

Burrow occupancy and productivity at coastal sooty shearwater (*Puffinus griseus*) breeding colonies, South Island, New Zealand: can mark–recapture be used to estimate burrowscope accuracy?

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Abstract. Breeding colonies of sooty shearwaters ('muttonbird', tītī, *Puffinus griseus*) on mainland New Zealand have declined in recent years. New data on burrow occupancy and colony productivity for seven sooty shearwater breeding colonies on the coast of Otago, New Zealand for the 1996–97 and 1997–98 breeding seasons are presented and analysed as part of a five-year data set. Detection of a burrow's occupants using a fibre-optic burrowscope may underestimate absolute occupancy rates, but is still of value in the analysis of trends. Detection probabilities estimated by the novel use of mark–recapture models corresponded with those of previous studies of the technique's accuracy. Mainland declines are associated with a lack of control of introduced mammalian predators at most mainland colonies superimposed on a global pattern of decline in the species' abundance. Large numbers of recovered carcasses and an absence of burrow activity at two small mainland colonies show the decline to extinction of these colonies over the five years of collecting data. At one mainland colony with intensive predator control, survival rates and parameter variances are comparable with those found on a predator-free offshore island. All other mainland colonies showed negligible breeding success. There was a significant positive relationship between egg survival and an index of relative adult survival, with an apparent threshold below which few eggs hatch. Adult survival during the breeding season is likely to be the most important parameter in maintaining a colony's viability.

Introduction

Breeding colonies of sooty shearwaters ('muttonbird', tītī, *Puffinus griseus*) were once widely distributed on the coastlines of both mainland islands of New Zealand, but have declined in recent years (Jackson 1957; Moors and Atkinson 1984; Hamilton *et al.* 1997; Jones 2000). Some colonies have disappeared whilst many others have significantly fewer birds than in the past (Hamilton and Moller 1995; Wilson 1999; Lyver *et al.* 2000; Jones 2000). Predation by introduced mammals is thought to be the main cause of this decline: feral cats (*Felis catus*), rats (*Rattus* sp.), stoats (*Mustela erminea*) and feral ferrets (*M. furo*) have all been identified as predators of sooty shearwater eggs, chicks or adults (Robertson 1976; Moors and Atkinson 1984; Hamilton 1998; Lyver 2000).

Understanding of the processes leading to the current situation is essential for restoration and management of those colonies that remain (Jones *et al.* 1997). The ability to

predict spatial and temporal variability in mortality risk would allow a more focussed effort and allocation of limited resources to where most benefit is likely to accrue. The sooty shearwater breeding season is prolonged (from late September to mid-May: Richdale 1963; Warham *et al.* 1982), so pinpointing exactly when and where predator control can be best directed for maximum effect is especially useful.

Assessments of the state of threatened populations are often made using mathematical modelling techniques such as population viability analysis (Shaffer 1981; Soulé 1987), or PVA, which examines the probability of a population persisting for a specified period. The ability of such models to predict population changes depends on the quality of the input data. A preliminary PVA model for mainland sooty shearwater populations was rather crude due to the fragmentary data set available at the time and some of the parameters used were based on average values of 'optimistic'

and 'pessimistic' estimates (Hamilton and Moller 1993, 1995). More recent data presented by Lyver *et al.* (2000) go some way to addressing these problems, but their methods of estimating daily and stage survival rates are most likely to have given flawed estimators of egg–early chick and early–late chick survival, specifically what Mayfield (1961) described as 'apparent success' (that is, the ratio of the number surviving to the number originally present).

The likelihood of a population persisting through time is dependent on the degree of variability in its demographic parameters (Dennis *et al.* 1991). Increased temporal variation is associated with decreased persistence (White 1999). The variance of a parameter estimate is the sum of two conceptually different components: process variation, which is the inherent stochasticity of the parameter in question; and sampling variation, which results directly from attempts to estimate the parameter (White 1999). The latter should therefore be excluded from estimates of parameter variation (Link and Nichols 1994). This distinction is often ignored, leading to inflated estimates of process variation and subsequent pessimistic estimates of population persistence by a model.

A more fundamental source of error in estimating demographic parameters arises from inherent inaccuracies in the methods used when collecting the data in the field. The use of tube-mounted cameras, or 'burrowscopes' is becoming increasingly common in studies of burrow-nesting seabirds (Dyer and Hill 1991; Lyver *et al.* 1998; Hamilton 2000), but there have been few attempts to quantitatively estimate the technique's accuracy (defined as the ability to detect shearwater eggs, chicks or adults in a burrow). Burrows may be up to 3 m long and may also be wet or contain soft, sandy soil or other obstructions such as rocks or tree roots that can make detection of occupants difficult (Hamilton *et al.* 1998). One method of assessing accuracy may be to treat the detection of a burrow's occupant as a 'capture' or 'recapture' in mark–recapture models. Detection probabilities can then be considered equivalent to capture probabilities. In this case, the burrow becomes the marked individual. Use of this method could allow estimation of the technique's accuracy without having to excavate all surveyed burrows to confirm the burrowscope findings, which is the method used by Hamilton (2000). This novel approach is trialled in this study.

In this paper we present new data on burrow occupancy, breeding success and juvenile stage-survival rates for a number of sooty shearwater breeding colonies on the coast of Otago, New Zealand for the 1996–97 and 1997–98 breeding seasons. Standardised estimates of burrow occupancy and pre-fledging survival for the preceding three seasons are also given. We explore the use of mark–recapture methods to estimate the accuracy of the burrowscope in detecting an egg or early chick. An index of relative risk to adult survival is estimated from carcass recoveries and related to offspring

survival. We then use the five-year data set to investigate temporal and spatial patterns of mortality risk and process variation therein, with special reference to the role of introduced predators. Our ultimate aim is to guide management of the remaining mainland colonies.

Methods

The breeding season of the sooty shearwater

The sooty shearwater is a colonial-nesting petrel that breeds during the Southern Hemisphere summer and migrates to the northern Atlantic and northern Pacific during the southern winter (Briggs and Chu 1986). Adult shearwaters return from their northern migration in late September/early October to begin courtship and preparation of the burrows in which they will eventually breed (Warham 1990). Burrows can be up to 3 m long and end in an enlarged nesting chamber (Hamilton 2000). Eggs (one per pair per year) are laid in late November or early December and hatch towards the end of January after incubation by both parents (Richdale 1944). Chicks fledge in late April or early May after provisioning by both parents, which becomes less frequent as the chicks age (Richdale 1963).

Study sites

Surveys were carried out at six mainland colonies and one near-shore islet during the 1996–97 and 1997–98 breeding seasons. The mainland colonies were at: Kakanui (K: 45°11.75'S, 170°54.00'E), Taiaroa Head (T.Hd: 45°49.80'S, 170°43.20'E), and on the Nugget Point peninsula, designated as: Nuggets 1 (N.1: 46°27.00'S, 169°48.30'E); Nuggets 2 (N.2: 46°27.70'S, 169°48.60'E); Nuggets 3/4 (N.3/4: 46°26.80'S, 169°48.50'E); and Nuggets 5 (N.5: 46°26.70'S, 169°48.30'E). The near-shore islet colony was on Tuhawaiki (Jack's) Island (T.I.: 46°30.20'S, 169°42.80'E). The dominant vegetation types at the colony sites may be classified as: rank exotic grasses with occasional shrubs, found at Kakanui, Taiaroa Head, Nuggets 1 and Nuggets 3/4 and on Tuhawaiki Island; and as coastal broadleaf native forest, found at Nuggets 2 and 5. The Kakanui site was not subject to any predator control; the Nugget Point colonies received sporadic low-level protection when the area was trapped each spring to protect yellow-eyed penguins (*Megadyptes antipodes*) breeding there; the Taiaroa Head colony benefits from predator-control programmes immediately adjacent to it that are in place for up to seven months each year (B. Thomas and S. Helyer, personal communications) to protect a colony of northern royal albatross (*Diomedea epomorphora sanfordi*) to the north and a yellow-eyed penguin colony to the south. Tuhawaiki Island is free of mammalian predators.

Data collection

Occupancy of burrows was determined using the burrowscope described by Lyver *et al.* (1998). We attempted to monitor all intact burrows at the smaller colonies. The large numbers of burrows at Taiaroa Head and on Tuhawaiki Island meant that sub-samples of these colonies were monitored. Colonies were surveyed during three distinct periods of the 1996–97 and 1997–98 breeding seasons: an 'egg' stage, in early December; an 'early-chick' stage, in late January; and a 'late-chick' stage, in mid-April to early May. Raw data from the three seasons prior to this (Lyver *et al.* 2000) are reanalysed here to aid in the description of trends and to ensure consistency of analyses. Not all colony sites were surveyed on all occasions during the five years due to personnel availability and logistic constraints. Data on occupancy and survival of late chicks on Tuhawaiki Island in 1998 are estimated from results in Uren (1999), who intensively studied 32 chicks in the same burrows as those used in this study using inspection hatches. These data were therefore not included in estimates of burrowscope accuracy.

All mainland colonies were checked for bird carcasses lying on the ground surface or in burrow entrances during the 1996–97 and 1997–98 seasons: each colony was searched for dead birds every month from November 1996 to April 1997 and fortnightly from October 1997 to April 1998. Data from the three preceding seasons (Lyver *et al.* 2000) are included to aid in the description of temporal variation.

Definitions and analyses

A burrow was designated as occupied if an egg or a chick was present during the egg or early chick stages, or a chick during the late chick stage. Occupancy rates for each colony and stage of the breeding season were estimated as the number of occupied burrows as a proportion of the total number of burrows surveyed. Only those burrows in which the burrowscope reached an end wall were included in the analyses; where this was not possible the burrow was designated 'unknown' and excluded from analyses. For those colonies that were sub-sampled, 95% binomial confidence intervals were calculated (Zar 1999, p. 527).

We used mark–recapture methods in order to estimate burrowscope accuracy. The form of the burrowscoping data (occupant found/not found) makes it amenable to this type of analysis. We used the program Release 3.0 (Burnham *et al.* 1987) to estimate the probability of finding an egg or early chick if it was there, which can be regarded as equivalent to 'capture probability' in mark–recapture terminology. With only two 'recapture' occasions (early and late chick) the initial capture rate for eggs, i.e. $p(\text{egg})$, is unidentifiable (Lebreton *et al.* 1992). To overcome this limitation we added an 'initial release' occasion to represent 'laying' to the recapture record for each burrow in which an egg or chick was found later in the same season. This assumes that eggs and early-stage chicks do not move between burrows, which is biologically reasonable. This allowed the software to estimate $p(\text{egg})$. The detection probability of a late chick appears only as a product term in the original mark–recapture models and individual components are therefore not able to be estimated independently.

As each burrow normally contains only one egg and young are effectively sessile until quite late in development, survivorship of eggs and chicks between sampling occasions was estimated using data in which individually marked burrows constituted sampling units. The apparent success estimator of survival used by Lyver *et al.* (2000) is positively biased because it fails to account for eggs that fail in the period between laying and first detection. This problem can be corrected for by the use of constant daily survival rates (Mayfield 1961, 1975; and subsequent modifications: Miller and Johnson 1978; Johnson 1979; Klett and Johnson 1982). Daily survival rates may then be used to estimate stage survival by raising the daily survival estimate to the power of the number of days in the stage.

Daily survival rates for each egg or chick were estimated using the 'Mayfield–40%' method (Miller and Johnson 1978; Johnson 1979). This estimator is based on Mayfield's (1961, 1975) original method, but assigns an exposure time of 40% of the interval between visits to lost eggs/chicks (as opposed to Mayfield's 50%) for long periods (>20 days) between observations. This simple method has been shown to very closely approximate much more complex maximum-likelihood estimators (Johnson 1979).

Daily probability of survival, $p_{(\text{surv})}$, is given by:

$$p_{(\text{surv})} = 1 - (\text{no. of deaths/exposure}),$$

where exposure = $t(n_s + 0.4n_d)$, t = interval between observations (days), n_s = number surviving during interval t , and n_d = number dying during interval t .

The standard error of this estimator is given by:

$$s = \sqrt{[(\text{exposure} - \text{deaths}) * \text{deaths}] / \text{exposure}^3}$$

and 95% confidence intervals are ± 1.96 (s.e.) (Johnson 1979). For estimating stage-survival over a period of t days, daily survival is raised

to the power t , as are the relevant confidence intervals. For sooty shearwaters, incubation of eggs lasts around 53 days and the nestling ('chick') period for 97 days (Richdale 1944, 1963; Warham *et al.* 1982). Our estimate of breeding success is the product of the two stage-survival estimates.

The counts of adult carcasses were used to derive an index of relative survival for adults at the colonies. We first derived a mortality rate:

$$\text{mortality} = \text{mean no. of carcasses per month} / \text{no. of birds present},$$

and,

$$\text{no. of birds present} = B * \text{OCC} * 2 * (\text{proportion breeding})^{-1},$$

where B = total number of burrows at the colony, OCC = mean occupancy rate at the colony during the egg stage (eggs are assumed to be a measure of breeding attempts and thus indicate the number of pairs of adult birds), and proportion breeding = 0.855. [Not all breeding-age birds breed in any one year. The proportion doing so was assumed to be constant at 0.855, which was based on data for the congeneric short-tailed shearwater (*Puffinus tenuirostris*) in Bradley *et al.* (2000) since no estimates are available for sooty shearwaters.]

For each estimate of relative mortality risk 95% confidence intervals (CI) were estimated by calculating mortality risk 1000 times. Each time the values of the parameters were selected randomly from a normal distribution based on the mean and standard deviation for each parameter. The resulting mortality risk index was then used to derive an index of relative survival. This was scaled against an estimate of adult survival based on data from a predator-free environment (Scofield *et al.* 2001) so that the mainland sites could be compared with Tuhawaiki Island:

$$\text{Relative adult survival} = (1 - \text{mortality risk}) * S_{\text{max}},$$

where S_{max} = adult survival rate in the absence of predators. It should be emphasised that this index is not an estimate of absolute survival and that it is assumed that birds at mainland colonies are subject to the same 'baseline' risks, from weather and food shortages, as those on offshore islands.

We summarise variation in vital rates at colonies over time and between colonies in each breeding season using coefficients of variation, V^* , corrected for small sample size (Sokal and Rohlf 1995, p. 58). The behaviour of populations whose demographic parameters show larger coefficients of variation is inherently more variable than those for which V^* is smaller (Starfield and Bleloch 1986, Ch.3). Prior to estimating V^* for the sub-sampled colonies, we removed sampling variance from estimates of total variance following Burnham *et al.* (1987). Coefficients of variation therefore reflect process variation only. The proportional effects of sampling variation on total variation are also demonstrated.

Results

Detection probabilities

Estimates of the accuracy of burrowscoping in detecting eggs or early chicks were possible for 12 colony–breeding stage combinations (Table 1). This limited number of estimates was due to: small colony sizes at many mainland sites, few chicks surviving to be detected at most mainland colonies and occasional gaps in the data set for a colony/year that precluded estimation of detection probabilities for any pre-fledging stage in that year. The probability of detecting an egg if present varied from 0.42 to 0.96 (mean = 0.80, s.e. = 0.581). The range for detecting an early chick was slightly narrower: 0.56–0.98 (mean = 0.87, s.e. = 0.102). These

Table 1. Burrowscope accuracy

Estimates are detection probabilities (with 95% confidence intervals shown in parentheses) for sooty shearwater eggs and chicks obtained using the program Release 3.0 (Burnham *et al.* 1987). Only reliable estimates (s.e. $\neq 0$) are included. A dash indicates that no reliable estimate was possible

Colony and season	Egg	Early chick
Kakanui, 1994–95	0.80 (0.595, 1.000)	–
Taiaroa Head, 1994–95	0.89 (0.840, 0.941)	0.98 (0.954, 1.000)
Taiaroa Head, 1995–96	0.96 (0.924, 0.994)	0.98 (0.950, 1.000)
Taiaroa Head, 1996–97	–	0.56 (0.326, 0.785)
Taiaroa Head, 1997–98	0.78 (0.621, 0.935)	–
Nuggets 1, 1994–95	0.78 (0.656, 0.899)	–
Nuggets 1, 1995–96	0.88 (0.762, 1.000)	–
Nuggets 1, 1997–98	0.42 (0.138, 0.696)	–
Tuhawaiki I., 1994–95	0.86 (0.741, 0.973)	–
Tuhawaiki I., 1995–96	–	0.94 (0.854, 1.000)

ranges are greatly extended by two outliers [p(egg) at Taiaroa Head in 1997–98 and p(early chick) at Nuggets 1 in 1996–97]. In the 1994–95 season the probability of detecting an early chick at Taiaroa Head was greater than that for an egg but, overall, the difference in mean detection probabilities between stages was not significant (two-sample *t*-test, assuming unequal variances). Insufficient estimates were available for some of the smaller colonies to investigate the effect of site on detection probabilities.

Burrow occupancy

The new data on burrow occupancy shows predictable within-season declines from egg to late chick stages for 1996–98 (Table 2). There are exceptions to this trend. At the Nuggets 1 colony in the 1997–98 season occupancy appears to increase between early and late chick: this is due either to missing an early chick during the middle monitoring period or because of an older chick moving to a different burrow just prior to the last period. The Nuggets 2 and 5 colonies showed no burrow activity during occupancy checks at all in the two seasons.

For the five-year data set (Fig. 1; Appendix 1), all six mainland colonies showed a general decline in egg-stage occupancy rate, with a slight increase in the 1995/96 season. Egg-stage occupancy is an important index of colony persistence as it can be regarded as an indicator of the number of breeding attempts and thus of population trends. Occupancy on the near-shore islet of Tuhawaiki stayed fairly constant over the monitoring period, ranging from 45.5% (95% CIs: 34.6–56.7) in 1994/95 to 48.6% (36.5–60.9) in 1997/98. Similar patterns can be seen in the early- and late-chick occupancy data.

To investigate possible predictors of demographic trends we looked at published data on sooty shearwater abundance from the Northern Hemisphere summers covering the same period as this study. There was a significant correlation between changes in abundance off western North America 1994–97 (Wahl and Tweit 2000, fig. 2) and egg-stage occupancy rates on Tuhawaiki I. in the following breeding season for the period 1994/95–1997/98 ($r = 0.998$, $P < 0.05$).

Superimposed on the long-term and intraseasonal trends is a pattern of inter-site variation in burrow occupancy (Fig. 2). Mean egg-stage occupancy rates for the five years varied from 6.8% (0.0–15.8) at Nuggets 5 to 60.5% (49.3–71.7) at Taiaroa Head, but differences were not statistically significant. Intra-site differences were more pronounced during early-chick (Kruskal–Wallis $H = 19.53$, d.f. = 6, $P = 0.004$) and late-chick ($H = 23.55$, d.f. = 6, $P = 0.001$) stages. No late-stage chicks were found at all at the Kakanui and Nuggets 2 and 5 colonies in any year and the mean occupancy rate at Nuggets 1 was only 1.1% (0.0–2.7) for this stage. The Taiaroa Head colony had a similar mean occupancy by late chicks to that of Tuhawaiki I.: 34.0% (26.6–41.5) and 32.1% (29.2–35.0) respectively.

Egg and chick survival

Survival of both eggs and chicks was similarly high at Taiaroa Head and Tuhawaiki I. (Fig. 3; full data set in Appendices 2 and 3). Both sites showed higher survival rates than Nuggets 2, 3/4 and 5 during the egg to early-chick stage.

Table 2. Burrow occupancy rates for juvenile development stages at monitored sooty shearwater breeding colonies, 1996–98

95% confidence intervals are shown where estimate is based on a sample. n = number of burrows examined. A dash indicates that data were not collected

Colony	1996–97 breeding season				1997–98 breeding season			
	n	Egg	Early chick	Late chick	n	Egg	Early chick	Late chick
Kakanui	32	–	6.3	–	18	44.4	0.0	0.0
Taiaroa Head	102	–	37.3 (27.5, 50.0)	30.4 (21.5, 40.5)	78	50.0 (38.0, 62.0)	24.4 (14.5, 35.7)	23.1 (14.2, 34.9)
Nuggets 1	101	0.0	0.0	0.0	118	6.8	0.0	1.7
Nuggets 2	50	–	0.0	–	37	0.0	0.0	0.0
Nuggets 3/4	80	–	0.0	0.0	91	8.8	0.0	0.0
Nuggets 5	80	–	0.0	–	74	0.0	0.0	0.0
Tuhawaiki I.	–	–	–	–	72	48.6 (36.5, 60.9)	34.7 (23.8, 47.1)	30.6 (19.9, 43.0) ^A

^AEstimate based on data in Uren (1999).

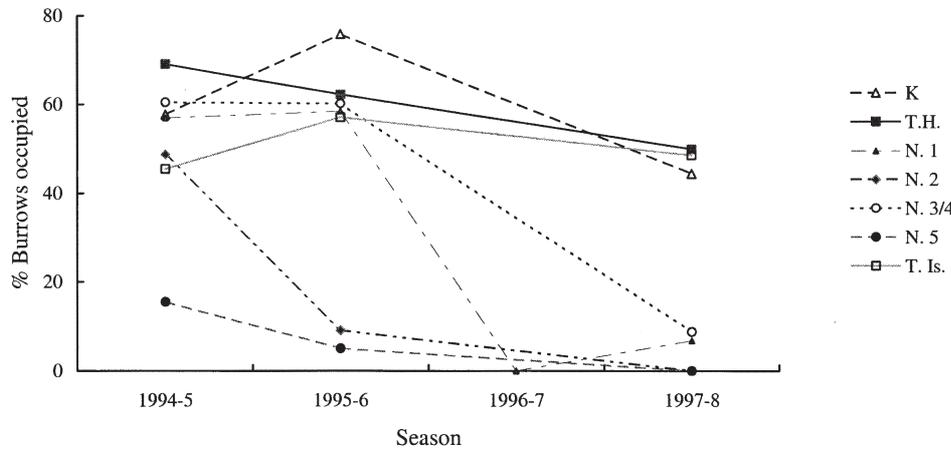


Fig. 1. Burrow occupancy rates for monitored sooty shearwater breeding colonies during the egg stage of the 1994-95 to 1997-98 breeding seasons.

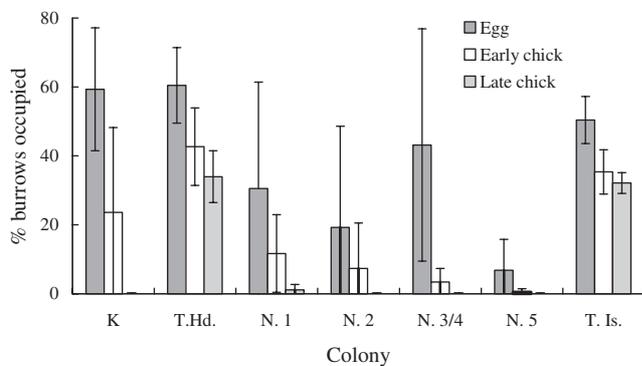


Fig. 2. Spatial variation in mean burrow occupancy rate during juvenile developmental stages for monitored sooty shearwater colonies 1993-94 to 1997-98. Error bars are 95% confidence intervals.

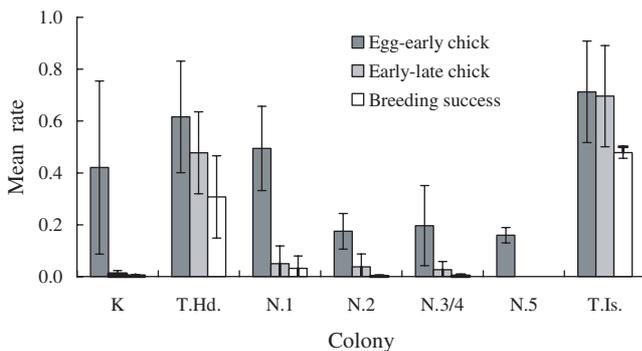


Fig. 3. Spatial variation in mean 'Mayfield-40% estimated' survival rates and of breeding success at monitored sooty shearwater colonies for the 1993-94 to 1997-98 breeding seasons. Error bars are 95% confidence intervals.

relevant for colonies N.2 and N.5., where the precision of mean estimates is further affected by zero occupancy rates. At colony N.2, no eggs were found in 1997-98 and no chicks from 1995-96 onwards; at N.5, no eggs were found in 1997-98 and chicks were recorded only once, in 1995-96. Survival decreased between egg-early-chick and early-late-chick stages at both N.1 and N.5 and, although the opposite trend was apparent in mean rates for Taiaroa Head and Tuhawaiki I., neither difference reached formal significance.

Although late chicks were not followed to fledging, breeding success rates for the colonies can be estimated as the product of stage survival estimates. This was markedly higher at Tuhawaiki I. (mean $48 \pm 2\%$) and Taiaroa Head ($31 \pm 16\%$) than at all other colonies, of which N.1 was the next highest ($3 \pm 5\%$).

Relative temporal variation in daily survival estimates for different colonies and years is summarised in Table 3. Coefficients of variation were small, at 2.23% or less, which reflects the use of daily survival probabilities: patterns of variation would be more apparent if expressed over longer periods. For the two colonies that were sub-sampled, total variance was partitioned into its components and only

Table 3. Summary of temporal variation in 'Mayfield-40%' estimates of juvenile sooty shearwater demographic parameters

All values are V^* (%): coefficient of variation corrected for small sample size (Sokal and Rohlf 1995, p. 59). The Taiaroa Head and Tuhawaiki I. colonies were sub-sampled; variance estimates for these colonies are based on process variance only. Figures in parentheses are the estimated percentage contribution of sampling variance to total variance in estimates for sampled colonies

Colony	Egg-early chick daily survival	Early-late chick daily survival
Kakanui	2.23	
Taiaroa Head	0.58 (14)	0.35 (36)
Nuggets 1	0.60	1.44
Nuggets 3/4	1.94	
Tuhawaiki I.	0.40 (23)	0.21 (39)

This pattern was even more marked later in the breeding season when both had much higher rates of chick survival than any of the other colonies. The wide confidence intervals of many of the estimates are due, in part, to limited data for some colonies. Because of missed sampling periods in the 1993-94 and 1996-97 seasons some estimates are based on as few as three seasons' data. This problem is particularly

process variance was used in inter-colony comparisons. Sampling variance made up 14–39% of the total variance for these estimates. At Tuhawaiki I. and Taiaroa Head, egg–early chick survival varied more than that for the later stage. The opposite is seen at colony N.1. Estimates are not available for some colonies because too few chicks survived in most years. At the Kakanui and Nuggets 3/4 colonies, variation in egg–early chick survival was much higher than at the other sites for which estimates were possible.

Adult mortality

Adult carcasses were found at mainland colonies throughout the breeding season. In the 1996/97 season 72 carcasses were collected (November–April), compared with only 11 in 1997/98 (October–April). The majority (58%) of the 1996/97 total was recovered in the period January–March 1997, when 10, 7 and 25 carcasses were found in successive months at the Nuggets 1 colony. Two adult carcasses found at each of the Nuggets 2 and 5 colonies in November 1996 were the only sign of activity at either colony in the last two years surveyed. During the burrowscope checks in 1997/98 at least 10 further carcasses were seen deep inside burrows, but as these checks were more than one month apart the birds could not be included in the monthly totals. Inter-month variation in carcass recovery rates was not significant. The index of mortality risk was much lower for adult birds at Taiaroa Head than at either Kakanui or Nuggets 3/4 (Table 4). In spite of there being many more carcasses discovered at Nuggets colonies 1, 2 and 5 the corresponding difference was not significant for these sites, probably because of the wide confidence intervals associated with the respective estimators. These intervals reflect the variation in the number of carcass recoveries per bird per month, but possibly underestimate the differences between colonies because at hardest-hit colonies there are likely to be many fewer adults present later in a breeding season.

To test whether there was a link between adult mortality and the success of early nests we regressed mean egg–early-chick stage survival against adult survival index, scaled to allow inclusion of data from Tuhawaiki I. The resulting curve (Fig. 4) suggests that there is a threshold adult survival rate

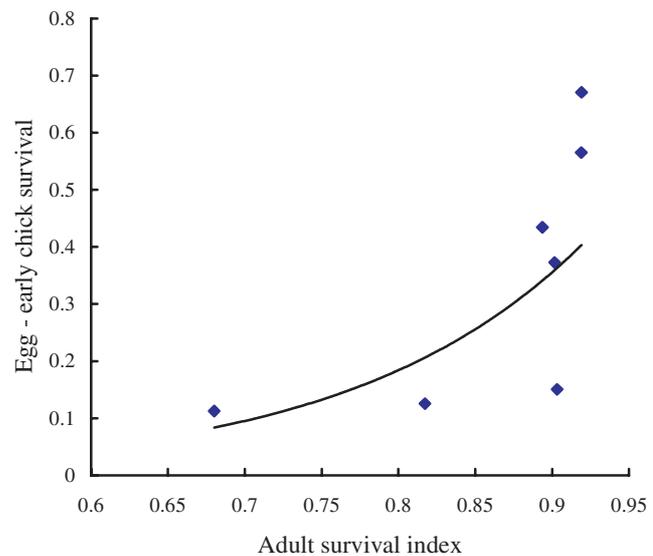


Fig. 4. Relationship between mean egg–early-chick stage survival and index of adult survival for all monitored sooty shearwater breeding colonies. The relationship is described by the equation: $\log(\text{egg survival}) = -7.34 + 0.088(\text{adult survival index})$ ($F = 7.18$, d.f. = 6, $P = 0.04$).

above which success of early nests climbs sharply. It is impossible to provide an absolute estimate of this threshold because we have based the relationship on an index of relative survival.

Discussion

Population parameter estimates used in models or to directly guide management actions depend on the accuracy of the methods used in the collection of the original data. An estimate of the ability of the technique used to detect the occupant of a burrow would allow estimation of how many eggs or chicks were likely to have been missed, which would permit more reliable estimates of colony size. Burrowscope accuracy is affected by burrow length, geometry, soil type and moisture (Dyer and Hill 1991; Hamilton 2000) and also by the ability and experience of the observers. In the first published attempt to estimate the technique's accuracy, Hamilton (2000) excavated burrows to compare the contents with what was found using a burrowscope. Accuracy during egg and early-chick stages was 66–89 and 65–97% respectively. This corresponds with our mark–recapture estimates of 42–96% and 56–98% for the corresponding periods. It should be noted that this comparison is made on the assumption of no prior knowledge of a burrow's contents by observers. The range would be considerably smaller if not for the two outlier estimates. Whilst quantitative analysis of predictors is not possible, it should also be noted that during both of the sampling periods in question the burrowscope was operated by relatively inexperienced two-person teams. This would suggest that results are likely to be consistent if trained and experienced operators can be used.

Table 4. Index of individual risk of death for adult sooty shearwaters at monitored mainland breeding colonies based on carcass recoveries in the 1993–94 to 1997–98 breeding seasons

Colony	Mortality risk per individual	Lower 95% CI	Upper 95% CI
Kakanui	0.0190	0.0020	0.0410
Taiaroa Head	0.0001	0.0000	0.0002
Nuggets 1	0.0276	0.0000	0.1790
Nuggets 2	0.1108	0.0000	1.0000
Nuggets 3/4	0.0173	0.0042	0.0650
Nuggets 5	0.2600	0.0000	1.0000

Our estimates are likely to be positively biased: by admitting only 'burrowscopic' burrows to the sample the true probability of detection is overestimated. This problem has its correlate in any mark-recapture study where there may be some members of a population that are present but never captured. This potential for systematic bias in estimates of burrowscope accuracy could only be addressed by combining Hamilton's excavation check on burrows in which nothing has been found using the burrowscope and testing to see whether some characteristic of a burrow could be used to predict an erroneous negative result.

Use of models to estimate detection probabilities may allow identification of predictors of burrowscope error. Our data set is limited because of the generally small colony size and low chick productivity of mainland colonies, which limits the number of estimates possible. Data from a larger-scale, longer-term study in a predator-free environment, such as the *Kia Mau Te Titi Mo Ake Tonu Atu* research programme currently underway on New Zealand's southern islands would permit testing of the effects of factors such as season, operator experience, weather, soil type, soil moisture content and burrow length on detection probability. If more than three sampling periods were used within a breeding season there would be no need to add the artificial 'first capture' to the data set in order to estimate the detection probability of an egg, as we have done here. If such assumptions and potential for bias can be addressed by more rigorous testing of the methods, the use of mark-recapture analysis to estimate burrowscope accuracy may provide a non-destructive method of accounting for errors and thereby estimating a correction factor to further improve estimates of occupancy and survival rates. It is certainly worthy of more detailed investigation.

Occupancy during the egg stage of the breeding season appears to be declining at all of the mainland colonies included in this study. This apparent trend may be the result of both global and local pressures on the species. The correlation between occupancy rates at our only predator-free colony and changes in abundance recorded in the northern Pacific in the preceding summer suggests that global-scale variations have had a 'background' effect on colony productivity. At the end of the austral summer sooty shearwaters migrate to spend the non-breeding season in the north Pacific, and, to a lesser extent, the north Atlantic oceans (Briggs and Chu 1986). Declines in abundance of up to 90% have been recorded for the species in the period 1987–95 off the west coast of North America (Veit *et al.* 1996 1997). These declines were associated with an increase in sea surface temperatures over the same period. Latest figures suggest that although numbers have increased slightly in the late 1990s they are still very low compared with a decade earlier (Bograd *et al.* 2000; Wahl and Tweitt 2000). Shorter-term declines have also been reported in association with El Niño Southern Oscillation climatic

events for sooty shearwaters and other petrel species in the southern oceans (Chastel *et al.* 1993; Guinet *et al.* 1998; Lyver *et al.* 1999).

Evidence from New Zealand's offshore islands supports the downward trend recorded for the northern populations. Hamilton *et al.* (1996) report a marked decline from 1988 onwards on Codfish Island (Whenua Hou) and Lyver *et al.* (1998) described concurrent declines in chick-harvest rates on Poutama Island. Changes in both burrow numbers and occupancy rates on the Snares Islands suggest that the population is much smaller than that recorded 30 years ago (Warham and Wilson 1982; Scofield and Hunter, unpublished). Possible mechanisms for this global decline are climate change, exerting its effects through oceanic food chains (Veit *et al.* 1996, 1997; Guinet *et al.* 1998) and high adult mortality rates resulting from fisheries bycatch (Ogi *et al.* 1991; De Grange *et al.* 1993; Scofield and Hunter, unpublished).

The Mayfield estimator, and variants thereof, is rapidly becoming the standard measure of nest survival (Manolis *et al.* 2000). When extrapolating daily survival probabilities to estimate nest survival there is a potential for bias in the assumption of a constant daily risk for the whole nesting period. Klett and Johnson (1982) showed that daily risk decreases with the age of the nest, causing survival estimators to be positively biased. This problem can be overcome by sub-dividing the nesting period into separate age classes/stages, as we have done. Daily survival probabilities can then be estimated for each stage and breeding success estimated as the product of stage-specific survival rates. Use of the Mayfield estimator assumes perfect knowledge of a nest's status. With burrow-nesting birds, this is unlikely, as the estimates of burrowscope accuracy have shown. There is therefore likely to be a systematic underestimation of survival that could be adjusted if a correction factor for burrowscope accuracy can be found.

The sooty shearwater colonies at Tuhawaiki I. and Tairaroa Head showed the highest rates of survival and the lowest site-specific variability through time. At the other mainland sites survival was low with higher intra-site variability or there were insufficient surviving chicks to permit estimation of breeding success. Nuggets 1 was comparable to the two most successful colonies during the egg-early-chick period, but followed the pattern of the other mainland sites during the later stages of the breeding season. At most mainland colonies survival rates were higher early in the nesting period. At Tuhawaiki I. and Tairaroa Head they were, at the least, equivalent. The general pattern in petrels is for losses during the egg stage to be greater than those for chicks (Warham 1990). Survival during the egg-early-chick stage was 56.5% ($\pm 21.5\%$) for Tairaroa Head and 67.1% ($\pm 19.6\%$) for Tuhawaiki I. This metric is roughly equivalent to 'hatching success', which Warham *et al.* (1982) recorded as 33–58% for sooty shearwaters, although the authors

suggested that this might be abnormally low due to disturbance by the researchers. Other published estimates of hatching success for petrels range from 46% for *P. tenuirostris* (Serventy and Curry 1984) to 86% for *Pterodroma ultima* (Brooke 1995). The latter estimate was obtained on an island where pre-fledging birds were subject to predation by kiore (*R. exulans*).

Egg–early-chick survival at Nuggets 1 colony was better and showed lower temporal variation than at other nearby colonies, which are subject to the same ecological pressures. This may be as a result of the N.1 colony's larger size. Both theoretical models and experimental evidence suggests that predation risk decreases with increasing colony size for a prey that are not the primary source of food for a local predator population (Sinclair *et al.* 1998; Lyver *et al.* 2000). This is the case for sooty shearwaters where predators depend mainly on rabbits (*Oryctolagus cuniculus*) and mice (*Mus musculus*) (Murphy and Dowding 1994; Alterio and Moller 1997; Ragg 1998)

As well as having the best pre-fledging survival rates of the mainland colonies, Taiaroa Head also had the lowest index of adult mortality. In deriving this index we assumed that carcasses were equally likely to be found at all sites and that the number found is an accurate indicator of predation. The index is likely to underestimate true temporal variation in risk because fewer adults attend colonies in the later months of the breeding season: unsuccessful breeders move offshore and there is a gradual erosion of breeder numbers due to the effects of predation. This will lead to an increased *per capita* risk, which becomes even greater as predator numbers increase in late summer (Gibb *et al.* 1978; King 1980, 1994; Ragg 1998; Jones 2001). This pattern clearly reflects the amount of protection from introduced mammalian carnivores received by the sites.

Predator control has been identified as a major predictor of persistence of mainland colonies (Jones 2000). Tuhawaiki I. is predator-free as a result of its separation from the mainland by a seawater channel and the absence of any small mammal prey there (Lyver *et al.* 2000). The Taiaroa Head colony lies between an albatross reserve that receives year-round protection and a privately operated yellow-eyed penguin sanctuary/tourist resource that is also trapped for much of the year. The sites on the Nugget Point Peninsula receive brief sporadic protection from late October to early December to coincide with the most vulnerable period for yellow-eyed penguin eggs and chicks (Department of Conservation, unpublished data) and the Kakanui site receives no predator control at all.

The five-year data set presented here clearly documents the decline to extinction of two small colonies at Nugget Point. Occupancy during the egg stage declined from 57% at N.2 and 15% at N.5 in 1994/95 to zero at both sites in 1997/98. High levels of predation on adult birds during the early breeding season are likely to be the cause of these

extinctions. Lyver *et al.* (2000) reported the recovery of 60 adult carcasses from the N.2 colony, during the 1995/96 season. The small size of the colony (average size <40 burrows) means that this level of loss is clearly unsustainable. The importance of good adult survival rates to the maintenance of a viable population was emphasised in the preliminary PVA by Hamilton and Moller (1995) and is reinforced by the correlation between adult and egg–early-chick survival rates demonstrated here. Sensitivity analyses of seabird population dynamics consistently rank adult survival highly and emphasise the importance of this vital rate to population maintenance and growth (Hamilton and Moller 1995; Weimerskirch *et al.* 1996; Russell 1999; Sæther and Bakke 2000; Hunter *et al.* 2000; Cuthbert *et al.* 2001) In long-lived seabird species the breeding population is made up of adults that may return to the same colony for a number of years. In the shorter term, survival of eggs and chicks is highly dependent upon there being two parent birds available for incubation and provisioning, and, where predators are present, to possibly act as a deterrent to smaller predators. Immediate effects on breeding success may be further compounded by ongoing depression of productivity because the death of one parent forces renewed pair-bonding in subsequent seasons. Breeding success is lower for new than for established pairs (Bradley *et al.* 2000).

PVA-modelling techniques have already been used to predict persistence of mainland sooty shearwater populations (Hamilton and Moller 1995). For K-selected species under acute risk, these methods may be the best short-term option to guide management action. In such models, if high levels of variation are included in initial parameter estimates there is likely to be increased variation in, and thus more pessimistic, model outcomes. This is especially important for those factors with large parameter uncertainties (Hunter *et al.* 2000). The evidence from this study underlines the importance of removing the sampling variance component of total parameter variances, with the former accounting for 14–39% of total variance in daily survival rates at sub-sampled colonies. Link and Nichols (1994) found a 14% increase in estimated standard deviation of a series of population size estimates when sampling variance was not removed and cast doubts on previously published data sets that fail to account for sampling variance. In a subsequent summary of survival estimates for three bird populations 35–100% of total variance was due to sampling variance (Gould and Nichols 1998).

Conclusions

Our results suggest a general decline in occupancy rates at mainland sooty shearwater colonies since at least 1994. Although the technique used to determine burrow occupancy is likely to underestimate absolute rates, it is still of value in the analysis of trends. We have used a novel way of estimating detection probabilities and suggest further

investigation of the utility of this method, especially in the derivation of an urgently needed correction factor for burrowscope data. The mainland declines may be linked in part to global declines in the species' abundance, but are most likely the result of predation pressure.

At the mainland colony with the most intensive predator control, survival rates are comparable with those found on a predator-free offshore island. Variance in vital rates is lower at these colonies than at other mainland sites. At the latter, survival estimates are often not possible because no eggs or chicks survive to fledging. Higher variance in demographic parameters at mainland colonies suggests a decreased likelihood of persistence. These patterns can be realistically assessed only if sampling variance is removed from estimates based on sampled populations. Two small mainland colonies have declined to extinction in the past five years. Adult survival during the breeding season is likely to be the most important parameter in maintaining a colony's viability and should be the focus of any management strategy.

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Appendix 1. Percentage of burrows occupied by eggs or chicks at monitored sooty shearwater breeding colonies

Season	K	T.Hd ^A	N.1	N.2	N.3/4	N.5	T.I. ^A
Egg stage							
1994–95	56.7	69.1 (62.6, 75.4)	57.0	48.7	60.5	15.49	45.5 (34.6, 56.7)
1995–96	75.9	62.3 (55.3, 68.8)	58.5	9.1	60.2	5.00	57.1 (46.3, 68.0)
1996–97	no data	no data	0.0	no data	no data	no data	no data
1997–98	44.4	50.0 (38.0, 62.0)	6.8	0.0	8.79	0.0	48.6 (36.5, 60.9)
Mean	59.3	60.5	30.6	19.3	43.2	6.8	50.4
Standard error	9.1	5.6	15.8	15.0	17.2	4.6	3.5
Early-chick stage							
1993–94	no data	56.4 (49.3, 63.3)	0.7	34.2	2.3	0.0	26.3 (9.1, 50.8)
1994–95	53.9	52.8 (45.6, 59.8)	31.1	2.6	0.0	0.0	39.8 (29.4, 51.0)
1995–96	34.5	42.6 (35.8, 49.7)	16.4	0.0	3.4	2.5	40.7 (30.1, 51.9)
1996–97	6.3	37.3 (27.5, 50.0)	0.0	0.0	0.0	0.0	no data
1997–98	0.0	24.4 (14.5, 35.7)	10.2	0.0	11.0	0.0	34.7 (23.8, 47.1)
Mean	23.7	42.7	11.7	7.3	3.4	0.5	35.4
Standard error	12.6	5.7	5.7	6.7	2.0	0.5	3.3
Late-chick stage							
1993–94	no data	46.6 (39.6, 53.7)	0.0	0.0	0.0	0.0	no data
1994–95	0.0	36.1 (29.6, 43.5)	4.0	0.0	0.0	0.0	30.7 (21.0, 41.7)
1995–96	0.0	33.7 (27.3, 40.5)	0.0	0.0	0.0	0.0	35.2 (25.2, 46.6)
1996–97	no data	30.4 (21.5, 40.5)	0.0	no data	0.0	no data	no data
1997–98	0.0	23.1 (14.2, 34.9)	1.7	0.0	0.0	0.0	30.6 (19.9, 43.0) ^B
Mean	0.0	34.0	1.1	0.0	0.0	0.0	32.1
Standard error		3.8	0.8				1.5

^AIndicates sub-sampled colonies (with 95% confidence intervals for estimates).^BEstimated from data in Uren (1999).**Appendix 2. Estimated Mayfield daily and stage-survival rates for eggs at monitored sooty shearwater breeding colonies 1994–98**

Key to symbols: *, no eggs found

Colony	Season	t (days)	n surviving	n dying	Daily p(survival)	Lower 95% CI	Upper 95% CI	Stage survival	Lower 95% CI	Upper 95% CI
Kakanui	1994–95	45	11	4	0.9929	0.9861	0.9998	0.687	0.475	0.991
	1995–96	60	10	12	0.9865	0.9789	0.9941	0.486	0.323	0.730
	1997–98	56	0	8	0.9554	0.9251	0.9856	0.089	0.016	0.463
Taiaroa Hd	1994–95	65	112	49	0.9943	0.9927	0.9959	0.738	0.677	0.803
	1995–96	64	102	53	0.9933	0.9915	0.9951	0.699	0.635	0.770
	1997–98	55	16	23	0.9834	0.9767	0.9901	0.412	0.286	0.591
Nuggets 1	1994–95	68	37	49	0.9873	0.9837	0.9908	0.507	0.419	0.613
	1995–96	70	23	70	0.9804	0.9758	0.9849	0.350	0.274	0.447
	1997–98	55	5	3	0.9912	0.9813	1.0011	0.626	0.368	1.000
Nuggets 2	1994–95	77	1	18	0.9715	0.9585	0.9845	0.216	0.106	0.436
	1995–96	67	0	4	0.9627	0.9268	0.9986	0.133	0.018	0.927
	1997–98	*								
Nuggets 3/4	1994–95	47	0	49	0.9468	0.9323	0.9613	0.055	0.024	0.123
	1995–96	66	3	50	0.9671	0.9581	0.9760	0.169	0.103	0.277
	1997–98	53	3	5	0.9811	0.9648	0.9975	0.364	0.149	0.876
Nuggets 5	1994–95	78	0	11	0.9679	0.9493	0.9866	0.178	0.063	0.489
	1995–96	69	0	4	0.9638	0.9289	0.9986	0.141	0.020	0.930
	1997–98	*								
Tuhawaiki I.	1994–95	82	30	10	0.9964	0.9942	0.9986	0.827	0.734	0.930
	1995–96	74	37	15	0.9953	0.9929	0.9977	0.778	0.686	0.884
	1997–98	49	20	15	0.9882	0.9823	0.9941	0.534	0.388	0.733

Appendix 3. Estimated Mayfield daily and stage-survival rates for chicks at monitored sooty shearwater breeding colonies 1994–98
Key to symbols: *, no eggs found; **, no early chicks found

Colony	Season	t (days)	n surviving	n dying	Daily p(survival)	Lower 95% CI	Upper 95% CI	Stage survival	Lower 95% CI	Upper 95% CI
Kakanui	1993–94	no data								
	1994–95	46	0	14	0.9457	0.9180	0.9733	0.004	0.000	0.073
	1995–96	61	0	10	0.9590	0.9341	0.9839	0.017	0.001	0.207
	1996–97	no data								
	1997–98	**								
Taiaroa Hd	1993–94	78	98	34	0.9961	0.9948	0.9974	0.684	0.602	0.777
	1994–95	46	83	40	0.9912	0.9885	0.9939	0.425	0.326	0.554
	1995–96	56	82	24	0.9953	0.9935	0.9972	0.635	0.529	0.761
	1996–97	30	25	13	0.9857	0.9779	0.9934	0.246	0.115	0.526
	1997–98	70	10	9	0.9905	0.9844	0.9967	0.398	0.218	0.725
Nuggets 1	1993–94	**								
	1994–95	46	6	41	0.9602	0.9483	0.9721	0.019	0.006	0.065
	1995–96	54	0	26	0.9537	0.9363	0.9711	0.010	0.002	0.058
	1996–97	no data								
	1997–98	77	2	10	0.9784	0.9651	0.9916	0.120	0.032	0.442
Nuggets 2	1993–94	89	0	14	0.9719	0.9574	0.9864	0.063	0.015	0.265
	1994–95	56	0	1	0.9554	0.8698	1.0409	0.012	0.000	1.000
	1995–96	**								
	1996–97	no data								
	1997–98	*								
Nuggets 3/4	1993–94	no data								
	1994–95	**								
	1995–96	54	0	3	0.9537	0.9025	1.0049	0.010	0.000	1.000
	1996–97	no data								
	1997–98	78	0	10	0.9679	0.9484	0.9875	0.042	0.006	0.295
Nuggets 5	1993–94	**								
	1994–95	**								
	1995–96	67	0	2	0.9627	0.9119	1.000			
	1996–97	no data								
	1997–98	*								
Tuhawaiki I.	1993–94	no data								
	1994–95	44	27	8	0.9940	0.9898	0.9981	0.557	0.371	0.835
	1995–96	47	30	7	0.9955	0.9921	0.9988	0.643	0.463	0.891
	1996–97	no data								
	1997–98	82	29	3	0.9988	0.9974	1.0002	0.889	0.778	1.000

Appendix 4. Apparent survival rates (%) of sooty shearwater eggs and early chicks at monitored colonies

Season	K	T.Hd ^A	N.1	N.2	N.3/4	N.5	T.I. ^A
Period I: egg- to early-chick stage							
1994/95	73.3	69.6 (61.7, 76.9)	43.0	5.3	0.0	0.0	75.0 (58.8, 87.3)
1995/96	45.5	65.8 (57.6, 73.4)	24.7	0.0	5.7	0.0	71.2 (56.5, 83.0)
1996/97	no data	no data	no data	no data	no data	no data	no data
1997/98	0.0	41.0 (24.9, 58.4)	62.5	— ^B	37.5	— ^B	57.1 (39.2, 73.8)
Mean	39.6	58.8	43.4	2.6	14.4	0.0	67.8
Standard error	21.4	9.0	10.9	2.6	11.7		5.4
Period II: early- to late-chick stage							
1993/94	no data	74.2 (65.7, 82.1)	0.0	0.0	0.0	0.0	no data
1994/95	0.0	67.5 (58.3, 75.8)	12.8	0.0	0.0	0.0	77.1 (59.6, 89.6)
1995/96	0.0	77.4 (68.2, 85.2)	0.0	0.0	0.0	0.0	81.1 (64.9, 92.0)
1996/97	no data	65.8 (48.6, 80.4)	no data	no data	no data	no data	no data
1997/98	0.0	52.6 (28.9, 75.6)	16.7	— ^B	0.0	— ^B	90.6 (74.7, 98.0) ^C
Mean	0.0	67.5	9.8	0.0	0.0	0.0	83.0
Standard error		4.3	5.0				4.0

^AIndicates sub-sampled colony (with 95% confidence intervals for estimates).

^BNo estimates possible since no eggs or evidence of activity were found at these colonies on first examination.

^CEstimated from data in Uren (1999).