Conservation and ecology of Hutton's shearwater (*Puffinus huttoni*)

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Published by Department of Conservation Head Office, PO Box 10-420 Wellington, New Zealand

This report was commissioned by Nelson/Marlborough Conservancy.

ISSN 1171-9834

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Reference to material in this report should be cited thus:

Cuthbert, R.J., 2001. Conservation and ecology of Hutton's shearwater (*Puffinus huttoni*). Conservation Advisory Science Notes No. 335, Department of Conservation, Wellington.

Keywords: Hutton's shearwater, *Puffinus huttoni*, breeding success, predation by stoats, Seaward Kaikoura Range, Manakau Ecological District.

Abstract

Hutton's shearwater (Puffinus huttoni) breeds at only two remaining colonies located in the Seaward Kaikoura Mountains. An introduced predator, the stoat (Mustela erminea), has been identified as the main potential threat to the continued survival of Hutton's shearwaters and a major aim of this research has been to evaluate that risk. The results showed that average breeding success (46.5%) and adult survival (93.1%) are within the same range as those found for other *Puffinus* species breeding in areas free from introduced predators. An average of 70.5% of burrows were occupied by a bird incubating an egg. This occupancy figure suggests that the population of Hutton's shearwaters may be closer to 106 000 breeding pairs rather than the 134 000 pairs previously estimated. Stoats are estimated to be killing an average of 0.25% of breeding adults and 12% of chicks in each season. This predation leads to a reduction of $0.86 \pm 0.22\%$ in the yearly population growth rate of a population model of Hutton's shearwaters. However, the overall population growth rate was still positive (0.44%), suggesting that stoat predation is not likely to be unsustainable for Hutton's shearwaters. Available breeding habitat and competition for breeding resources may be limiting factors for the current population of Hutton's shearwaters. Protecting the remaining colonies from feral pigs (Sus scrofa) and establishing new breeding areas should be high management priorities.

1. Introduction

Hutton's shearwater (Puffinus huttoni) is an endangered seabird that breeds in the Seaward Kaikoura Mountains. Their breeding range was formerly more widespread, with historical records from both the Seaward and Inland Kaikouras (Harrow 1976; Sherley 1992). The contraction in breeding range has left the two remaining colonies of Hutton's shearwaters in rugged mountainous country at altitudes of 1200 - 1800 m. These breeding colonies were only discovered in 1964 (Harrow 1965), some fifty years after the species was first described (Mathews 1912). While there is indisputable evidence for the contraction in breeding range (Harrow 1976; Sherley 1992) the cause of this contraction is unknown. Predation and habitat destruction by introduced mammals have been suggested as possible agents of decline (Bell 1986; Sherley 1992). Whether the remaining breeding population of Hutton's shearwaters is stable is also unknown, although anecdotal evidence suggests that the density of burrows may have declined since the colonies were discovered (Sherley 1992). Of particular concern is the presence in both remaining colonies of an introduced predator, the stoat (Mustela eminea) (Harrow 1976; Sherley 1992).

The main purpose of this report is to summarise our present knowledge on the breeding ecology and status of Hutton's shearwaters.

2. Study areas

The two remaining breeding colonies of Hutton's shearwaters are located at altitudes of 1200-1800 m in two remote valleys of the Seaward Kaikoura Mountains (42° 14'S, 173° 28'E). The study was mainly conducted at the larger colony in the Kowhai Valley, which consists of around 30 spatially distinct subcolonies that are separated by areas of scree and bluffs (Figure 1). Shearwater Stream colony was visited on five occasions over the three years of this study. In addition, eight known extinct colonies (Harrow 1974; Sherley 1992) and many of the surrounding valleys were explored for signs of shearwater activity.

3. Methods and materials

3.1 LOGISTIC SUPPORT

Support for this project was provided by the DOC Kaikoura Field Centre, who facilitated the construction of a Portacom hut in the Kowhai Valley. Transport into the colony was provided by Kaikoura Helicopters. The burrowscopes and fieldwork equipment were constructed by staff at the Department of Zoology, University of Otago.

3.2 FIELD METHODS

3.2.1 Breeding habitat

Breeding habitat was measured and quantified from a sample of 118 random quadrats. At each site I recorded the presence/absence of shearwater burrows, the number of burrow entrances and the number of live and dead *Chinocloa* tussocks within a 4 x 4 m quadrat. Aspect and slope-angle over the quadrat were measured to the nearest degree. Two 250 cm³ soil samples were taken from each quadrat. Soil samples were sieved through a 5 mm and 2 mm mesh, and the volume of rock >5 mm and rock <5 mm were measured by water displacement. After all birds had fledged from the colony, I revisited 46 of the quadrats and measured soil depth using a 1 m long and 5 mm diameter fibre-glass probe (soil-depth was the mean penetration distance of five points within the quadrat).

3.2.2 Weights and measurements

Breeding birds from 120 study burrows were sexed by cloacal measurements at, or shortly after, egg-laying (Boersma & Davies 1987). All birds caught were weighed to the nearest 2.5 g with a Pesola spring balance. The mass of sexed breeding birds was measured during the pre-egg, incubation and chick-rear-

ing periods. These periods were defined in relation to the laying and hatching date of each pair. Body measurements were taken from all study birds using vernier calipers and a stopped ruler. Hatched chicks from study burrows were weighed on every other day until fledging had occurred.

3.2.3 Monitoring burrow occupancy and breeding success

During the incubation period of the 1996/97 season, I compared the accuracy of using field sign and a burrowscope (Dyer & Hill 1991; Lyver et al. 1998). Over three weeks (14/11 to 2/12/96) seven observers independently checked 148 marked burrows. Each observer scored the burrow as "used" or "unused" on the basis of the field sign at the burrow entrance. The presence of fresh diggings, scratches in the soil, faeces, feathers and broken fragments of fresh vegetation were taken as indicators that the burrow was "used" (Sherley 1992; Furness 1995). At the end of this period, all 148 burrows were checked with the burrowscope.

To test the accuracy of the burrowscope I checked a sample of 103 burrows first with a burrowscope and then through an inspection hatch. Inspection hatches consisted of a covered hole, dug above or in reach of the nest chamber. Inspection holes were either covered with a suitably sized rock or plastic tray, or else were constructed from 150 mm diameter plastic drain tubing, covered with a screw or push-on lid. These burrows were checked towards the end of the chick-rearing period and should provide a best estimate of the accuracy of burrowscopes.

In the 1997/98 and 1998/99 seasons I monitored occupancy and breeding success in three different ways that would cause varying levels of disturbance. These groups were: burrows checked with a burrowscope, burrows checked infrequently through inspection hatches, and burrows checked frequently through inspection hatches. The burrowscope and infrequently checked inspection hatch burrows were monitored in mid November (early incubation), early January (late incubation/early chick-rearing) and late February (late chickrearing). Incubating birds were removed from the inspection burrow, banded and weighed, and returned to the burrow after the egg had been measured. The frequently checked burrows were inspected every other day during the pre-egg period and for the first 4 - 10 days after egg laying. All incubating birds were removed from the burrow, banded and measured at first capture. These burrows were then left undisturbed for the rest of the incubation period and were next checked at the estimated hatching date. The chick was then weighed and measured on at least every other day for the rest of the chick-rearing period.

3.2.4 Breeding success

For the seven year period from 1989/90 to 1995/96 I used data gathered by Department of Conservation staff (Paton & Davies, in press). These data were collected from three different sub-colonies (sub-colonies 1, 9 & 14 of Figure 1, known as "camp", "top" and "hoheria" respectively) with a sample of 18 to 38 marked burrows (depending on the year) monitored within a 10 x 10 m plot. Checks were made in mid November, early January and late February. Burrows were checked through a rock-covered hole dug above each nest chamber.

In the 1996/97 breeding season I increased the number of inspection hatch burrows in sub-colonies 1 and 9 to sixty and established a further 40 inspection hatch burrows in sub-colonies 5, 15 & 32 (Figure 1). A further 40 marked burrows checked with the burrowscope were established in sub-colonies 9, 30 and 31. These burrows were distributed at approximately 5 m intervals along transects that traversed each sub-colony. This made a total of 360 study burrows, which were inspected on three occasions over each season.

Reproductive parameters were defined in the following way. Burrow occupancy was the proportion of burrows that contained a bird incubating an egg during the nest check in early incubation. Hatching success was the proportion of eggs that successfully hatched. Fledging success was the proportion of hatched chicks that survived to the nest check in late chick-rearing. Breeding success was the proportion of eggs that survived to the late chick-rearing check. Total productivity was the proportion of burrows that produced a fledged chick. The overall mean, standard error and 95% confidence limits were estimated using the methods of Burnham et al. (1987: 260-278).

3.2.5 Adult survival

Incubating birds were banded with an individually numbered monel band. Usually only one bird in each study burrow was caught in any year, and sample sizes in the first six years (1990/91 to 1995/96) were small. Some study burrows were "lost" between years, either because birds dug beyond the limits of the inspection hatch, or because the inspection hatch could not be relocated. Adult survival was, therefore, estimated only from those burrows that were checked in every year from the time they were added to the study.

Annual adult survival from 1990/91 to 1998/99 was estimated from mark/recapture analysis using the program (White & Burnham 1997). Two different models were fitted to the data set mark: constant survival and variable probability of capture (S, P,) and variable survival and variable probability of capture (S, P,). Capture effort varied greatly between years, so a variable probability of capture was most appropriate to the data set. The mark/recapture records used in this analysis are presented in Appendix 1.

3.2.6 Predation

I monitored predation in two main ways: by monitoring the fates of individual chicks and adults in marked study burrows and by regularly walking transects to find dead birds lying on the ground within the colony.

I used study burrow data gathered by Department of Conservation staff from 1989/90 to 1995/96 and from this study to estimate the proportion of dead chicks and adults down burrows. In the 1997/98 and 1998/99 seasons, 120 of the 350 study burrows were checked every two days for the first 4 - 8 days after egg laying, and every day during the chick period. From these burrows, I calculated the proportion of eggs and chicks that "disappeared".

At the start of the 1996/97 season I established transacts which totalled 6 km in length, within sub-colonies 4, 5, 9, 15, 18, 30 and 32. Transacts were fixed and marked, and followed a "zig-zag" route that traversed through each sub-

colony. Transects were walked every 15 days during all three seasons. I recorded the perpendicular distance of each carcass from the transect line and used the program DISTANCE (Laake et al. 1993) to estimate the density of carcasses.

Predation estimates from transects will be biased if stoats cache carcasses and/or withdraw them into shelter for feeding. To evaluate this, I trapped and radio-tracked stoats in the 1997/98 and 1998/99 seasons. Stoats were caught in wooden Edgar traps baited with fresh rabbit meat. All animals caught were fitted with two-stage radio-collars (SirTrack Ltd). Stoats were tracked with a hand-held receiver and Yagi antenna. If the animal was stationary I located its position on the ground (to the nearest 1 - 2m). All sites were marked and then searched over the following days for carcasses on the ground and down burrows.

I recorded information on the location and position of each body and any associated sign of feeding on the carcass (Table 1). All bodies were collected and carefully dissected to find and measure the location of killing bites or injuries (Lyver in press), and to classify the pattern of eating (Table 1).

Total chick predation was estimated from the mean proportion of stoat-killed chicks found down burrows from the last ten breeding seasons (1989/90 to 1998/99) and from the mean proportion of chicks that disappeared from the daily checked burrows (1997/98 to 1998/99). Total adult predation was calculated from the proportion of stoat-killed adults found down burrows over the ten seasons (1989/90 to 1998/99) and from the proportion of stoat-killed adults found on the ground within the colony over the last three seasons (1996/97 to 1998/99). The proportion of stoat-killed adults on the ground was estimated from the density of dead bodies found on transects and from the density of breeders and non-breeders within the colony (calculated from mean burrow density and burrow occupancy).

3.3 STATISTICAL ANALYSES AND FURTHER METHODS

Unless otherwise specified, all results are presented as the mean \pm standard deviation and statistical tests are two-tailed. Binomial confidence limits are estimated following Zar (1996: 513-527). The methods described above provide a broad overview of the work undertaken in this project. More detailed descriptions of the methodology and statistical analyses used can be found in Cuthbert (1999), copies of which are located with the Nelson/ Marlborough Department of Conservation and at the University of Otago.

4. Results

4.1 BREEDING COLONIES

In areas with soil and vegetation the presence of burrows was positively related to the angle of the ground and tussock density and negatively related with the soil content of rocks larger than 5 mm in diameter. There was no relationship between the presence or absence of burrows with the aspect of the ground or with rocks smaller than 5 mm. The average values of these parameters, in areas of burrowed and non-burrowed ground, are shown in Table 2. The measurements of soil-depth indicated that burrows were generally located in areas of deeper soil.

Within the Kowhai Valley and Shearwater Stream colonies almost all areas of suitable habitat appear to be utilised for burrowing, and within the Kowhai Valley burrows occurred at an average density of 9.1 (6.8 burrows per 4 x 4 m plot) (n = 50). This burrow density is over twice that found in the closely related and similar sized Manx shearwaters (*Puffinus puffinus*) breeding on the mountainous island of Rhum, NW Scotland (Hutton's shearwaters = 0.57 ± 0.42 burrows/m2 (n = 50); Manx shearwaters = 0.28 ± 0.21 burrows/m2 (n = 101) (Furness 1995)).

Breeding burrows are generally of a simple and non-branched nature, with the majority of burrows having one entrance that leads to a single nest chamber. From a sample of 112 burrows fitted with an inspection hatch, 26 (23.2%) were of a branched structure and 14 (12.5%) had more than one entrance. Although 23.2% of burrows were of a branched structure, on no occasion did I record more than one incubating pair within a burrow.

4.2 DESCRIPTION OF HUTTON'S SHEARWATERS

4.2.1 Weights and measurements of adults

Adult males were larger than females in all measured body-dimensions with the exception of wing-length (Table 3). Males were significantly heavier than females in all three periods of the breeding season although there was considerable overlap between the ranges of mass observed (Table 4). There was also significant variation between periods, with both males and females at their lowest mass during chick-rearing (Table 4).

4.2.2 Eggs and incubation

There was no difference between the mean laying date in the 1997/98 season (9 November \pm 9.6 days, n=88) or the 1998/99 season (8 November \pm 6.2 days, n=88) (t=0.46, n.s.). Egg-laying was spread over a wide range of dates in both years (23/10 to 1/12/97 = 38 days, and 29/10 to 24/11/98 = 27 days). In the 1997/98 season the mean egg-length was 60.3 ± 2.0 mm (n=89, range 56.1 to 66.1 mm), with a mean egg-width of $40.3 3 \pm 1.3$ mm (n=89, range

36.1 to 42.6 mm). Mean incubation period in the 1997/98 breeding season was 50.3 ± 2.0 days (n = 50; range 46 to 56 days).

4.2.3 Chick growth

Chicks gained mass rapidly before reaching a maximum at around 60 days old, and then mass declined until fledging (Figure 2). There were significant differences between the rate of mass gain and the maximum mass of chicks in the 1997/98 and 1998/99 seasons (Table 5), but in both seasons chicks reached their peak mass at an average of about 60 days of age. In the 1997/98 seasons chicks fledged after an average of 83.8 \pm 3.8 days within the burrow (n=43, range 75 to 94 days) and at an average mass of 404 ± 40 g (n=44). Chicks approaching fledgling age spent four to five nights in their burrow entrance before fledging, but only rarely were fledging chicks seen or caught out of their burrows on the ground. On no occasion were chicks seen exercising their wings at night before fledging, an activity documented in other petrel species.

4.3 BREEDING SUCCESS AND SURVIVAL

4.3.1 Monitoring breeding success and burrow occupancy

The average occupancy status of burrows classified using field sign was not significantly different from that found with a burrowscope (field sign = 71.3 \pm 20.5%; burrows cope = 60.8%;one-sample t-test, t = 1.35, n.s.) although there was a very large range of occupancy values scored (Table 6) and significant differences between observers (Log-likelihood (26 = 410.4 p < 0.001). Field sign on average classified 36.5 \pm 7.5% of burrows differently from the results from a burrowscope.

A total of 113 inspection hatch burrows were burrowscoped and then checked through an inspection hatch. The burrowscope was unable to classify the content in ten instances (8.9%) because burrows were either too tight or twisted for the burrowscope tube. Of the remaining 103 burrows, the burrowscope was accurate in classifying the contents (chick present/absent) in 93 instances (90.3%). Of the ten burrows that were incorrectly classified, nine were branched. This was from a total of 18 out of 103 branched burrows (17.5%), suggesting that most inaccuracy occurred in burrows with a more complex branched structure.

There were no significant differences in hatching success or fledging success between the three burrow checking regimes (Table 7), suggesting that handling birds during incubation or chick-rearing did not cause higher levels of disturbance and desertion than using a burrowscope. There were, however, significant differences between the three burrow checking regimes and the proportion of burrows that were recorded to contain an incubating bird (Table 7). Of the burrows checked with the burrowscope, 71% were observed to contain an incubating bird, in comparison with occupancies of 87% and 81% in the frequently and infrequently checked inspection burrows, respectively.

4.3.2 Occupancy and breeding success

Because the burrowscope was unable to accurately assess the content of some burrows, overall burrow occupancy was only estimated from burrows checked through inspection hatches. The proportion of burrows containing an incubating bird varied from year to year (Table 8, Figure 3a) with an average occupancy of 70.5% (with 95% C.I. from 61.8 to 77.4%). Breeding success from 1989/90 to 1998/99 was highly variable, ranging from 27 to 66% (Table 8, Figure 3b). The average breeding success over this period was 46.5%, with 95% confidence limits from 37.4 to 55.6%.

Significantly more breeding failures occurred during the incubation period compared to the chick-rearing period (t 17 = 5.23, p < 0.001). Hatching success averaged 57.3% (with 95% C.I. of 47.5 to 67.1%) over the ten seasons of the study, compared to an average fledging success of 85.2% (with 95% C.I. of 81.0 to 89.4%) from the nine seasons for which data were available. Hatching success was significantly more variable than fledging success (between-year variation of hatching success = 14.2%, fledging success = 2.0%; variance test, F(2),9,8=50.41, p < 0.001) (Figure 3 c & d).

4.3.3 Adult survival

The most parsimonious mark/recapture model was one with constant yearly survival and varying probability of capture. Using this model, annual adult survival from 1990/91 to 1998/99 was estimated to be $93.1 \pm 1.3\%$ (\pm s.e.), with 95% confidence intervals of 88.9 to 95.8%.

4.1 PREDATION

4.4.1 Stoat caches of chicks

Twelve stoats in the 1997/98 season and four in 1998/99 were caught from a total of 1472 and 1080 "effective trap nights" (Nelson & Clark 1972). No ferrets or rats were caught during this trapping period. Nine stoats (four males and five females) were radio-tracked during the chick-period of the 1997/98 season, and two males were tracked during the incubation and early chick period of the 1998/99 season. A total of 345 radio-tracking fixes were obtained from 208 different sites. Nine dead adult shearwaters were found, six of which were down burrows. On no occasion did I retrieve more than one dead adult shearwater at a site found through radio-tracking. Seven caches of chicks were found, three of which contained ten, six and four chicks, while the remaining four caches contained two chicks. A further 28 single dead chicks were found as a result of the radio-tracking. The ages of these dead chicks (estimated from their size) suggests that stoats were mainly removing young chicks from their burrows (Figure 4).

4.4.2 Egg and chick predation

A total of 74 eggs in 1997/98 and 49 eggs in 1998/99 were checked every day during the first few days of incubation (day 0 up to day 8), for a total of 422

and 209 egg/days respectively. No eggs disappeared from burrows during this period, suggesting that if egg predation occurred, it was very infrequent.

Dead chicks were recovered from study burrows in all years except for the 1990/91 season (Table 9). The overall mean proportion of dead chicks found down burrows was 6.6%, All 13 dead chicks found down burrows in the 1996/97 - 1998/99 seasons showed signs of stoat predation. Similar proportions of chicks disappeared from burrows in the 1997/98 (7/128 = 5.5%) and 1998/99 (2/39 = 5.1%) seasons. The pooled mean of these two estimates was 5.4%. Total chick predation over the last ten seasons is estimated to be 12.0% (95% C.I. from 2.5 to 17.4%).

4.4.3 Adult predation

A total of 96 dead adults were found on transects during the 1996/97 to 1998/99 breeding seasons. Adults were found more frequently during the pre-egg and incubation periods in comparison to the chick-rearing period (pre-egg and incubation = 1.28 ± 0.73 bodies/km, n = 16 transect sessions; chick-rearing = 0.61 ± 0.42 bodies/km, n = 18 transect sessions; t32 = 3.25, p < 0.005). Using the criteria in Table 1, the cause of death was classified for 52 of the 96 dead adults found. Stoats were the major cause of mortality, with evidence for stoat predation found on 57.7% (30/52) of these carcasses (Table 10). Of the 44 carcasses where the cause of death could not be determined, 41 showed sign of harrier feeding.

The average density of dead adults found on the ground over the three seasons was 20.8 ± 2.6 dead adults/ha. Using the average proportion of stoat-killed adults found on transects, the overall density of stoat-killed adults was estimated to be 11.8 ± 1.5 adults/ha. Burrows within the colony occurred at an average density of 6181 burrows/ha. With an average of 69.6% of burrows being occupied and including non-breeding birds which are estimated to comprise two thirds of the population (Brooke 1990), the overall density of birds was calculated to be 24 583 birds/ha. The total proportion of stoat-killed adults on the surface is estimated to be 0.05 %.

Dead adults were only found down study burrows in two breeding seasons between 1989/90 to 1998/99 (Table 9). Six adults were found out of a sum total of 1538 burrows checked over the ten seasons. The pooled mean of these estimates is 0.20%. Both dead adults found in the 1996/97 season showed signs of stoat predation. The total estimated proportion of adults killed down burrows and above-ground in each season is estimated to be 0.25% (95% C.I. from 0.08 to 0.43%).

5. Discussion

5.1 GENERAL ECOLOGY OF HUTTON'S SHEARWATERS

The breeding habitat of Hutton's shearwaters falls within the pattern described for other burrowing petrels. The majority of burrows were found on moderate to steeply angled slopes. This presumably facilitates take-off, as Hutton's shearwaters have difficulty taking off from level ground (personal observation). The sloping ground may also reduce the likelihood of burrows flooding in periods of heavy rain (Thompson & Furness 1991). Soil-depth and the volume of larger rocks within the soil were the other factors that appeared to be important for the location of burrows, probably because of ease of burrowing.

Within both remaining breeding colonies of Hutton's shearwaters all areas of habitat suitable for burrowing appear to be utilised and the density of burrows within the Kowhai colony is over twice that recorded for the closely related and similar-sized Manx shearwater (Furness 1995). Moreover, there is a large level of competition at the start of each season for a breeding burrow (Cuthbert 1999). These results suggest that available breeding habitat within the two colonies could be a factor limiting the population (Newton 1998).

Breeding males are on average of greater size and mass than breeding females; a pattern reported for most shearwater and petrel species (Brooke 1990; Warham 1990). Although males are larger, there was a large range of overlap between the sexes in all measured body dimensions, and body size alone is an unreliable means sexing birds.

In the 1997/98 and 1998/99 seasons egg laying was spread over 38 and 27 days, respectively. Heavy winter snowfall in the 1997/98 season explains some of the variation between the two seasons, because winter snow prevented some birds from accessing their breeding burrows. The incubation period in Hutton's shearwaters of 50.3 days is almost identical to the 51 days recorded for Manx shearwaters (*Puffinus puffinus*) (Brooke 1990) and 49 days recorded for Audobon's shearwaters (*Puffinus lhermini eri*) (Warham 1990, table 14.2).

While the duration of incubation is similar, the average age at fledging (83.8 days) in Hutton's shearwaters was considerably longer than the 71 and 75 days recorded for Manx and Audobon's shearwaters. Hutton's shearwater chicks followed the growth pattern reported for other *Puffinus* species (Warham 1990), with mass being gained rapidly to a maximum point, and then steadily lost until chicks fledged. The observed rate of mass gain (c. 10-13 g/day) was lower than that reported for Manx shearwaters (c. 15g/day; Brooke 1990) and these differences may potentially explain the extended fledging period.

Unlike other shearwater species (Brooke 1990; Warham 1990), Hutton's shearwater chicks did not appear to come out of their burrow and "exercise" in the weeks before fledging. This behaviour makes banding of large numbers of fledglings a difficult task and reduces the ability to accurately esti-

mate recruitment in Hutton's shearwaters. Why Hutton's shearwater chicks refrain from exercising on the colony is unknown, but it may be related to the presence of two native predators, Australasian harrier (*Circus approximans*) and kea (*Nestor notabilis*), which have been observed in the colonies at night.

The results of this study indicate that, despite the alpine habitat of the breeding colonies, most aspects of the breeding biology of Hutton's shearwaters fit with the general pattern observed in other species of *Puffinus*. The duration of chick-rearing was longer than that recorded in similar sized species, and this may be due to difficulty in provisioning the chick, either because of food resources at sea or the costs of flying in to the breeding colony.

5.2 MONITORING OCCUPANCY AND BREEDING SUC-CESS

This study has demonstrated that using field sign to assess the occupancy status of burrows is likely to produce erroneous results. Although average burrow occupancy from field sign was not significantly different to that found from using the burrowscope, this was more a matter of coincidence rather than agreement between the two methods, because the use of field sign classified over one third of burrows incorrectly. It seems unlikely that incorrectly classified burrows were the result of any systematic error in the interpretation of field sign, because observers only agreed in 77.8% of classifications (and observers would be expected to agree in 50% of cases by chance alone). These results cast severe doubt on the ability of monitoring studies that use this methodology. Monitoring large trends in the population of Hutton's shearwaters could be done by simply monitoring burrow density (see Appendix 2).

Of the burrows that could be fully checked, burrowscopes were accurate in classifying the contents in 90.3% of cases. Incorrectly classified burrows were generally branched or sharply twisting, suggesting that most inaccuracies in using burrowscopes occur in burrows of more complex structure. The result of these inaccuracies is that burrowscopes are likely to underestimate the true level of burrow occupancy. Burrowscopes were, however, a reliable means of measuring breeding success of Hutton's shearwaters for nests where occupancy could be detected. However, problems with reliability (key periods of the 1996/97 and 1997/98 breeding seasons were missed) suggest that using the burrowscope as the main, or only, means of monitoring breeding success could be risky. One other problem with burrowscopes (not assessed in this study) is the potential for between-observer errors. Using a burrowscope effectively takes a large degree of concentration and experience, and therefore unless the same personnel are used in a long-term study, interpreting trends could be confounded by observer errors.

Inspection hatches appear to be the simplest and most reliable means of monitoring burrow occupancy and breeding success, and Hutton's shearwaters seem tolerant of this method. No differences were found between hatching success or fledging success for the three different monitoring regimes. This suggests that handling incubating Hutton's shearwaters through inspection

hatches did not result in an increased number of egg desertions as has been reported for other petrel species. Therefore, the data collected over the ten seasons that Hutton's shearwaters have been monitored using inspection hatches should give a reliable and accurate estimate of breeding success. Inspection burrows also have the advantage that birds can be banded to allow estimation of adult survival, and any carcasses can be recovered for autopsy. The disadvantage of inspection burrows is that they require maintenance in most years, to ensure that the nest chamber has remained within reach of the hatch. Some burrows are also likely to be dug up by kea. Siting inspection hatch burrows in solid areas of the colony and ensuring that hatches are secure and/or covered with large rocks should reduce the latter problem. Inspection hatches constructed from plastic tubing proved to be the most robust and easily monitored form of inspection burrow.

5.3 PRODUCTIVITY AND SURVIVAL

In spite of the presence of stoats the overall values of breeding success and annual adult survival recorded in this study are very similar to those reported for other *Puffinus* species breeding in areas free from introduced mammalian predators (Table 11). These results suggest that the impact of stoats on the breeding biology and population of Hutton's shearwaters could be low. The majority of breeding failures occurred during the incubation period, a pattern that has been reported in a number of studies on petrels (e.g. Chastel et al. 1993; Johnstone & Davies 1990). In contrast, once the chicks had hatched, their survival prospects were high (85.2%) (and the fledging period is when the greatest numbers of stoats will be present in the area (King 1990)).

An average of 70.5% of burrows were occupied by a bird incubating an egg. If this is an accurate estimate of the proportion of breeding birds, the breeding population of Hutton's shearwaters is likely to be lower than that calculated by Sherley (1992). Sherley estimated that 89.1% of burrows were occupied and that the breeding populations of Kowhai Valley and Shearwater Stream colonies were 124 600 and 9800 pairs respectively. With an average burrow occupancy of 70.5%, the breeding populations of Hutton's shearwaters within Kowhai Valley and Shearwater Stream may be closer to 98 600 and 7750 pairs respectively.

The overall value of productivity (number of young fledged per burrow) for Hutton's shearwaters was 32.8%. This figure is remarkably similar for all five *Puffinus* species where data are available, despite there being differences between breeding success and burrow occupancy. This pattern suggests that other processes, in particular density dependence, may be important for regulating total productivity of shearwater species.

Annual adult survival in Hutton's shearwaters appears to be very similar to the range of values recorded in other congeneric species breeding in environments free from introduced predators (Table 12). The results of these studies suggest that annual adult survival in species of *Puffinus* may be closer to 93% than the 90 to 92% previously reported (Wooller et al. 1992).

These differences, although apparently small, are important because annual adult survival will greatly affect the duration of an individual's breeding life and overall lifetime reproductive success and will have a large influence on the growth rate of the population (Croxall & Rothery 1991; Hamilton & Moller 1995; Cuthbert 1999). With an average adult survival of 93.1%, a breeding bird will on average have a reproductive life of 14.0 years (expectation of further life calculated as (2-m)/2m, where m is mean annual mortality). In comparison, adult survival of 90% will give a mean expectation of further life of 9.5 years. These results suggest that even small changes to adult survival are likely to be important for the population growth rate of Hutton's shearwaters and underlines the importance of accurately estimating this parameter.

5.4 PREDATION

Stoats are the primary predators of breeding Hutton's shearwaters and account for nearly 57.7% of observed adult mortality. A feral cat was present in the colony for one month of the 1998/99 season, but cats were otherwise absent from the colony. No ferrets or rats were caught during the trapping period of this study. This, combined with the relative ease with which these species are trapped (Cross, et al. 1998; Innes 1990; Moors 1990), suggests that ferrets and rats are generally absent from the colony.

It is important to assess the reliability of the predation estimates. This is especially so because autopsy-based studies often underestimate predation because most kills are consumed or decayed before they are found by observers (Hartman et al. 1997; Newton 1998).

Radio-tracking indicated that adults were generally not cached by stoats (which will lead to an underestimate of predation), although two sites were found by chance which both contained four adult shearwaters - indicating that in some circumstances adults are cached, but that this behaviour is relatively uncommon. In contrast, the frequent caching of chicks indicated that transects were an unreliable means of assessing chick mortality and, because of this, chick predation was estimated from the proportion of dead chicks found down burrows and the proportion that "disappeared" from burrows.

Most stoat predation occurred on chicks rather than adult shearwaters (12% of chicks and 0.25% of breeding shearwaters). This is important, because Hutton's shearwaters are likely to be much more sensitive to the loss of adults (Croxall & Rothery 1991; Hamilton & Moller 1995; Cuthbert 1999). It is therefore "fortuitous", with respect to the impact of stoat predation on Hutton's shearwaters that stoats switch from a diet of predominantly adults to a diet almost exclusively of chicks (Cuthbert 1999) and that they take a larger proportion of chicks than adults.

The estimated level of stoat predation on Hutton's shearwaters is in marked contrast to the rates of predation recorded on other birds within New Zealand, including sooty shearwaters (Hamilton & Moller 1995; Lyver et al in press), yellow-eyed penguins (Megadyptes antipodes) (Ratz, submitted), kaka

(Nestor, meridionalis) (Wilson et al. 1998), yellowheads (Mohua ochrocephalus) (Elliot 1992) and kiwi (Apteryx sp.) (McLennan et al. 1996). Two obvious differences between Hutton's shearwaters and these other species are the relative size and density of the Hutton's shearwaters breeding colony, and their high altitude. The two remaining colonies of Hutton's shearwaters contain around 100 000 and 8000 breeding pairs and there is likely to be double that number of non-breeders visiting the colony (Brooke 1990). These very high numbers and densities of birds will provide a measure of "safety in numbers", as the number of stoats present within the colony can only remove a very small fraction of the total number of Hutton's shearwaters. Stoat predation of Hutton's shearwaters is, therefore, inversely density-dependent, whereby with increasing numbers of prey, a decreasing proportion are killed by predators (Newton 1993).

Inverse density-dependent predation has been shown to occur in several introduced-predator and endemic-prey systems (Sinclair et al. 1998) and is predicted to occur when predator numbers are limited by factors other than their primary prey (Newton 1998). Such a situation is likely for stoats in the breeding colonies of Hutton's shearwaters. Stoat numbers are usually limited by a lack of available prey over the winter period and at least half of all stoat mortality may occur at this time (Erlinge 1983; King & McMillan 1982). This situation is likely to be even more severe within the shearwater colonies, because during the winter months Hutton's shearwaters are absent for over four months and there is no alternative abundant prey source.

The high between-year variation in predation reported for yellowheads and kaka (Elliot 1996; Wilson et al. 1998) has been attributed to periodic irruptions in stoat numbers which generally occur in the year following mast-seeding by beech trees (*Nothofagus* sp.) (King 1983). The historical reductions in the range and extent of beech forest in the Kaikoura region (Wardle 1991) and the high alpine environment of Hutton's shearwaters may preclude such processes from operating within the shearwater colonies. However, the extent to which mice and stoat numbers may respond to mast-seeding of the dominant vegetation, snow tussock (*Chionochloa* sp.) (Kelly et al. 1992) is unknown and is an area that needs further investigation.

5.5 I MPACT OF STOAT PREDATION

To assess the overall impact of the observed predation I developed a population model of Hutton's shearwaters using all the available information on breeding parameters and survival from this study and data from other *Puffinus* species where none was available for Hutton's shearwaters. Details on the structure and parameter values entered into this model can be found in Chapters 5 and 6 of Cuthbert (1999).

The overall model indicated a median yearly population growth rate of 0.44%, suggesting that the population is slowly increasing or stable. While the overall population growth rate of the model indicates that Hutton's shearwaters are not at great risk of decline, the wide range of growth rates predicted by the model (Figure 5) indicates that it is impossible to be absolutely sure that the population is "safe".

I used the approach of Robinson & Redford (1991) to assess whether stoat predation was likely to be greater than the maximum "harvest rate" sustainable by the population. No measures of the maximum population growth rate of Hutton's shearwaters are available. Instead, I used information on the observed population growth rate of two other long-lived annual breeding petrel species; the northern fulmar (*Fulmarus glacialis*) and Laysan albatross (*Diomedea immutabilis*), breeding in environments free from introduced predators. These species have grown at an annual rate of around 7 and 7.1% respectively (Cramp, et al. 1974; Gould & Hobbs 1993), and these increases are the result of productivity rather than immigration. Therefore, I have taken 7% as the growth rate that Hutton's shearwaters may be able to realise under natural conditions in the absence of predation (Slade et al. 1998).

If the estimates of predation over the last ten years are representative of the true predation rate, the observed impact of stoat predation on the population model's annual growth rate is almost an order of magnitude smaller (0.86 \pm 0.22%) than the 7% growth rate that may be realised by a species like Hutton's shearwaters. This suggests that the predation rate is well below the potential yearly growth rate and that the impact of stoats is not, on its own, likely to be unsustainable for the population.

6. Conclusions

6.1 CONSERVATION OF HUTTON'S SHEARWATER

The results of this study suggest that the estimated impact of stoat predation is unlikely to be causing a decline in the breeding population of Hutton's shearwater, despite the year-round presence of stoats (and on occasion other mammalian predators) and the fact that stoats are definitely preying upon eggs, chicks and adult shearwaters. This minimal impact is related to a number of factors, which include the relative abundance of shearwaters compared to stoats, limitation of stoat numbers by factors outside the breeding season of Hutton's shearwaters, prey selection by stoats, and the sensitivity of the shearwater population to losses in different breeding and survival parameters. The estimated impact of predation on Hutton's shearwaters is in marked contrast to other studies of stoat predation within New Zealand and emphasises the need to document the effect of a predator, rather than simply consider its presence a cue for control (Caughley & Gunn 1996).

The results suggest that factors other than predation may be more important for limiting the present breeding population size of Hutton's shearwaters. Bird populations may be limited by a number of factors, including food resources, climatic conditions, breeding sites and parasites (Newton 1998). Food resources are widely held to be the ultimate factor limiting the size of seabird populations (Birkhead & Furness 1985; Wooller et al. 1992). Presently we have limited knowledge of the food of Hutton's shearwaters (West & Imber 1985) and no knowledge on the availability or distribution of these feeding resources.

The availability of suitable habitat and breeding burrows may well be factors that are currently limiting Hutton's shearwaters. Within the two remaining colonies all areas of suitable habitat appear to be utilised for burrowing, burrows occur at a high density, and there is strong evidence of competition for burrows. Under these circumstances, a surplus of non-breeding birds is likely to be excluded from the breeding population, so that breeding habitat and burrows will ultimately limit the population (Manuwal 1974; Newton 1998).

Additionally, the relatively small impact on the population of Hutton's shearwaters of the predation observed in this study is likely to be further mitigated if breeding space is limiting the population, because any losses from predation are likely to be compensatory, rather than additional, to existing mortality. That is, predation of chicks and pre-breeders will be merely removing individuals that otherwise would be excluded from the breeding population, and losses of breeding birds will be replaced by non-breeding individuals (Newton 1993; Newton 1998).

The availability of breeding habitat underlines the critical importance of protecting the two remaining colonies of Hutton's shearwaters. Loss or degradation of this habitat is likely to have a far greater impact on the population than the current levels of mortality imposed by stoats. Protecting the two remaining breeding colonies from invasion by feral pigs (Sus scrofa) and not allowing large numbers of browsing mammals to build up in the area, should be high management priorities. Feral pigs are currently found on the boundaries of the Kowhai Valley and Shearwater Stream colonies, and are only separated from areas of burrowed ground by steep terrain. Pigs were also recorded within, or in easy access of, all the extinct colonies of Hutton's shearwaters and it is this factor alone that appears to distinguish those colonies that have become extinct and those that have survived. Other factors that have been suggested as possible causal agents of decline (e.g. habitat destruction by browsing chamois (Rupicapra rupicapra), red deer (Cervus elaphus) and feral goats (Capra hircus), erosion and stoat predation) are either present in both the extinct and surviving colonies or would operate on such a scale as to affect all colonies (e.g. fall-off in at-sea prey availability).

Although circumstantial, the present distribution of feral pigs in the Kaikouras and their documented ability to root up and prey upon burrowing seabirds (Challies 1975; Harper 1983; Holden 1994; Howell & Webb 1990) strongly suggests that pigs were partly responsible for the historical reduction in breeding range. Even without the threat imposed by pigs, dependence on just two breeding localities is not a safe option, and establishment of other breeding colonies should be given serious consideration.

6.2 RECOMMENDATIONS FOR FUTURE RESEARCH AND MANAGEMENT

While the results of this study have generally given an encouraging picture of the health of the Hutton's shearwater population and the likely impact of stoat predation, there are still key areas of uncertainty that need to be clarified before the conservation status of Hutton's shearwaters can be re-assessed. The current assessment of the conservation status of Hutton's shearwaters is based on the values of breeding success and adult survival (which are comparable with other *Puffinus* species breeding in areas free from introduced predators) and the low rates of predation observed within the colony. While this is encouraging, longer-term assessment of survival, breeding parameters and predation are needed. Re-analysing a long-term data set, Brook & Kikkawa (1998) found that 15 years of data were required to accurately estimate breeding and survival parameters before they were sufficiently accurate to be of use in a population viability model. Present breeding parameters and adult survival are based upon ten and nine seasons of data, respectively. As the resources and set-up to continue monitoring are in place (e.g. the research hut, marked study burrows, banded adults and experienced personnel), it would be advisable to continue with the existing monitoring of these parameters so that more accurate estimates can be calculated.

Recruitment into the population also has a large influence on the population model, yet it is a parameter for which there are currently no estimates available for Hutton's shearwater. Hutton's shearwaters banded as chicks are beginning to return to Camp and Top colony as 3- and 4-year old birds and the capture of these birds and banding of more fledglings should be a priority. This research is made difficult by the behaviour of Hutton's shearwater chicks at the time of fledging. As a consequence, if accurate estimates of recruitment are to be obtained, it is important to maintain a sufficient number of inspection burrows so that fledging chicks can be caught and banded each season.

Predation parameters should also be estimated in the course of the continued monitoring of adult survival and breeding success. Records should be kept of the number of dead adults and chicks found down study burrows (with information on the cause of death, as categorised in Table 1). A record should also be kept of the number of dead adults and chicks found on the ground with the study burrow areas of Camp and Top sub-colonies.

The estimated low impact of stoats on Hutton's shearwaters is attributable to a number of factors previously discussed. Amongst these is the low abundance of over-winter prey available to stoats. The impact of stoats would also be likely to be much greater if another prey species (e.g. rabbits (*Oryctolagus cuniculus*)) established itself in the colony or surrounding area, as the new species could provide an alternative food source for the winter period. Ensuring that no alternative prey species becomes established in the area should be a priority. Other potential over-winter food sources are the remains of introduced chamois and red deer (which are currently kept at low numbers in the colony through culling). Culling chamois and deer should either be done early on in the season and/or it should be ensured that all carcasses are removed to eliminate their potential as a winter food source for stoats.

It is also important to ensure that feral pigs do not invade the remaining colonies (in particular Kowhai Valley, which is more accessible than Shearwater Stream). The boundaries of Kowhai Valley colony should be hunted out in the early spring and summer (when pigs are most active) of every season. These hunting trips could be combined with colony visits to monitor breeding and survival parameters.

In the longer term, Hutton's shearwaters will remain at risk because there are only two breeding colonies. The establishment of more breeding areas should be a priority for future research and management. Suitable sites might include some of the extinct colonies where good areas of habitat still exist and some of the grassy areas on Mt Fyffe, which also have the advantage of good access. Hutton's shearwaters could be made to use new areas, either by translocation of chicks or (preferably) by luring non-breeding birds into an area.

In addition to the conservation and management of the breeding areas, the atsea feeding ecology of Hutton's shearwaters is very poorly known and has not been touched upon by the present research. Questions on what species Hutton's shearwaters are utilising, seasonal change in diet and foraging areas are vital for a fuller understanding of the ecology of this species and to evaluate potential at-sea threats.

In summary, I recommend that the key areas for future research and management are:

- to obtain a more precise estimate of annual adult survival and betweenyear variation of adult survival and breeding parameters,
- to band and recapture fledglings to obtain an estimate of recruitment,
- to determine if stoat irruptions do occur in the shearwater colonies in years following heavy tussock seeding and, if this is the case, to determine if the subsequent predation is on chicks or adult shearwaters,
- to obtain a better understanding of the food and feeding areas of Hutton's shearwaters and investigate if these resources are likely to be threatened,
- to ensure that feral pigs do not gain access to the remaining colonies and to keep numbers of browsing mammals within the colonies at low levels,
- to investigate the establishment of a new breeding colony, through identifying sites with suitable habitat characteristics that are accessible to management and protection, and to assess the response of Hutton's shearwaters to tape-luring during the early stages of the breeding season,
- to increase public awareness and understanding of the natural, scientific and cultural values of Hutton's shearwaters, to ensure that future research and conservation of this species is fully supported by the local community.

7. References

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8. Acknowledgements

This project would not have been possible without the support and work of a great number of people. I am grateful for the hard work and dedication of all my field assistants and in particular to Erica Sommer, Mike Dunlop, Sheryl Hamilton, Caren Shrubshall, Alan Wiltshire and Geoff and Lyndsey Harrow. Thanks to Faith Barber, Keith Dunlop, Mike Morrisey and Dave Walford of the Kaikoura Field Centre for logistical support and help in the field. Many thanks to Kath Walker and Peter Gaze for their enthusiasm and uninhibited support for this project, and to Lloyd Davis and David Fletcher for guidance with fieldwork and analysis. I am also very grateful to Alison Davies and Brian Paton who gave me free access to their data.

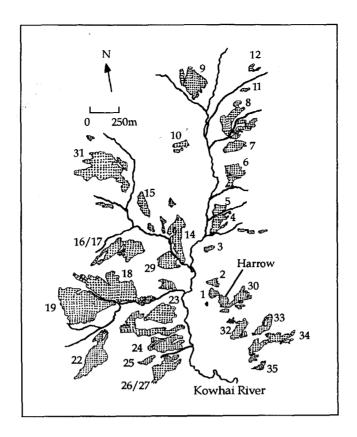


Figure 1. Map of the Kowhai valley colony. Stippled areas represent sub-colonies. Numbering of sub-colonies follows figure 2 of Sherley (1992), with the exceptions of areas 18 and 19 which were formerly labelled as 18b and 18a respectively, and sub-colonies 32, 33, 34 and 35 which were not demarcated by Sherley (1992).

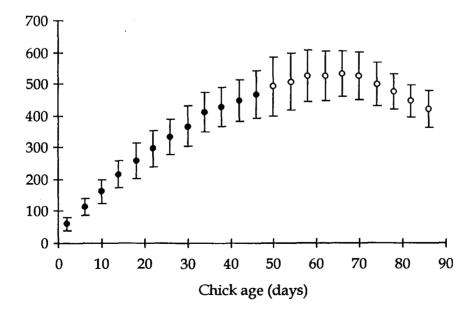


Figure 2. Mass gain of chicks in the 1997/98 breeding season (mean \pm SD), n = 45.

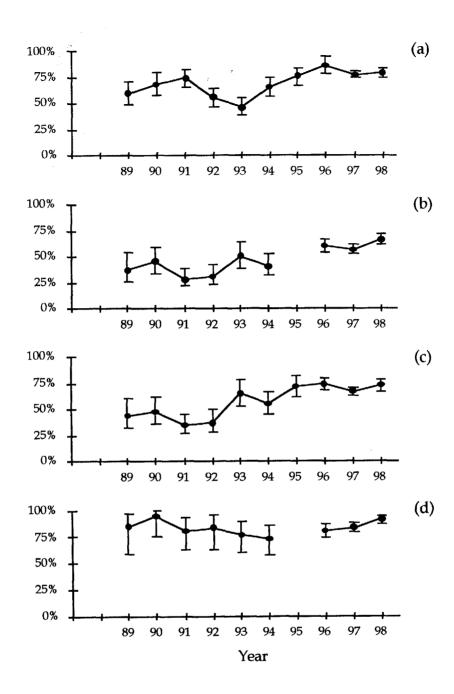


Figure 3. (a) burrow occupancy, (b) breeding success, (c) hatching success and (d) fledging success of Hutton's shearwaters from the 1989/90 to 1998/99 breeding seasons, means (95% CI).

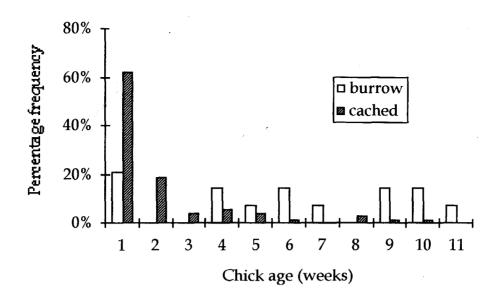


Figure 4. Frequency and age of dead chicks found down burrows and found cached, after radio-tracking stoats.

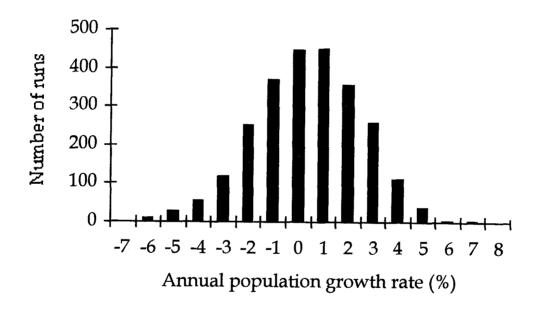


Figure 5. Frequency distribution of the population's annual growth rate, for all 2500 runs of the model.

TABLE 1: INJURIES AND SIGN USED TO CLASSIFY THE CAUSE OF DEATH OF ADULT SHEARWATERS FOUND ON TRANSECTS.

Classification	Sign	Injuries
Flying Accident	Beneath bluff	Broken bill, broken wing
Trapped	Stuck in entrance	Intact body
Starvation		Intact body, mass of adult or chick < 99% confidence intervals
Stoat	Down burrow Between or under tussocks Chewed feathers Stoat scats present	Paired punctures < 9.5 mm apart Puncture/bite to back of head/neck Flesh consumed from neck and/or upper breast only Skinned
Cat		Paired punctures between 9.5 - 21mm Flesh removed from breast or back with neck intact Thoracic cavity entered by hole chewed though keel/sternum
Kea	Digging close to body	Broken large bones Fat consumed but flesh intact Injuries to back, breast, wing, or legs but neck intact
Harrier	Body found on tussock or rock Large quantities of plucked feathers Harrier feathers	Plucked skin Notched keel bone Just wings and sternum present

TABLE 2: HABITAT MEASUREMENTS IN KOWHAI VALLEY COLONY FROM RANDOM QUADRATS, MEAN \pm S.D. (N) AND T-TESTS.

	Burrows present	Burrows absent	t	p
Slope angle (°)	35.4 ± 6.7 (50)	27.8 ± 12.7 (62)	4.19	<0.001
# live tussocks	17.3 ± 11.9 (50)	10.2 ± 11.4 (62)	3.24	<0.01
Rocks < 5mm (cm3)	$36.4 \pm 26.6 (50)$	$39.8 \pm 23.2 (62)$	0.71	n.s.
Rocks > 5mm (cm ³)	$57.2 \pm 47.3 (50)$	81.9 ± 63.1 (62)	2.43	< 0.02
Soil penetrability (m)	$0.34 \pm 0.16 (19)$	0.18 ± 0.14 (27)	3.57	<0.01

TABLE 3: BODY MEASUREMENTS OF FEMALE AND MALE BREEDING BIRDS (MEAN \pm S.D. (N) AND RANGE) AND T-TESTS.

	Females Mean ± s.d.	Range	Males Mean ± s.d.	Range	t	p
Bill-length	36.7 ± 1.1 (50)	34.2 - 39.0	37.7 ± 1.3 (54)	34.7 - 40.5	4.15	<0.001
Bill-depth	10.1 ± 0.3 (46)	9.5 - 11.0	$10.7 \pm 0.5 (45)$	9.3 - 11.6	7.20	<0.001
Bill-width	$9.2 \pm 0.5 (50)$	8.3 - 10.6	$9.6 \pm 0.5 (54)$	8.8 - 11.0	4.15	<0.001
Head-length	$82.6 \pm 1.9 (50)$	77.6 - 87.5	$84.5 \pm 1.8 (54)$	81.1 - 88.0	5.21	< 0.001
Head-width	$26.9 \pm 0.7 (50)$	25.8 - 28.7	$27.6 \pm 0.6 (54)$	25.7 - 28.9	5.73	< 0.001
Tarsus-length	43.8 ± 1.3 (49)	41.6 - 48.9	44.3 ± 1.1 (54)	42.1 - 47.1	2.03	< 0.05
Wing-length	$226 \pm 6 (50)$	215 - 242	226 ± 5 (54)	216 - 240	0.35	n.s.

TABLE 4: BODY MASS OF FEMALE AND MALE BREEDING BIRDS (MEAN \pm S.D. (N) AND RANGE) DURING THE PRE-EGG, INCUBATION AND CHICK-REARING PERIODS.

	Females Mean ± s.d.	Range	Males Mean ± s.d.	Range
Pre-egg	358.8 ± 18.3 (35)	315 - 392.5	373.7 ± 19.8 (42)	330 - 417.5
Incubation	$367.9 \pm 24.6 (87)$	322.5 <i>-</i> 425	$378.1 \pm 23.2 (90)$	325 - 430
Chick-rearing	$331.7 \pm 22.3 (58)$	292.5 - 400	350.2 ± 20.3 (62)	305 - 42 5

TABLE 5: MASS GAIN OF CHICKS OVER THE FIRST 40 DAYS OF CHICK-REARING, ESTIMATED MAXIMUM MASS AND AGE AT MAXIMUM, (MEAN \pm S.D. (N) AND RANGE) AND T-TESTS.

	1997,	/98	1998	/99		
	Mean ± s.d.	Range	Mean ± s.d.	Range	t	p
Mass gain	9.8 ± 1.8 (46)	5.8 - 13.3	12.9 ± 2.1 (40)	6.0 - 15.8	7.20	<0.001
Max mass	$546 \pm 62 (45)$	393 - 695	$588 \pm 69 (40)$	391 - 685	2.98	< 0.01
Age at max	61.1 ± 7.4 (45)	40.6 - 74.0	59.2 ± 4.4 (40)	51.2 - 70.1	1.46	n.s.

TABLE 6: ESTIMATED NUMBERS OF OCCUPIED AND UNOCCUPIED BURROWS AND % OCCUPANCY FOR 148 BURROWS CHECKED WITH THE BURROWSCOPE AND FROM FIELD SIGN FOR OBSERVERS 1 TO 7.

	B-scope	1	2	3	4	5	6	7
occupied unoccupied	90 58	96 51	102 45	142 6	111 36	124 24	46 102	111 37
% occupancy	60.8	65.3	69.4	95.9	75.5	86.6	31.1	75.0

TABLE 7: BURROW OCCUPANCY, HATCHING AND FLEDGING SUCCESS FOR THE THREE DIFERENT CHECKING REGIMES AND G-TESTS.

	Hatch frequent	Hatch infrequent	Burrow- scope	G-tests
Burrow Occupancy	86.6%	81.3%	71.0%	15.0
	(123/142)	(230/283)	(174/241)	p < 0.001
Hatching Success	64.4%	69.3%	70.7%	1.54
	(%/149)	(149/215)	(118/167)	n.s.
Fledging Success	87.2% (82/94)	85.2% (127/149)	88.8% (103/116)	0.74 n.s.

TABLE 8: BREEDING PARAMETERS AND YEARLY SPECIFIC SAMPLE SIZES FROM 1989/90 TO 1998/99 (BURROWS WERE NOT CHECKED AT THE END OF THE 1995/96 SEASON, SO FLEDGING AND BREEDING SUCCESS COULD NOT BE CALCULATED FOR THIS SEASON).

Season	<i>N</i> 1	Occupancy %	N2	Breeding success %	Hatching success %	N3	Fledging success %
89/90	50	60	30	37	4 3	13	85
90/91	55	69	38	4 5	4 7	18	94
91/92	83	<i>7</i> 5	62	27	34	21	81
92/93	90	56	50	30	36	18	83
93/94	87	4 6	40	50	65	2 6	7 7
94/95	84	65	55	40	55	30	73
95/96	73	<i>7</i> 7	56	-	71	-	-
96/97	52	87	156	60	74	114	81
97/98	228	83	320	56	67	213	84
98/99	197	83	195	66	72	146	91

N1 = Number of study burrows for calculation of occupancy

TABLE 9: NUMBERS OF DEAD ADULTS AND CHICKS FOUND IN STUDY BURROWS AND PERCENTAGE MORTALITY IN ESTIMATING ADULT MORTALITY THE NUMBER OF PAIRS WAS MULTIPLIED BY TWO.

89/90	90/91	91/92	92/93	93/94	94/95	95/96	96/97	97/98	98/99
50	55	83	90	87	84	<i>7</i> 3	350	386	280
0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.3	0.0	0.0
13 1 7.7	18 0 0.0	21 1 4.8	18 3 16.7	26 4 15.4	30 4 13.3	_* _* _*	174 5 2.9	139 7 5.0	148 1 0.7
	50 0 0.0 13	50 55 0 0 0.0 0.0 13 18 1 0	50 55 83 0 0 0 0.0 0.0 0.0 13 18 21 1 0 1	50 55 83 90 0 0 0 0 0.0 0.0 0.0 0.0 13 18 21 18 1 0 1 3	50 55 83 90 87 0 0 0 0 4 0.0 0.0 0.0 0.0 2.3 13 18 21 18 26 1 0 1 3 4	50 55 83 90 87 84 0 0 0 0 0 4 0 0.0 0.0 0.0 0.0 2.3 0.0 13 18 21 18 26 30 1 0 1 3 4 4	50 55 83 90 87 84 73 0 0 0 0 4 0 0 0.0 0.0 0.0 2.3 0.0 0.0 13 18 21 18 26 30 -* 1 0 1 3 4 4 -*	50 55 83 90 87 84 73 350 0 0 0 0 4 0 0 2 0.0 0.0 0.0 2.3 0.0 0.0 0.3 13 18 21 18 26 30 -* 174 1 0 1 3 4 4 -* 5	50 55 83 90 87 84 73 350 386 0 0 0 0 4 0 0 2 0 0.0 0.0 0.0 2.3 0.0 0.0 0.3 0.0 13 18 21 18 26 30 -* 174 139 1 0 1 3 4 4 -* 5 7

^{*}Study burrows were not checked during the fledging period of this season.

N2 = Number of eggs for calculation of breeding and hatching success

N3 = Number of hatched chicks for calculation of fledging success

TABLE 10: ESTIMATED CAUSES OF MORTALITY OF 52 DEAD ADULTS FOUND ON TRANSECTS FROM 1996/97 TO 1998/99.

Cause of death	n of bodies	% frequency	95% C.I.
Stoat	30	57.7	(43.2 - 71.3)
Cat	7	13.5	(5.6 - 25.8)
Kea	2	3.8	(0.5 – 13.2)
Accident	13	25.0	(14.0 – 38.9)

TABLE 11: DURATION OF STUDY (YEARS), BURROW OCCUPANCY, HATCHING, FLEDGING AND BREEDING SUCCESS AND ESTIMATED TOTAL PRODUCTIVITY OF FIVE *PUFFINUS* SPECIES.

Species	years	Occupancy %	Hatching Success %	Fledging Success %	Breeding Success %	Total Prod.
Hutton's	10	70.5 ± 12.4	57.3 ± 14.2	85.2 ± 2.0	46.5 ± 12.3	32.8
Sooty	3	53 ± 5	76 ± 8	831	63 ¹	33.4
Manx	15	58* ± 22	68.9 ± 13.7	87.7 ± 11.7	59.5 ± 15.0	34.5
Short-tailed	32	69	-	-	48 ± 18	33.1
Wedge-tailed	3	79	-	-	43	34.0

^{*} Only three years of data available for estimate

TABLE 12: DURATION OF STUDY (YEARS) AND ESTIMATED ANNUAL ADULT SURVIVAL AND BETWEEN YEAR VARIATION OF FOUR *PUFFINUS* SPECIES.

Species	Years	Survival %	Variation %
Hutton's	9	93.1	4.8
Sooty	15	93.1	5. <i>7</i>
Manx	10	90.5	5.0
Short-tailed	30	90 - 92	-

¹ Only two years of data available for estimate

Appendix 1

Banding records of breeding birds in Camp and Top used in the survival analysis.

Burrows removed where they have been lost from study for period 1990 to 1998. No birds in viable burrows banded in 1989 1 = caught; 0 = not caught; first year of capture and banding for each bird is the first column to the left with a 1.

Colony	Burrow #	Band $\#(x)$	1990/91	1991/92	1992/93	1993/94	1994/95	1995/96	1996/97	1997/98	1998/99
Camp	CA10	5872	0	1	0	0	0	0	0	0	0
Camp	CA10	9090	1	1	0	0	1	1	1	1	1
Camp	CA13	5869	1	1	0	0	1	1	0	1	1
Camp	CA13	9093/9065	0	0	1	0	0	0	0	1	1
camp	CA14/20	5881	0	1	1	0	0	0	0	1	1
camp	CA1 6/R39	5956	0	0	0	0	1	1	0	1	1
camp	CA1 7	5870	1	1	0	0	0	0	0	1	1
camp	CA1 7	9094	0	0	1	0	1	1	0	1	1
camp	CA19	6054	1	1	1	0	0	1	0	1	1
camp	CA19	9096	1	1	1	0	1	1	0	0	0
camp	CA1 B	3939	0	0	0	1	1	0	0	1	0
camp	CA1 B	5012	0	0	0	0	0	0	0	1	1
camp	CA1 B	10512	0	0	0	0	0	1	1	1	1
camp	CA20A	6043	0	0	1	0	0	0	0	1	1
camp	CA21	5889	0	1	0	0	0	0	0	0	0
camp	CA21	5990	0	1	0	0	0	0	0	0	0
camp	CA24	5809	0	1	0	0	0	0	0	0	0
camp	CA24	5989	0	1	0	0	0	0	0	0	0
camp	CA24	6045	0	0	1	1	0	0	0	0	0
camp	CA25	5877	0	1	0	0	0	0	0	0	0
camp	CA25	6094	0	1	1	0	0	0	0	0	0
camp	CA26	6044	0	1	1	0	1	0	0	1	1
camp	CA26	10514	0	0	0	0	0	1	0	1	1
camp	CA5	9087	1	1	0	0	0	1	0	1	1
camp	CA65	9088	1	1	0	0	0	0	0	1	1
camp	CA68	9056	0	1	1	0	0	0	0	0	0
top	T01/29	4790	0	0	0	0	1	0	0	1	1
top	T02	5835	0	1	0	0	0	0	0	1	1
top	T02	5845	0	1	0	0	0	0	0	0	0
top	T02	6066	1	1	0	0	1	0	0	1	1
top	T02	9835	0	0	0	0	1	0	0	0	0

top	T020	6069	1	0	0	0	1	0	0	0	1
top	T023	3922	0	0	0	1	1	0	0	1	1
top	T023	4789	0	0	0	0	1	1	0	1	1
top	T023	5712	0	1	1	0	0	0	0	1	0
top	T023	5713	0	1	1	0	0	0	0	1	0
top	T025	5832	0	1	0	0	0	0	0	1	1
top	T025	9116	0	0	1	1	1	1	0	1	1
top	T025	9196	0	0	0	0	1	0	0	0	0
top	T027/26	5740	0	0	0	0	1	0	0	1	1
top	T027/26	5994	0	1	0	0	0	1	0	1	1
top	T030	5724	0	0	1	0	0	0	0	1	0
top	T030	5744	0	0	0	0	1	1	0	0	1
top	T030	6041	0	0	1	0	0	0	0	0	0
top	T032	3920	0	0	0	1	0	0	0	0	0
top	T032	5652	0	0	0	0	1	0	0	1	1
top	T032	5717	0	0	1	0	0	0	0	0	0
top	T032	9133	0	0	1	0	0	0	0	1	0
top	T033	5003	0	0	0	0	1	1	0	1	1
top	T035/32	3932	0	0	0	1	0	1	0	1	1
top	T036	5708	0	0	0	0	1	1	0	1	1
top	T036	10515	0	0	0	0	0	1	0	1	1
top	T04	3918	0	0	0	1	0	0	0	1	1
top	T04	5736	0	0	0	0	0	1	0	1	1
top	T04	6063	1	1	0	0	0	0	0	1	0
top	S1	12372	0	0	0	0	0	0	0	1	1
top	S 1	12579	0	0	0	0	0	0	0	1	1
top	S2	12545	0	0	0	0	0	0	0	1	1
top	S2	12559	0	0	0	0	0	0	0	1	1
top	S 3	12471	0	0	0	0	0	0	0	1	1
top	S 3	12469	0	0	0	0	0	0	0	1	1
top	S4	12573	0	0	0	0	0	0	0	1	1
top	S4	12580	0	0	0	0	0	0	0	1	1
top	S5	12318	0	0	0	0	0	0	0	1	1
top	S5	12578	0	0	0	0	0	0	0	1	1
top	S 6	12349	0	0	0	0	0	0	0	1	1
top	S6	12583	0	0	0	0	0	0	0	1	1
top	S 9	12341	0	0	0	0	0	0	0	1	1
top	S 9	12399	0	0	0	0	0	0	0	1	1
top	S11	12226	0	0	0	0	0	0	0	1	1
top	S11	5725	0	0	0	0	0	0	0	1	0
top	S12	5802	0	0	0	0	0	0	0	1	1
top	S13	12565	0	0	0	0	0	0	0	1	1
top	S13	12577	0	0	0	0	0	0	0	1	1
top	S14	12541	0	0	0	0	0	0	0	1	1
top	S14	12582	0	0	0	0	0	0	0	1	1
top	S15	12566	0	0	0	0	0	0	0	1	1
top	S15	12572	0	0	0	0	0	0	0	1	1
top	S16	12413	0	0	0	0	0	0	0	1	1
top	S16	12588	0	0	0	0	0	0	0	1	1
top	S17	12584	0	0	0	0	0	0	0	1	1

top	S17	12586	0	0	0	0	0	0	0	1	1
top	S18	12569	0	0	0	0	0	0	0	1	1
top	S18	12575	0	0	0	0	0	0	0	1	1
top	S20	12562	0	0	0	0	0	0	0	1	1
top	S20	12570	0	0	0	0	0	0	0	1	1
top	S21	12219	0	0	0	0	0	0	0	1	0
top	S21	12567	0	0	0	0	0	0	0	1	1
top	S22	12571	0	0	0	0	0	0	0	1	1
top	S22	12581	0	0	0	0	0	0	0	1	1
top	S23	12551	0	0	0	0	0	0	0	1	1
top	S23	12563	0	0	0	0	0	0	0	1	1
top	S23	5721	0	0	0	0	0	0	0	1	0
top	S24	12561	0	0	0	0	0	0	0	1	1
top	S26	12494	0	0	0	0	0	0	0	1	1
top	S26	12352	0	0	0	0	0	0	0	1	1
camp	R1	10889	0	0	0	0	0	0	0	1	1
camp	R1	12168	0	0	0	0	0	0	0	1	1
camp	R2	5664	0	0	0	0	0	0	0	1	0
camp	R2	10927	0	0	0	0	0	0	0	1	1
camp	R3	5658	0	0	0	0	0	0	0	1	1
camp	R3	5962	0	0	O	0	0	0	0	1	1
camp	R4	12177	0	0	0	0	0	0	0	1	1
camp	R4	12178	0	0	O	0	0	0	0	1	1
camp	R5	5015	0	0	0	0	0	0	0	1	1
camp	R5	6285	0	0	0	0	0	0	0	1	1
camp	R6	12253	0	0	0	0	0	0	0	1	1
camp	R6	5047	0	0	0	0	0	0	0	1	1
camp	R7	12181	0	0	0	0	0	0	0	1	1
camp	R7	6345	0	0	0	0	0	0	0	1	1
camp	R8	6347	0	0	0	0	0	0	0	1	1
camp	R8	12453	0	0	0	0	0	0	0	1	1
camp	R9	12184	0	0	0	0	0	0	0	1	1
camp	R9	12540	0	0	0	0	0	0	0	1	1
camp	R10	12172	0	0	0	0	0	0	0	1	1
camp	R10	12173	0	0	0	0	0	0	0	1	1
camp	R11	12183	0	0	0	0	0	0	0	1	0
camp	R11	12539	0	0	0	0	0	0	0	1	0
camp	R13	12179	0	0	0	0	0	0	0	1	1
camp	R13	6346	0	0	0	0	0	0	0	1	1
camp	R14	10930	0	0	0	0	0	0	0	1	1
camp	R14	12180	0	0	0	0	0	0	0	1	1
camp	R15	12196	0	0	0	0	0	0	0	1	1
camp	R15	12197	0	0	0	0	0	0	0	1	1
camp	R16	12169	0	0	0	0	0	0	0	1	1
camp	R16	5013	0	0	0	0	0	0	0	1	1
camp	R17	12199	0	0	0	0	0	0	0	1	1
camp	R17	12198	0	0	0	0	0	0	0	1	1
camp	R18	12200	0	0	0	0	0	0	0	1	0
camp	R18	6208	0	0	0	0	0	0	0	1	1
camp	R19	12455	0	0	0	0	0	0	0	1	1

camp	R19	12558	0	0	0	0	0	0	0	1	l
camp	R21	12533	0	0	0	0	0	0	0	1	1
camp	R21	12536	0	0	0	0	0	0	0	1	1
camp	R22	12201	0	0	0	0	0	0	0	1	1
camp	R22	12434	0	0	0	0	0	0	0	1	1
camp	R24	12190	0	0	0	0	0	0	0	1	1
camp	R24	8525	0	0	0	0	0	0	0	1	1
camp	R29	10829	0	0	0	0	0	0	0	1	1
camp	R29	12182	0	0	0	0	0	0	0	1	1
camp	R30	12195	0	0	0	0	0	0	0	1	0
camp	R30	12537	0	0	0	0	0	0	0	1	1
camp	R31	12191	0	0	0	0	0	0	0	1	1
camp	R31	12192	0	0	0	0	0	0	0	1	1
camp	R32	10803	0	0	0	0	0	0	0	1	0
camp	R32	10899	0	0	0	0	0	0	0	1	1
camp	R33	12185	0	0	0	0	0	0	0	1	1
camp	R33	12186	0	0	0	0	0	0	0	1	1
camp	R34	12187	0	0	0	0	0	0	0	1	0
camp	R34	12188	0	0	0	0	0	0	0	1	0
camp	R36	12189	0	0	0	0	0	0	0	1	0
camp	R36	12259	0	0	0	0	0	0	0	1	0
camp	R37	12175	0	0	0	0	0	0	0	1	1
camp	R37	12176	0	0	0	0	0	0	0	1	0
camp	R38	12538	0	0	0	0	0	0	0	1	1
camp	R38	12454	0	0	0	0	0	0	0	1	1
camp	R39	5900	0	0	0	0	0	0	0	1	0
camp	R39	9956	0	0	0	0	0	0	0	1	1

Appendix 2

MONITORING BURROW DENSITY OF HUTTON'S SHEARWATER WITHIN THE KOWHAI COLONY

Because burrows were marked and followed for three seasons, it was possible to record changes in the number of burrow entrances. This was done only for burrows checked with a burrowscope, as the structure of these burrows was unaltered by this methodology. A total of 6 out of 109 burrow entrances were filled in with soil and/or collapsed from the 1996/97 to 1997/98 seasons (5.5%), and 12 out of 156 burrow entrances were similarly lost, from the 1997/98 to 1998/99 seasons (7.7%). As a consequence of this turnover in burrow entrances, the density of burrows, in conjunction with observations on the areas of sub-colonies, is likely to be a simple way of following large trends in the population. Monitoring of burrow density could be repeated at 5 to 10 year intervals, and should be undertaken in the Kowhai Valley and Shearwater Stream colonies.

The burrow density of eight sub-colonies was estimated in the 1997/98 and 1998/99 breeding seasons. Burrow entrances were counted during February and March of both these seasons. A burrow entrance was defined as a Shearwater burrow sized hole, that was greater than 0.4m long (i.e. that extended beyond the reach of the observer's forearm). Multiple entrances which obviously joined one burrow (i.e. where it could be felt that entrances joined one another) were counted as a single entrance. The number of burrow entrances were counted within a 4 x 4m quadrat. These quadrats were located randomly at approximately 5 to 10m intervals along transects that traversed through each sub-colony. The four corners of the quadrat were pinned out with bamboo canes. The whole of the quadrat was searched on hands and knees for burrow entrances, with the under-sides of tussocks and all loose vegetation checked. Burrows entrance that fell on the edge of the quadrat were only counted if it was judged that more than half of entrance was within the quadrat. A minimum of 25 quadrats was needed to obtain an adequate estimate of burrow density of each sub-colony.

Eight sub-colonies were monitored in the 1997/98 and 1998/99 seasons (Table 13 and Figure 2). These sub-colonies were originally chosen for monitoring breeding success and predation, and they are not the only sub-colonies that could be monitored for detecting trends in the number of burrows. The upper sections of sub-colonies 30 and 31 were very fragile, and these areas were not sampled. If the number of monitored sub-colonies were expanded, then sub-colonies 18 and 19 are an obvious choice, as they are both reasonably accessible and generally solid. Sub-colonies 7, 8, 14 (Woody) and "Harrow" (uphill from Camp colony) are all very fragile, and these areas should be avoided. Sub-colony 15 is best accessed by the large scree that falls to the north (upstream side) of sub-colony 14. This route avoids walking through sub-colony 14 (the previously chosen access route). The number and contents of any trampled burrows should be accurately recorded. If a collapsed burrow contains a chick, then the burrow should be adequately repaired with a rock, tussock or wooden board covering the hole.

TABLE 13: SUB-COLONY NAME AND NUMBER (FROM FIGURE 1), MEAN SD NUMBER OF BURROW ENTRANCES COUNTED WITHIN EACH 4 X 4M QUADRAT, AND NUMBER OF QUADRATS WITHIN EACH SUB-COLONY.

Sub-colony Name	Sub-colony number	Mean ± s.d.	Number of quadrats
Camp - Top - Col Woody New	1 4 5 9 15 30 31 32	7.73 ± 2.36 6.16 ± 2.35 8.36 ± 2.98 11.92 ± 4.51 14.42 ± 4.36 10.80 ± 3.48 8.42 ± 4.35 10.76 ± 4.20	37 38 28 52 48 25 19