X21233 growth pattern after male X17294 stopped provisioning at point S.

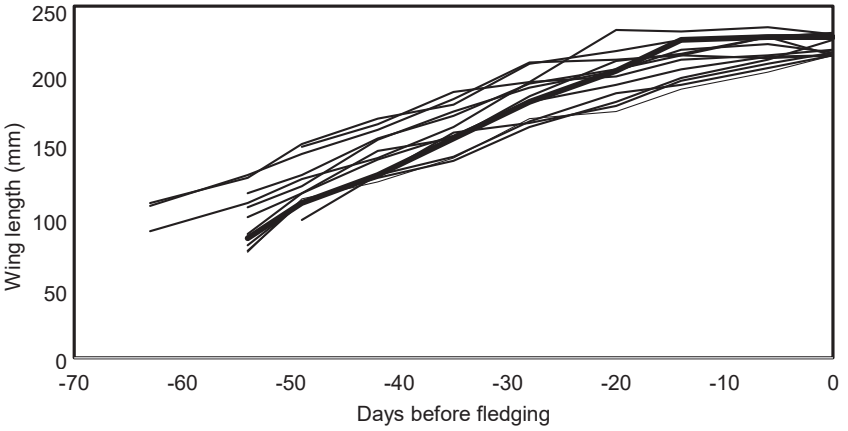

Figure 14. The variability of wing growth curves for 12 Hutton's shearwater chicks at Te Rae o Atiu in 2016-17. The heavy line is the average curve for chicks at the Kōwhai River colonies extracted from Cuthbert & Davis (2002).

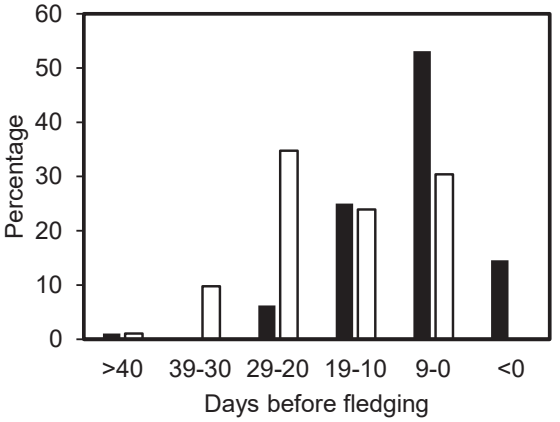

Figure 15. The frequency distribution of the number of days that the adults stopped feeding chicks before they fledged. Open bars = females; solid bars = males.

In 6% of cases, a parent ceased to feed its chick over 30 days before fledging, for reasons unknown (not death, as they were back the next season having left their partner to continue feeding the chick until fledging). One example was a chick whose 5-year-old male parent ceased feeding it 44 days before fledging. The female (also 5-years-old) continued to feed it until it fledged at 310 g (this was 77% of Kowhai River average fledging mass of 404 g; Cuthbert & Davis 2002; Fig. 13). This pair divorced prior to the next season. Although the chick departed at a very light mass, it returned as a 3-year-old and bred. Another (10 yo) female ceased provisioning her chick 54 days before fledging, and a further nine females ceased visiting their nests 30–38 days before their chicks fledged (all did so). All these females returned and bred the following season, with two of the 11 pairs having undergone divorces.

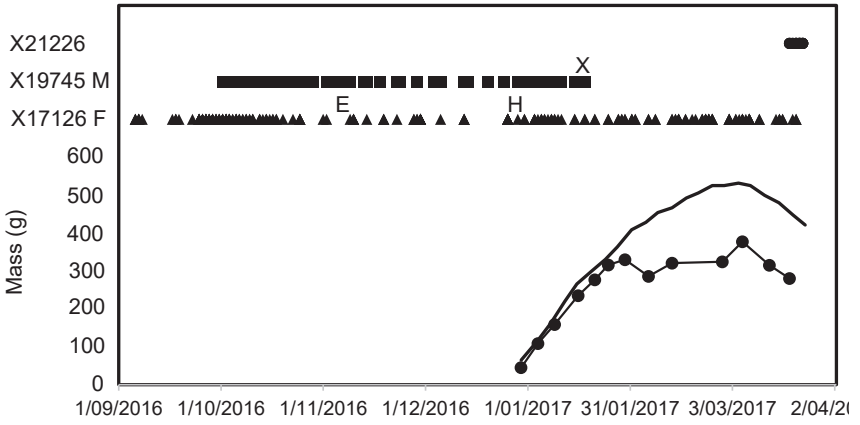

Figure 16. Timeline of Hutton's shearwaters entering and leaving nestbox 12, 2016-2017, showing the success of female X17126 provisioning chick X21226 alone for 64 days until fledging on 26 March. ▲Female X17126; ■ male X19745; ● chick X21226; E = egg laid; H = hatched; X = date X19745 was last recorded; solid line = Kōwhai River chick growth (extracted from Fig. 1a in Cuthbert & Davis 2002); line with dots = X21226 growth.

Two males (4 yo and 5 yo) were lost, presumed dead, as they were not recorded again, 64 and 71 days before their chicks fledged; their 10 yo mates continued to feed the chicks until they fledged. One female fed chick X21226 for 64 days (Figs 13 & 16) until it fledged with a mass of 280 g, (*c*. 69% of the average fledging mass of Kōwhai River chicks). The chick was not seen again after fledging. Another female fed her chick for 71 days until it fledged, and a 10 yo male fed his chick for 54 days after his mate failed to return.

PIT-tag records showed chicks first left nestboxes on average 8 nights (sd = 3.6 nights, CI = 0.7 nights, n = 115) before fledging. A few birds left on their first night out of the nest, and at least one emerged for 20 nights before fledging (Fig. 17). At least 18 chicks were recorded at nestboxes other than their own; two were recorded at two other nestboxes and one at three others. Chicks were last recorded at their nestboxes on the day of leaving between 19:37 h and 05:55 h; 54% were last recorded between 20:00 h and 21:00 h and another 23% between 00:00 h and dawn (Fig.18); sunset is about 19:30 h NZDST at this time of year.

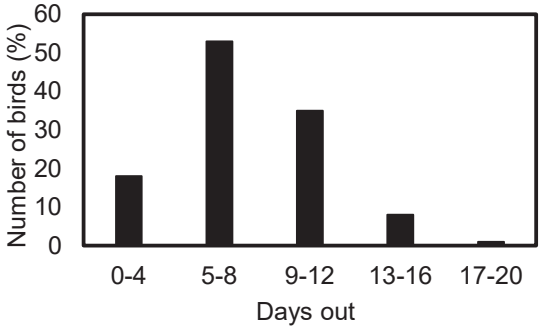

Figure 17. Frequency of days that Hutton's shearwaters at Te Rae o Atiu emerged before fledging.

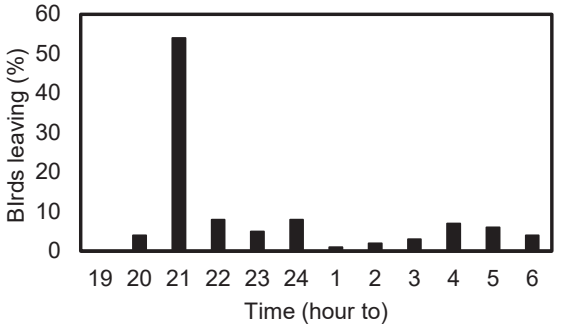

Figure 18. Frequency of the time that Hutton's shearwaters fledglings at Te Rae o Atiu last exited the nestboxes. Sunset is about 19:30 h NZDST at 23 March, the average fledging date.

Fidelity of pairings and nestboxes

In 12 years of breeding activity from 2010-11 to 2021-22, 219 pairings of 46 females and 52 males that produced eggs were identified. Seventeen partnerships (7.8%) ended when one or both partners were lost between seasons. The other 202 pairings showed a high degree of variability with respect to fidelity to partners, with 73 (36.3%) ending in divorce (i.e. both parents known to be present in a later year). In their final year together, 40% of pairings that divorced successfully fledged a chick whereas the other 60% did not; the difference was not significant ($\chi^2 = 3.08 < \chi^2_{P=0.05} = 3.84$, df = 1).

Regression analyses of the proportion of each age group that divorced significantly decreased with age: males (%) = 55.4 – 3.0 x age (years) ($r = 0.739 > r_{P=0.95} = 0.532$, $r^2 = 0.546$ df = 12); females (%) = 60.4 – 3.3 x age (years) ($r = 0.851 > r_{P=0.95} = 0.553$, $r^2 = 0.266$, df = 11).

Thirty-five females (85%) and 35 males (88%) had at least one divorce, four females and four males had >3 divorces. The longest partnership persisted for 9 years in the same nestbox from 2013 to 2021, and a second 9-year partnership moved between three nestboxes, staying for four consecutive years in each of the first two. At the other extreme, one male had six divorces and lost one mate in 13 years, another male had seven divorces in a row before staying with the same mate for 4 years, and a female had four divorces and one mate loss in 10 years.

Two pairings only showed 'long-term' nestbox fidelity, for 9 and 6 years. Other females stayed in the same nestbox for up to 11 years but with multiple changes of partners. There were only four instances of males staying in a nestbox for more than 4 years, with the longest being for 9 years.

DISCUSSION

This study has provided known-age breeding data for Hutton's shearwaters at a new colony that was established by translocations to Te Rae o Atiu on the Kaikōura Peninsula from 2005 to 2013 (Rowe & Howard 2023) and that has been monitored ever since. The two natural Hutton's shearwaters colonies are in the Seaward Kaikoura mountains between 1200 and 1800 m a.s.l. and 20 km inland, whereas Te Rae o Atiu is adjacent to the sea at 80 m a.s.l.; therefore the logistics required to get to the colonies is vastly different. At Te Rae o Atiu, birds bred in a cluster of 108 wooden nestboxes spaced about 1.5 m apart. Thus, monitoring is easier compared to the long, narrow, stony, winding burrows up to 2 m long at the natural colonies (Cuthbert 1999, 2017). New technology, namely PIT tag recorders attached to the nestbox tunnels, provided bird identity and time of movement data. An additional benefit for the birds was that competition for nesting sites at Te Rae o Atiu was less than at the mountain sites.

As with other shearwaters in the Manx group, we found Hutton's shearwaters little impacted by observer handling (Harris 1966a, b; Warham 1990) with no nest desertion detected in our study.

There are a number of factors that need to be kept in mind when considering comparisons of Te Rae o Atiu birds to those at the natural Kowhai River colonies, and other shearwater species. At 2022-23 the Te Rae o Atiu colony consisted of 86 birds made up of: 19 birds from the 2006 to 2008 translocations and aged 15–17 years; 27 birds from the 2012 and 2013 translocations aged 10 or 11 years; 39 Te Rae o Atiu bred chicks aged 3–10 years; one bird of unknown age that was first caught as an unbanded adult at the colony. The average age of the breeding birds with eggs or chicks in 2022 was 10 years for males and 11 years for females. Thus, the colony is made up of young birds, and lacks the older birds that are expected at a long-established colony. While there are no studies of longevity of Hutton's shearwaters, Kowhai River birds have been captured at 20–23-years-old and one at 32 years (Rowe & Taylor 2020). This suggests that the older birds at Te Rae o Atiu now present may have many more years of breeding to come, and it could be many years before the age distribution at the new colony approaches that of the mountain colonies. Therefore, results with time/age factors will need to be qualified as they could change with more older birds present.

A small number of Hutton's shearwaters return from their first overseas migration to Te Rae o Atiu as 2-year-olds; however, the majority first return as 3- or 4-year-olds, which is slightly older than the 2- to 3-year-olds for Newell's shearwaters (KESRP 2021) and Manx shearwaters (Harris 1996b; Brooke 1990). Most petrel species, including Manx shearwaters, have been found to have breeding males returning to a colony earlier in a season than females (Warham 1990). Our Hutton's shearwater data did not show this trend, with no significant difference between average times for males and females to return in the six years 2017 to 2022. This may be a consequence of the young average age in the colony and the lack of competition for burrows.

One unexpected finding was the extent to which adult Hutton's shearwaters visited other nestboxes during a season – birds visited up to 23 nestboxes, and one nestbox was visited by 29 different birds. Cuthbert (2017) only noted up to five or six birds visiting a Kōwhai River burrow early in the season when they were attempting to acquire a burrow, or they may, as Warham (1990) noted, wander while awaiting the arrival of females. The late season visits to other nestboxes here confirm similar, but smaller scale, observations at Kōwhai River, where 10 of 27 PIT-tagged adults entered some of the other 25 scattered burrows with PIT-tag readers installed (Rowe 2018). We have not found reports of this occurring later in the season by other petrel species, and surmise it could be a normal phenomenon only found as a result of the intensive PIT-tag records obtained at Te Rae o Atiu, or it is an artifact of the translocation and the lack of competition in the newly established population.

Most Hutton's shearwater females went on a pre-laying exodus of about 12 days (range 5–22 days), with males tending to remain about the colony. This is similar to Manx shearwaters (10–14 days; Harris 1966b; Brooke 1990; Warham 1990), Balearic shearwaters (13.5–21 days; ACAP 2021; Guilford *et al.* 2012), Yelkouan shearwaters (13 days; Gatt *et al*. 2019), and Newell's shearwater (14 days; Raine *et al.* 2022). Estimating exoduses can be rather subjective, as some Hutton's shearwater females made up to three overnight visits back to Te Rae o Atiu during the exodus, which is contrary to its strict definition, but is behaviour that Warham (1990) reported for Antarctic prions (*Pachyptila desolata*). Because of the range in length of Hutton's shearwaters exoduses, with some birds making brief visits ashore, it is possible that some birds were feeding closer to the colonies than others, but there is no pre-laying tracking evidence to confirm this. During chick rearing, Hutton's shearwaters mainly foraged south of Banks Peninsula (Bennet *et al.* 2019); other shearwater species are known to visit different sites during the exodus compared to when gathering food for chicks, e.g. Yelkouan shearwater (Gatt *et al.* 2019).

The youngest Hutton's shearwater breeders at Te Rae o Atiu were 4-year-old males and 5-year-old females. These ages for first breeders are similar to those for translocated fluttering shearwaters at Maud Island, Marlborough Sounds (5 years; Bell *et al*. 2005), Manx shearwaters (4–5 years; Harris 1966b, with some breeding as young as 3–4 years; Harris 1966a; Brooke 1990), and Yelkouan shearwaters (3–4 years; Anon 2020).

Shearwaters generally lay one egg without replacements in the event of failures (Marchant & Higgins 1990; Warham 1990) and this is the norm for small shearwaters, e.g. Balearic shearwater (ACAP 2021), Yelkouan shearwater (Anon 2020), black-vented shearwaters (Keitt *et al*. 2000) and Newell's shearwater (FWS 2021; KESRP 2021). This was the case for 265 layings at Te Rae o Atiu; however, in seven instances we found two eggs in the one nestbox in the one season. One of these eggs was considered to be a replacement laying, and was the only one of these 14 eggs to hatch (and the chick subsequently fledged; Rowe *et al.* 2024).

The average laying date of Hutton's shearwaters at Te Rae o Atiu, 6 November (range 2-12 November by year), was similar to 8 and 9 November at the Kōwhai River colonies (Cuthbert & Davis 2002) even

though Te Rae o Atiu is 1200 m lower in altitude and not affected by snow cover. Laying at Te Rae o Atiu is asynchronous and spread over 66 days, 20 October to 25 December; the last date was 14 days later than any other laying. At the Kowhai River colony, the spread was over 38 days, 23 October to 1 December (Cuthbert & Davis 2002); 2.7% of Te Rae o Atiu layings were later than these dates. Excluding the single late egg, the laying period of 52 days is closer to, but still 14 days longer than, at the Kōwhai River, where laying can be influenced by snow cover. The spread was also longer than for fluttering shearwaters at 39 days (Berg *et al*. 2018). It is possible that the long tail of the egg laying distribution was due to replacement layings made observable through the use of accessible nestboxes (Rowe *et al*. 2024), although was only confirmed in the one instance.

PIT-tag records showed that 73% of females were at their nestbox for the first night only after their pre-laying exodus to lay the egg. At least 22% of females were known to have stayed two to four nights; they may not have laid on arrival or had laid and were undertaking the first incubation shift. This fits with Warham's (1990) observations that many shearwaters lay the first night back, although some may delay laying for at least 2 days. Warham also suggested that delayed departures of females may be a consequence of the absence of mates that usually undertake the first prolonged incubation shift. Hutton's shearwater males were in attendance on the night of egg-laying in 66% of cases. At least 36% of them took the first incubation shift by staying one or more days; 21% of males left the night of laying and the status of the rest was uncertain. Where we determined who undertook incubation the first day after laying, in 42% of cases no adults were present, and the egg was left unattended. A similar situation seems to occur with the Manx shearwater, where many females leave the night of laying and the average time until a male begins incubating the first shift is a little more than one day (Brooke 1990).

Hutton's shearwater eggs at Te Rae o Atiu were incubated on average for 52 days, only slightly longer than the 50.3 days at Kōwhai River (Cuthbert 2001; Cuthbert & Davis 2002). This was similar to the incubation periods for other small shearwaters; e.g. 50 days for fluttering shearwaters at Burgess Island (Berg *et al*. 2018), and 51 days for Manx shearwaters (Harris 1966b; Brooke 1990; Gillies *et al*. 2022).

During incubation, our weekly observations found instances when no birds were present on eggs; however, this did not appear to impact egg viability. Intermittent incubation, with associated chilling of the egg, occurs in many petrel species when the returning partner is delayed (Warham 1990), including Manx shearwater (Matthews 1954; Brooke 1990) and black-vented shearwaters (Keitt *et al*. 2000). Hatching success of Hutton's shearwater at Te Rae o Atiu was 59%, similar to the Kōwhai River colonies at 57.3% (Cuthbert 2001) but lower than for fluttering shearwaters at Burgess Island, 73.8% (Berg *et al*. 2018). We expected a higher success at Te Rae o Atiu than at Kowhai River, as the Te Rae o Atiu colony is in a protected predator-free site. However, the birds here were young breeders, and hatching success has improved as they aged.

The time from hatching to fledging for the Hutton's shearwater at Te Rae o Atiu, 87 days, was similar to the 84 days for birds at the Kōwhai River colonies despite those birds having to fly 1200 m higher and 20 km further inland (Cuthbert 2001; Cuthbert & Davis 2002). Cuthbert and Davis (2002) suggested that the longer fledging period at Kowhai River compared to, say, the Manx shearwater at 71 days (Brooke 1990) was due to a lower rate of mass gain, but the similar growth regimes at Te Rae o Atiu and Kowhai River infer that there may be an unknown species-specific phenomenon at play.

Fledging success at Te Rae o Atiu (89%) was higher than at Kōwhai River 85.2% (Cuthbert 2001), similar to fluttering shearwaters on Burgess Island (88%; Berg *et al*. 2018), but lower than reported for Manx shearwater (95%; Harris 1966a, b). The fledging success rate suggests that if an egg can be incubated through to hatching, there is a high chance the chick will fledge, a finding reported for other petrels by Warham (1990). Because there was a high fledging success, productivity was controlled by incubation success, which improved with age of the female parent. The productivity for Hutton's shearwater here was 52% compared to 47% at the Kōwhai River colonies (Cuthbert 2001), 36% for black-vented shearwaters (Keitt *et al*. 2003), 67% for Yelkouan shearwaters (Bourgeois & Vidal 2007), 75% for Manx shearwaters (Harris 1966b), and 72% for fluttering shearwaters at Maud Island (Bell *et al*. 2005) and 64% at Burgess Island (Berg *et al*. 2018).

The mass of Te Rae o Atiu fledglings ranged between 267–565 g (average 415 g) and averaged 75% of their peak mass, a loss similar to Kōwhai River birds at 79% (Cuthbert & Davis 2002). Hutton's shearwater chicks appear to lose less mass from their peak until fledging than some small shearwaters including the Manx shearwater 73% (Brooke 1990) but more than fluttering shearwaters at Burgess Island 89% (Berg *et al*. 2018) or black-vented shearwaters 88% (Keitt *et al*. 2003).

Pre-fledging parent-reared shearwaters at Te Rae o Atiu were recorded at the exit to the tunnels, presumably to imprint on the site by roaming about, but also visiting other nestboxes. This averaged eight nights (range 0–20 nights) before the last recording (and assumed fledging) and confirms earlier observations: Te Rae o Atiu translocated chicks averaged 7.7 nights, range 1–17 nights (Rowe

2014); Kōwhai River native chicks range 1–18 nights (Rowe 2018). Pre-fledging Hutton's shearwater chicks have previously been reported to visit other nestboxes in the days up to fledging (Rowe 2014, 2018) as have fluttering shearwater chicks at Mana Island (Gummer & Adams 2010).

Observers of pre-fledging birds at Kōwhai River noted that the birds spent several nights at the mouths of the burrows, rarely came out and were never seen to exercise their wings before leaving (Harrow 1976; Cuthbert 2001; Cuthbert & Davis 2002). This was also observed for fluttering shearwaters at Burgess Island (Berg *et al*. 2018) with all birds seen outside the burrows leaving the colony that night. Exercising wings before fledging is an activity observed in other petrel species (Brooke 1990; Warham 1990) including black-vented shearwaters (Keitt *et al*. 2000) and Manx shearwaters (Harris 1966b). Wing exercising has now been observed for Hutton's shearwaters at Te Rae o Atiu using trail cameras (Rowe *unpubl. data*, HSCT video files March 2017) and at Kōwhai River using thermal imaging (Howard *pers. obs.*, thermal video available).

In common with some other shearwater species (Warham 1990) there is a tendency for Hutton's shearwater adults to cease feeding chicks several days before they depart. Manx shearwaters desert their chicks on average for 8–9 days (range 1–23, n = 204) before they fledge (Harris 1966b; Brooke 1990). The average for Te Rae o Atiu Hutton's shearwater parents was longer for females (17 days) than males (8 days), and chicks fasted on average 6.3 days before leaving. Brooke also noted that the desertion period was longer for chicks that hatched later ($r = 0.249 > r_{P=0.05} = 0.138$, n = 204); however, that was not the case at Te Rae o Atiu ($r = 0.130 < r_{P=0.05} = 0.273$, n = 49). At Te Rae o Atiu and at Kōwhai River (Rowe 2018) there are records of adult males still in attendance 7 days after their chicks had departed. Warham (1990) also noted cases of petrels in attendance after chicks have departed. Warham (1990) suggested several scenarios that would cover this range, from true desertion (when an adult needs to look after itself and abandons the chick), to a chick refusing food as they have adequate reserves and are ready to leave the colony whether the parents are still coming back or not. The experience with translocated Hutton's shearwaters chicks showed that they fledged when they were ready despite being offered food up until the day they left (e.g. R. Williams, 2012, *Hutton's shearwaters translocation report, March-April 2012*, unpublished report for the Hutton's Shearwater Charitable Trust; Wildlife Management International Ltd., 2013, *Hutton's shearwater: report on the translocation of chicks to Te Rae o Atiu, March 2013*, unpublished report for the Hutton's Shearwater Charitable Trust). Marchant & Higgins (1990) stated that Hutton's shearwater fledglings mostly left their burrows before midnight (0100 h NZDST) on their night of departure. The PIT-tag records here confirm that, with only 19% leaving after midnight.

An unexpected result of PIT-tag monitoring was the number of parents that last visited 71–30 days before their chick fledged, with the remaining parent able to provide enough sustenance for the chick to fledge. Three such cases were due to loss of a parent, while in another three cases the missing parent returned the following breeding season. Rowe (2018) also reported adult males ceasing to feed up to 61 and 73 days before chick fledging at Kōwhai River; however, it was not known whether this was due to death of the parent. We are unaware of other reports of single seabird parents being able to successfully feed a chick over such a long period until it fledged. It is likely that this phenomenon has only been discovered here because of the intensive monitoring in place.

Divorce probably occurs in most petrel species (Warham 1990); however, Manx shearwaters tend to have the same partner and burrow year after year with divorces uncommon (Brooke 1990). The frequency of divorce by Hutton's shearwaters at Te Rae o Atiu is high, with over 85% of birds having had two to seven partners. Unlike Manx shearwaters (Brooke 1990), the frequency of divorces was not significantly different between pairs that failed breeding compared to those that successfully fledged chicks. The high numbers of divorces are likely to be a consequence of the population consisting of mainly young breeders, as the divorce rate decreased with age; in 2022-23, 32% of birds in pairs that laid eggs were under 10 years-old.

In summary, Hutton's shearwaters at Te Rae o Atiu near sea-level had breeding ecology that was similar to birds breeding above 1200 m in the source colony, and that was similar to other small shearwaters of the Manx group. The main difference compared to related species was the longer chick fledging period, which was similar for both Te Rae o Atiu and Kowhai River populations. Other unusual behaviour observed at Te Rae o Atiu, such as birds visiting multiple nestboxes, the variability of pre-laying exoduses, and high divorces rates can probably be attributed to the young age of breeding birds in this new colony.

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This work was performed under permits and authorities issued by DOC, and was carried out under DOC protocols.

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