A COMPARATIVE ANALYSIS OF POPULATION ESTIMATION METHODS FOR A BURROW-NESTING SEABIRD: A NOVEL GROUND-COUNT METHOD AND CLOSED POPULATION CAPTURE-RECAPTURE MODELLING

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By: Janet Moore

ABSTRACT

Spatial variation in nesting patterns can cause variation in population size estimates. This thesis research shows that more accurate estimates can be made of population sizes of breeding burrow-nesting seabirds by mapping Bonin Petrel (*Pterodroma hypoleuca*) nesting colonies into low, medium, and high burrow densities and then randomly conducting burrow density and occupancy surveys, as compared to more traditional censusing methods. Results from closed population modelling, using the Program MARK, indicate that capture-recapture studies may be useful in estimating the total population size of Bonin Petrels. Capture-recapture studies are more time/cost-effective than ground-count studies, are less harmful to the study species, and can estimate both breeding and total population sizes of any burrow-nesting seabird species worldwide. Support for distinguishing breeding females from breeding males and non-breeding individuals through cloacal size is provided, and the importance of habitat (and *Verbesina encelioides*, an invasive species) to Bonin Petrel nesting patterns is discussed.

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GENERAL INTRODUCTION AND RESEARCH OBJECTIVES

Seabirds are long-lived animals that spend most of their lives at sea. They are predators near the top of marine food webs and thus are extremely dependent on oceanographic conditions (Diamond and Devlin 2003). Research has shown that seabird breeding success is affected by changes in prey availability in the waters around their colonies (Furness 1978; Cairns 1987; Montevecchi et al. 1988; Monaghan et al. 1989; Bost and LeMaho 1993). Seabirds are often highly selective of prey size and so theoretically could also affect long-term prey abundance and availability (Cairns 1992). They can indicate changes in population size of commercial prey stocks. Seabird population changes have been shown to parallel changes in commercial prey species availability (Montevecchi and Berutti 1990; Barrett 1991; Hatch and Sanger 1992; Bertram and Kaiser 1993). Consequently, seabirds are often cited as indicators of relative productivity and health of the marine environment (Croxall et al. 1988; Furness et al. 1993; Kushlan 1993; Parrish and Zador 2003). To quantify the effects caused by changes in the marine environment, reliable information is required on the abundance and breeding population size of seabirds (Harding et al. 2005).

The United States Fish and Wildlife Service's (USFWS) Pacific Region is responsible for the management of seabirds that breed in Hawaii and the U.S. Pacific Islands. In 2004, the USFWS convened workshops with experts in seabird monitoring, and one main goal stemming from these meetings was "to integrate seabird monitoring into an overall assessment of the health of marine/coastal ecosystems of the United States Pacific Islands" (Citta et al. 2007). In developing a seabird monitoring and conservation plan for the Pacific Region, the USFWS requested an assessment of their Pacific seabird monitoring program. The assessment (Citta et al. 2007) included a review of monitoring methods, analysis of existing USFWS data to evaluate the statistical power of current monitoring, and recommendations for statistically rigorous seabird monitoring protocols. Although population size and reproductive success monitoring was undertaken by, or in collaboration with the USFWS throughout the 1990s, the assessment states that "no (monitoring) data" were available for Bonin Petrels (*Pterodroma hypoleuca*) on Midway Atoll, where this study takes place. The authors of this report recommend that Bonin Petrels be recognized as a "stewardship species", because a large proportion of their global population (>50%) breeds in the U.S. Pacific Islands, and that Bonin Petrels are included in any future USFWS monitoring plans (Citta et al. 2007).

Although Bonin Petrels once inhabited the main Hawaiian Islands, they were extirpated following human occupation, primarily due to habitat loss and predation (Seto and O'Daniel 1999). The remaining Hawaiian population of Bonin Petrels breed on remote and low-lying small coral atolls (French Frigate Shoals, Laysan and Lisianski Islands, Pearl and Hermes Reef, Midway Atoll and Kure) as well as on Japan's Bonin and Volcano Islands. The largest colony of Bonin Petrels in the Northwest Hawaiian Islands breeds on Sand Island, Midway Atoll (28° 15'N, 177° 20'W) and is where this study takes place. Midway Atoll lies within the Papahānaumokuākea Marine National Monument, created on 15 June 2006, and forms part of the remote Northwest Hawaiian Islands (NWHI), approximately 1850 km northwest of Honolulu (Figure 1.1).

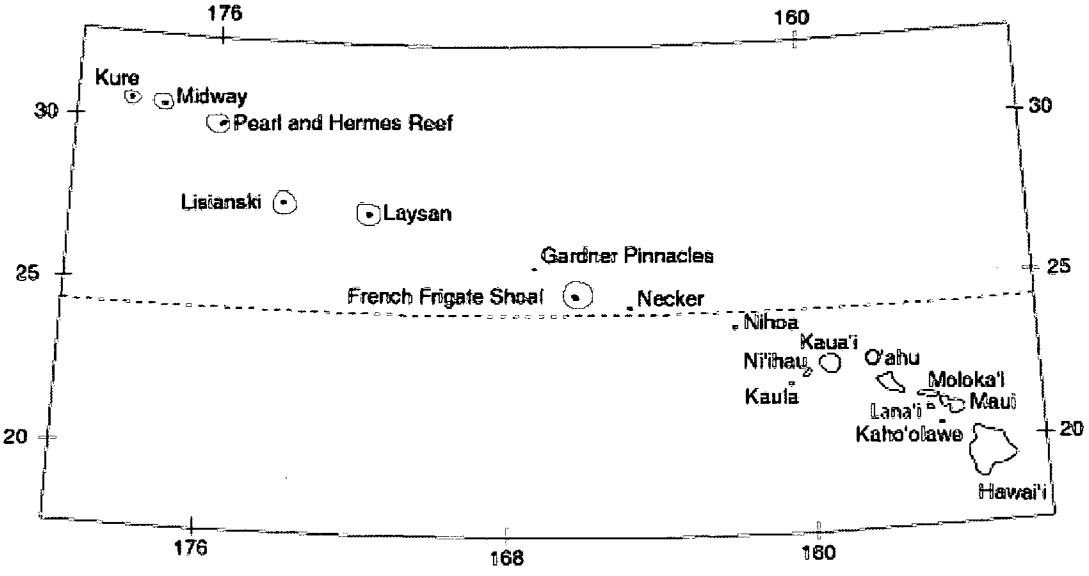

Figure 1.1: The Hawaiian Islands and study site, Midway Atoll. Areas shaded blue depict islands where Bonin Petrels are breeding in the Northwestern Hawaiian Islands. Source: http://bna.birds.cornell.edu and the Cornell Lab of Ornithology.

Midway Atoll is comprised of three islands, Sand (485 ha), Eastern (136 ha) and Spit (2 ha). The landscape of Sand and Eastern Islands have been significantly altered since the early 1900's, when the Commercial Pacific Cable Company took occupancy constructing cable houses and residences and importing over 9000 tonnes of soil from Guam and Hawaii to support non-native flora for sustenance and personal pleasure (http://www.fws.gov/midway/cable.html, accessed 11 March 2009). In 1935, Pan American Airways constructed an airport, runway and supportive infrastructures (e.g., hotel, power, water plants and shops, etc.). Under the jurisdiction of the U.S. Navy since 1903, significant transformations of Sand and Eastern Islands followed, and were particularly conspicuous after Midway was ordered a national defence area in 1941, during World War II. USFWS staff were permanently stationed on Sand Island in 1991, albeit Midway was designated as an overlay Refuge since 1988, and even prior to this time has been managing wildlife within the Atoll. In 1996 the United States Department of Interior's Fish and Wildlife Service (USFWS) took control from the U.S. Navy.

Presently home to over two million seabirds (18 breeding species), Midway also supports the largest breeding colony of Laysan Albatrosses (*Phoebastria immutabilis*) and the three largest breeding colonies of Red-tailed Tropicbirds (*Phaethon rubricauda rothschildi*), White Terns (*Gygis alba rothschildi*) and Black Noddies (*Anous minutus melanogenys*) found in the Northwestern Hawaiian Islands (Seto 1994). Midway is also home to about 65 resident endangered Monk seals (*Monachus schauinslandi*), threatened Hawaiian Green Sea turtles (*Chelonia mydas*), provides daytime resting grounds to approximately 250 Spinner dolphins (*Stenella longirostris*), and provides habitat that supports considerable numbers and species of reef fish. Further information regarding Midway's wildlife and historic importance is available from the USFWS's Refuge website http://www.fws.gov/midway/.

Bonin Petrels are small (30 cm long; wingspan 63–71 cm; mean body mass 203.7 g ± 25.5 SD) (Harrison 1988; Seto 1994), nocturnal, and monomorphic seabirds. Sexually monogamous, they breed during the winter, and breed farther north than any other *Pterodroma*, or gadfly petrel. Courtship, pair formation, burrow excavation, and nest-site preparation occur from August through December of each year. Bonin Petrels nest underground in burrows, most of which are 0.25 m – 2 m in length, but can be as long as 3 m (Seto 1994). Burrows are approximately 1 m deep, and end in an enlarged nesting chamber (Grant et al. 1983). Both males and females excavate the burrows, and nest cups are composed of grasses, ironwood tree (*Casuarina equisetifolia*) needles, or small feathers from the petrels themselves (Seto 1994). Bonin Petrels prefer to dig burrows in sandy soils and in areas with native bunch grass (*Eragrostis variabilis*), but also breed under stands of ironwood trees and under dense native naupaka shrubs (*Scaevola sericea*) (Clapp and Wirtz 1975). Egg laying commences during the second week of January and ends approximately one month later (Seto and O'Daniel 1999). Females synchronously lay just one egg per season, and both males and females share in incubation. Incubation shifts last from 1-11 and 1-13 days for females and males respectively (Seto and O'Daniel 1999). The mean incubation period is 49 days ± 1.3 SD (n = 46; Seto 1994), consistent with petrel eggs of the same mass (Seto and O'Daniel 1999). However, the incubation period is twice as long as the value predicted on the basis of egg mass for other bird species (Grant et al. 1982). Bonin Petrel eggs begin to hatch in May, chicks begin fledging in late May, and continue to do so until the third week in June. The mean fledging age is 82 days ± 3.0 SD (range 77–89, n = 44; Seto 1994). Similar to most other seabirds, Bonin Petrels come to land to breed, but spend most of their time at sea. Bonin Petrels primarily feed on fish species that inhabit deeper waters during the day, but surface at night, such as lantern fishes (*Myctophidae spp.*) and hatchetfishes (*Sternoptychidae spp.*) (Harrison and Seki 1987). Squid (*Ommastrephidae spp.*) are another important food source (Harrison et al. 1983).

For seabirds, it is important to have baseline population size estimates at both local and wider scales from which to measure change, or to identify important breeding areas for site conservation (Walsh et al. 1995). While resources for conducting population censuses are often limited, efforts should however, concentrate on providing an accurate count (Walsh et al. 1995). Generally speaking, wide-spread counts of species or colonies of seabirds are suggested every 5-10 years, while more targeted counts, using plots positioned within representative habitats for example, are recommended every one to five years (Walsh et al. 1995). Monitoring seabird productivity, or breeding success, is also important to detect or reflect changes in environmental conditions. Yearly productivity monitoring within representative plots for example, would provide insight into immediate threats to a seabird population from reduced prey species availability that wider-scale, less frequent population censusing may not alone reveal.

Breeding population census techniques differ according to the nesting behaviour of the bird species. Direct counts of seabirds that nest synchronously and underground in burrows (e.g., petrels and shearwaters), or crevices (e.g., puffins), are often impractical because of their large population sizes, and sometimes because colonies are geographically isolated from one another. Therefore, it is recommended that counts are conducted in plots positioned in habitats representative of the total area being used, that sampling is conducted during the known egg-laying period, and in plots of equal size (Birkhead and Nettleship 1980; Walsh et al. 1995; Citta et al. 2007). Counts from sample plots have two distinct aims: 1) extrapolation from the sample counts to produce whole-colony population size estimates, and/or; 2) detection and quantification of population changes in representative samples (Walsh et al. 1995). The number and size of plots selected for sampling involves a trade-off between statistical efficiency and practicality (Citta et al. 2007). The larger the proportion of a colony covered, the greater the chance of results being representative of the whole population (Walsh et al. 1995). A greater number of smaller sized plots are preferable to fewer, larger plots. However, too many small plots may take a disproportionately long time to count and become more prone to inaccuracy (Walsh et al. 1995). For Bonin Petrels, Citta et al. (2007) recommend that long-term population and productivity plots are large enough to contain 20 nests.

Sample plots can be randomly, systematically, or stratified and randomly positioned. Randomly positioning plots is a valid technique for obtaining an unbiased, statistically representative sample of a population (Walsh et al. 1995; Williams et al. 2002). However, one disadvantage of this method is that plots may end up being clumped together, leaving some parts of a breeding colony underrepresented. One solution is to use a stratified random sampling method, which involves dividing the total area where birds are breeding (e.g., an island) into smaller areas, and then randomly positioning an equal number of sample plots based on the relative proportion each stratified area encompasses. Areas can be stratified based on differences in habitat, burrow density (Harris and Rothery 1988; Small 1999; and this study), or simply by dividing the total breeding area into a number of smaller areas. Stratified random sampling improves the precision of sample results, and many ecologists and statisticians consider this the best sampling technique for ecological studies (Southwood 1978; Walsh et al. 1995). This method is particularly advantageous in situations where breeding densities vary markedly (Walsh et al. 1995), as in the case of Bonin Petrels on Midway Atoll.

Systematic sampling is another method used to census ground-nesting or burrow-nesting seabirds, where study plots or quadrates are placed at regular or fixed intervals throughout the breeding area (Walsh et al. 1995; Williams et al. 2002; U.S. Geological Survey 2009). Study plots can be placed along transect lines criss-crossing or radiating from the centre of a breeding area, or the colony can be divided into grid squares of equal size, and plots are positioned at the centre of each square (Anker-Nilssen and Rostad 1993; Walsh et al. 1995). The starting point should be randomly selected. Milne (1959) found that the resulting statistics using this method to estimate population size were "at least as good, if not rather better" than if data were derived using randomly positioned sample plots. For burrow-nesting seabirds, Savard and Smith (1985) found that burrow density in systematically placed plots was less variable and the results were more precise than in randomly positioned plots. This method is also advantageous compared to random sampling because it can be easier and quicker to carry out in the field, and can provide information on the extent of colony boundaries (Tasker et al. 1988; Anker-Nilssen and Rostad 1993). One theoretical disadvantage of this method is that transect lines and sample plots could be positioned to follow some pre-existing nesting pattern which could inadvertently bias the resultant population estimate (Walsh et al. 2007). Also, where a population is forced to breed in a number of smaller colonies, because of anthropogenic habitat alterations, such as on Midway Atoll, this method would not be as practical as the stratified and random sampling approach. Considerable time would be spent travelling to, and setting up plots in areas not suitable for nesting Bonin Petrels; where ground surfaces are covered by concrete/building or where surface conditions appear suitable, but where underlying conditions are not suitable. For example, some areas on Sand Island have been used to bury solid waste, while others are prone to flooding because of perched water levels. Sampling in a considerable number of plots where there are no burrows would result in a downwardly breeding population size estimate.

The recommended breeding census unit is the "apparently occupied site" (AOS) (Walsh et al. 1995). Burrow density and occupancy are census units for burrow and crevice-nesting species. Operational definitions of an "apparently active" burrow can vary, and are specific to the species of bird studied. Generally speaking, a burrow may be considered apparently active if it is appropriately sized and has an unconcealed entrance, and where there are conspicuous signs of recent activity, such as foot prints in the burrow entrance, evidence of fresh digging, and/or excrement, feathers, egg shell fragments etc. found at the entrance and/or in the burrow (Walsh et al. 1995).

Operational definitions of an occupied burrow (or an apparently occupied site; AOS) can include courting or incubating pairs, or more commonly when an egg or fresh egg fragments are found within a burrow (Walsh et al. 1995; Oxley 1997). A burrowscope, or underground surveillance camera, is a common and direct method to survey burrows for occupancy, however other direct and indirect methods can also be used. For example, grubbing, or directly reaching into suspected burrows for signs of occupancy has traditionally been used for species where burrows are relatively short, or an arms length (e.g., Leach's Storm Petrels, *Oceanodroma leucorhoa*) (Oxley 1997; Stenhouse et al. 2000; Robertson et al. 2002; Regehr and Chardine 2003; Ambagis 2004). This method is not practical for species where burrows extend beyond approximately 0.75 m, such as the Bonin Petrel. The use of indirect methods to assess for occupancy, which are generally less invasive to the study species, can also be used. For example, sound recordings, or playbacks of species specific calls have been successful for Leach's Storm-Petrels, Spectacled Petrels (*Procellaria conspicillata*) and other similarly nesting species (Ryan and Moloney 2000; Ambagis 2004). However, this method may not be as practical in high density breeding areas, or areas where other wildlife are extensively calling or otherwise generating considerable noise. On Midway Atoll, over one million albatrosses are breeding at the same time as Bonin Petrels, and petrel vocalizations in one burrow, as opposed to another, may be difficult to distinguish between. Lattices of small twigs, or popsicle sticks have also been used to indirectly assess occupancy (Oxley 1997). If, for example, the lattice of twigs is displaced from the entrance, it is assumed to be an occupied burrow. However, this later technique is not practical in situations where other bird species or wildlife are likely to interfere with the placement of twigs or sticks.

While the techniques to estimate the breeding population size of burrow and crevice nesting species are widely documented, methods to estimate their total population size are not as well established. One possible method is to use capture-recapture (CR) and modelling to estimate the total population size. However, there are few published studies that explore the accuracy and performance of modern closed population capture-recapture models; models most suited for estimating the total population size of Bonin Petrels on Midway Atoll. Recent and on-going statistical modifications and improvements to the closed population models in Program MARK will require persistent validation of the use of one class of model(s), as opposed to another. Although CR and modelling do provide total population size estimates, in order to estimate the breeding population size, distinction between breeding and non-breeding individuals must be made at the time of capture. Further challenges to studying Bonin Petrels include identical plumage between non-breeding and breeding individuals, and no obvious morphometric differences existing between the sexes (Seto 1994).

A more recent and promising method to estimate the total population size of nocturnal and migrating birds involves the use of radar (Peckford and Taylor 2007). While this method could be adapted to estimate the total population size of Bonin Petrels on Midway Atoll, considerable investment would be necessary to modify the required radar system, develop a computer program(s) to decipher the radar data, and species specific flight information would also be required.

Since population data for Bonin Petrels is so sparse (Citta et al. 2007), considerable effort was taken to ensure that the census methods used in this study were robust and would provide precise and accurate baseline estimates of both the breeding and total populations on Midway Atoll. Because spatial variation in nesting patterns is common for burrow-nesting birds, the range of burrow densities and occupancies from plot sampling tend to vary considerably, and thus, estimates may be inaccurate. Also, conducting ground censuses are labour intensive and time consuming, so frequently, only small portions of colonies can be sampled and also contributes to problems associated with accuracy and precision (U.S. Geological Survey, Patuxent Wildlife Research Centre, http://www.pwrc.usgs.gov/monmanual/taxa/colonialwaterbirds/burrowcolony.htm, accessed 18 March 2009).

In order to improve the accuracy of breeding population size estimates for burrow-nesting seabirds, monitoring methods should be aimed at reducing the confidence intervals of the population estimates. While conducting more burrow density and occupancy plot surveys is one obvious solution, it is often impractical and can be damaging to the nesting habitat, because burrows are prone to collapse when conducting plot surveys. One alternative is to stratify Bonin Petrel nesting colonies into areas of low, medium, and high burrow density by marking the breeding colony boundaries using GPS waypoints. The waypoints can then be connected using ArcGIS to create a detailed nesting pattern map based on burrow density. Burrow density and occupancy plot sampling can subsequently be undertaken proportionate to the areas encompassed by each of the low, medium, and high burrow density areas as originally mapped. While the primary goal in producing such a detailed map is to improve the accuracy of the breeding population size estimate, it can also be used to correlate nesting patterns with local conditions, such as habitat, proximity to water or anthropogenic influences, and also the nesting patterns of other co-nesting species and wildlife. Correlation of these patterns can be quantified using Land Cover maps and ArcGIS, or from habitat and vegetation data collected concurrently with burrow density and occupancy plot surveys (Appendix A1).

Recent advancements in mapping software, accurate GPS units, and broad-scale availability of quality satellite and digital imagery will undoubtedly provide the impetus for improving methods to ground-census breeding colonies of burrow-nesting seabirds, and improve the precision and accuracy of population size estimates.

The most significant negative impact to Bonin Petrels was caused by the accidental introduction of the predatory black rat (*Rattus rattus*) in 1943 aboard cargo (Fisher and Baldwin 1945). Populations once recorded at 500,000 Bonin Petrel individuals (Hadden 1941) declined to 10,000 breeding individuals (Ludwig et al. 1979). Populations have since rebounded following a successful rat eradication program that concluded in 1997 (USFWS pers. comm.). However, no estimate of their population size has been done since 1995, which was prior to rats having been extirpated from the Atoll. The breeding estimate at that time was 64, 132 individuals (Seto 1995). A study, such as the one I have undertaken, is therefore timely and provides important insight into censusing this, and similarly nesting species.

Research Objectives

One of the objectives of my study was to estimate the breeding population size of Bonin Petrels on Sand Island in 2008 (Chapters 1), more than one decade after the eradication of the black rat. The census method used in this study combines traditional techniques, where burrow density and occupancy plots are randomly positioned, but also includes initial and detailed GIS mapping of nesting colonies. Improved mapping methods are central to setting up this stratified, random, plot-based study design.

A second objective was to use a capture-recapture study and closed population modelling to determine whether modern models produce accurate estimates of the total population size of Bonin Petrels (Chapter 2). Program MARK was selected because it is widely available, commonly used by wildlife biologists in the United States and Canada, and incorporates closed population models that account for time effects, behavioural response and species specific heterogeneities (e.g., incubation shifts and flight patterns). Although the behaviours of Bonin Petrels are not well documented, the assumption of population closure was made, because the capture period was short, and the study site is relatively isolated from other islands where Bonin Petrels breed.

To determine if modelled population size estimates are precise, a comparative estimate was required. From the mistnetting capture study, the proportion of breeding female Bonin Petrels was determined from cloacal and brood patch categorization. This value was then doubled to account for their mate, and represents the total proportion of breeding individuals on Midway Atoll. The breeding estimate calculated from the ground-count census was deemed equal to the proportion of captured breeding birds, and the total population size was subsequently derived based on the remaining proportion of non-breeding individuals captured. Identifying breeding female Bonin Petrels is, however, challenging. Molecular studies to confirm the success of using cloacal size to identify breeding female Bonin Petrels from males, and non-breeding individuals, have not yet been done. Thus, a third objective of this research was to evaluate if there is a significant difference in the size of cloacae between male and female Bonin Petrels. Data collected in 1998 and 1999 by the USFWS, where cloacal measurements were taken from Bonin Petrels breeding in artificial nestboxes buried underground (Chapter 1) were used. Justifying the methods used to sex breeding females provides further evidence that the total population size estimates derived from the capture study and based on ground-count censusing techniques are accurate.

A fourth objective was to document Bonin Petrel nesting patterns and preferences in relation to local conditions (Chapter 3). Midway Atoll has a longstanding history of human occupation and war; local conditions have been conspicuously altered. Invasive species, such as *Verbesina (Verbesina encelioides)*, were accidentally introduced, while other species, such as ironwood trees, were purposefully introduced as wind barriers. Both of these non-native species have reduced the available nesting habitat to indigenous avifauna on Midway Atoll (USFWS pers. comm.; Feenstra and Clements 2008). However, no studies have been done to quantify the impact *Verbesina* has on nesting bird habitat (Feenstra and Clements 2008). Therefore, to better understand nesting patterns and preferences of Bonin Petrels in relation to land cover (e.g., "*Verbesina* dominated" areas), this chapter has been included to quantify this relationship and further exemplifies the benefits of improving ground-count census methods, where more detailed mapping is undertaken.

CHAPTER 1. ESTIMATING THE POPULATION SIZE OF BONIN PETRELS USING A NOVEL GROUND-COUNT METHOD AND MISTNETTING, SAND ISLAND, MIDWAY ATOLL

1.1 ESTIMATING THE POPULATION SIZE OF BONIN PETRELS AND PAST EFFORTS

Chapter 1 details an improved stratified and random ground-count breeding census technique, herein referred to as the CTBS (Censusing Technique for Burrow-Nesting Seabirds). The CTBS complements published U.K. and U.S. study protocols (Walsh et al. 1995; Citta et al. 2007) by more accurately stratifying Bonin Petrel breeding areas and improving colonial mapping methods. The resultant CTBS breeding population size estimate is compared to an estimate that was produced using this same data, but derived based on the mean burrow density and occupancy from plot samples positioned randomly, and throughout the entire area where Bonin Petrels were found nesting on Sand Island. Both the Canadian Wildlife Service and the USFWS commonly use either systematic or random burrow density and/or occupancy plot sampling; where the breeding population size is calculated from the mean values obtained from plot sampling which are multiplied by the total area occupied by breeding birds (Oxley 1997; Stenhouse et al. 2000; Diamond 2001; Robertson et al. 2002; Regehr and Chardine 2003; Ambagis 2004). These commonly adopted approaches are broadly referred to as "traditional methods" in this study. Practically speaking, while systematic sampling is an efficient technique, the habitat on Midway Atoll is fragmented, and a stratified and random approach was more suitable and ensured that sampling was solely conducted in areas where Bonin Petrels were breeding. Also, the CTBS improves the accuracy of the breeding population size estimate because it is derived from mean burrow density and occupancies from plot sampling yet calculated independently for each of three unique nesting categories (low, medium, and high burrow density) and then summed to yield a total breeding population size estimate. The other obvious advantage of the CTBS is that the importance of land cover to breeding patterns can be evaluated from the nesting pattern map. Further study results provide information relating to Bonin Petrel burrow density and occupancy from data collected in collaboration with the USFWS in 1994 (Seto 1994; Seto 1995) and 1998 (by the author, unpublished). The total population size of Bonin Petrels is also derived based on the proportion of breeding and non-breeding individuals captured during a mistnetting study. The minimum age of first breeding for Bonin Petrels is also confirmed from birds captured by the USFWS in 1994, 1995, and 1999 using mistnets.

Prior to this study, the most recent population size estimate was made by Seto (Seto 1995) who used a similar, yet less rigorous method, to estimate breeding populations on Sand Island, Midway Atoll. For example, a specific burrow density study was not completed at the time of her research, and burrow density was not considered to the same extent as in this study when producing breeding population size estimates. Three irregularly shaped plots of different areas were selected to conduct occupancy surveys (using a burrowscope), as opposed to conducting island-wide surveys, and results from the occupancy surveys were solely used to calculate the breeding population size. The burrow density map Seto used as the basis for identifying the total area occupied by nesting Bonin Petrels was created three years prior, in 1991, by USFWS volunteer Chris Kirkpatric (Kirkpatric 1991). Between November 1990 and February 1991, Kirkpatric hand sketched a map that showed the total nesting area used by Bonin Petrels and, similar to this study, categorized colonies into low, medium, and high nesting densities. GPS units and ArcGIS were not available to Kirkpatric. Kirkpatric sub-sampled for burrow density using 100 m^2 plots in approximately 57% of the total nesting area occupied (280,813 m^2). Kirkpatric did not produce any population size estimates at this time, likely because he did not conduct occupancy surveys. Using Kirkpatrics' map, Seto selected the three occupancy plots to "scope" based on each site being relatively isolated from each other, and each representing a breeding colony of low, medium, and high burrow density. Seto produced three breeding population size estimates by multiplying the results from occupancy surveys by the total area occupied specific to each density category. Summation of these three estimates provided a total breeding population size estimate.

Seto also mistnetted and banded Bonin Petrels within each of the three occupancy plots, and used combined sexing methods, from cloacal measures and brood patch development (a technique also used in this study, see Methods), to calculate the proportion of breeding birds in comparison to the total number of birds captured. From the CR study, Seto applied Bailey's modification of the Lincoln-Peterson Index (LPI), a precursor to modern-day models, to calculate the total population size of Bonin Petrels. The LPI assumes that each individual bird captured has an equal chance of recapture (Amstrup et al. 2005). Seto's research indicated that this assumption was violated due to the inherent incubation behaviours of Bonin Petrels, and thus invalidated her total population estimates using this particular CR and modelling method.

The total population size estimate derived from modelling was subsequently evaluated against the total population size estimate derived based on the results of her occupancy survey, similar to the methods used in this study. The proportion of breeding individuals as determined using combined sexing measures from CR were deemed equal to the number of breeding individuals derived from the ground-count occupancy survey. The number of non-breeding individuals was calculated based on the proportion of non-breeding individuals captured during mistnetting, and the non-breeding and breeding numbers were summed to yield a total population size estimate for Sand Island.

The CTBS likely provides more accurate breeding population estimates than traditional methods and those used by Seto, because: the entire breeding colony is mapped at the same time as breeding population size estimates are produced; the map systematically provides representation of the total areas encompassed by unique nesting densities (low, medium, and high nesting densities) from initial marking and mapping; mean burrow densities and occupancy are determined based on sub-sampling throughout the entire range of breeding birds as influenced by unique local ecological conditions and anthropogenic influences; and both burrow density and occupancy are used to calculate breeding size estimates independently in each of the initially mapped nesting density categories.

1.2 METHODS

1.2.1 Study Site

This study was primarily undertaken on Sand Island, however a burrow density map was also created for Eastern Island, Midway Atoll. Sand Island is approximately 2.9 km long and 1.9 km wide. Considerable portions of land are covered by airplane runways, airplane staging areas and buildings, while a tiny portion (<3%, 0.3 acres) has been converted into wetlands to support the recent successful re-introduction of the critically endangered Laysan Duck (*Anas laysanensis*). Sand Island is believed to support the majority of breeding Bonin Petrels in the world (USFWS pers. comm.). Although Bonin Petrels have started breeding on Eastern Island, colonies are sparse and individual numbers are low. In addition, 24% (32 ha) of Eastern Island is covered by abandoned runways, and the U.S. Navy, following a decision to raise the islands height by 2 m, used in-fill materials unsuitable for burrow-nesting seabirds (e.g., heavy stone, concrete, and coral). Rats had also heavily populated Eastern Island because control efforts were not established. In contrast, significant rat control measures were taken on Sand Island in, and around, human occupied areas following their accidental introduction in 1943. In 2007, Midway Atoll was officially declared rat free (USFWS pers. comm.). Spit Island is believed to support just five active Bonin Petrel pairs (USFWS pers. comm.) and remains largely unoccupied because of naturally occurring dense and hard packed coralline substrate which is unsuitable for burrowing seabirds.

1.2.2 The Breeding Population Size of Bonin Petrels, Sand Island

The method documented here was attempted, albeit not completed, in 1999 by USFWS volunteer researchers Dr. Cleo Small and Bruce Casler (Small 1999). As far as the author is aware, this study is the first effort at formally documenting the extent of colonial mapping and burrow density and occupancy plot surveys required to produce more accurate breeding population estimates compared to if traditional methods had been used. A breeding population size estimate of Bonin Petrels, using this stratified and random sampling technique (CTBS), was derived from summation of the products of burrow density (from “apparently active” burrows, refer below) and occupancy calculated independently in low, medium, and high burrow density nesting areas as initially mapped.

This estimate was subsequently evaluated against an estimate derived using the same data, but as the product of mean burrow density, occupancy and total nesting area, which is similar to using traditional and systematic methods to census burrow-nesting seabirds.

Mapping Colonies

(29 January 2008 – 7 February 2008)

Two researchers circumnavigated Sand and Eastern Islands, and using Garmin (GPSMAP® 60CSx) hand-held GPS units, "marked" all low, medium, and high density nesting colonies using colour-coded waypoints specific to each category. Demarcation of the perimeters was solely done by visually estimating the proximity of one burrow entrance to another, irrespective of whether burrows were apparently active (refer below). The distances between burrow entrances were not measured. The closer the entrances were to one another, the higher the density. Approximately 4 m, 2 m, and 1 m separated burrow entrances in low medium, and high burrow density colonies respectively. Colonies of approximately 10 or fewer burrows were excluded if they were dispersed over a proportionately large area, and when relatively few burrows were found in an area bounded by walkways or other structures.

Throughout the two-week survey, colony boundaries were uploaded daily from the GPS units using GPSBabelGUI (2007) and imported onto a satellite image of the Atolls islands using ArcGIS 9.2 (ESRI, 2006). Three shape files were created, and colour-coded polygons were drawn specific to the burrow density they represented by connecting the waypoints (using editing tools). Using an underlain geo-referenced grid-frame, originally created by Rod Low, USFWS, and a statistical function available in

ArcMAP ("calculate geometry"), the areas (m^2) for each of the three nesting categories were derived, and subsequently summed to provide the total nesting area.

This nesting density map was used as the basis for establishing where burrow density, and latterly, occupancy sub-sampling plots were positioned. In effect, creating this map ensured that sampling was conducted solely within known nesting areas, thereby avoiding sampling in areas without birds, common with traditional systematic methods, and that sampling was stratified and conducted proportionately within low, medium, and high nesting densities on Sand Island. This maximized the probability that sampling results from burrow density and occupancy surveys reflected present-day conditions and respected the spatial variations in nesting.

Burrow Density

(11 February 2008 – 5 March 2008)

Using 100 m^2 circular plots randomly placed island-wide (Sand Island), the number of apparently active burrows found within areas proportionate to a minimum of 2.5% of each of the low, medium, and high density colonies were recorded (herein after referred to as burrow density). Because the area used by nesting Bonin Petrels were similar for each nesting density, a similar number of plots were sub-sampled in each of the three nesting categories. A random number generator, using the X and Y coordinates in 10 m intervals derived from the underlain grid-frame, was used to identify where plots would be positioned. To minimize the time spent travelling to and from these randomly selected sampling points, these X and Y coordinates were sorted. The coordinates were subsequently entered into a GPS unit which was then used to locate the sample sites in the field (± 5 m). Three lightweight ropes were tied to a centre stake and the opposite ends to another stake. One stake was positioned at the centre of each randomly selected sample site. The three ropes (radius = 5.65 m) were then used to circumnavigate the 360° 100 m^2 plot, thereby eliminating need for more permanent site marking and facilitating survey by a sole researcher. A burrow was deemed apparently active and was recorded when: 50% or more of the entrance was contained within the sampling frame, the entrance was deemed large enough to allow passage of a Bonin Petrel (approximate width 16 cm and height 9 cm; Seto 1994), it was not completely obstructed by vegetation, and it was at least 0.5 m in length (<5% of burrows were found between 0.25-0.5 m; Seto 1994). While burrows were found with larger entrances, there were few in number, and were assumed to be used by Wedge-tailed Shearwaters (*Puffinus pacificus chlororhynchus*), and discounted. Wedge-tailed Shearwater burrow entrances are approximately 19.4 cm wide (SD ± 3.2 cm, range 11.0–26.0, n = 64) and approximately 12.0 cm high (SD ± 2.3, range 8.0–15.0, n = 64; Byrd et al. 1984). Another burrow-nesting seabird, Tristram's Storm-petrels (*Oceanodroma tristrami*), once used Midway Atoll, but was extirpated by rats (McClelland 2008). If populations of these other two similarly nesting species increase, distinguishing between their burrows will be necessary. Bonin Petrel burrow densities in each of the low, medium, and high nesting colonies, were derived following analysis of these plot surveys.

Burrow Occupancy

(18 February 2008 – 5 March 2008)

A single check of apparently active burrows was done using a burrowscope; a video surveillance camera with infra-red lights housed in a long flexible tube with a viewing monitor (originally constructed by Seto; Seto 1994). An apparently active burrow was deemed occupied when a Bonin Petrel egg was found, irrespective of whether an adult was present and incubating or if it was viable. This study commenced following the known egg-laying period based on data collected in 1993, 1994 (Seto 1994), and 1998 (by the author for the USFWS) when 100% of females had laid their eggs on, or before, 2 February (1993 and 1994) and 13 of February respectively.

Although an attempt was made to survey for occupancy using a method similar to that for burrow density, due to persistent burrowscope failure, and to maximize the number of burrows that could be surveyed for occupancy given time restrictions, surveys were primarily conducted opportunistically in considerably larger plots. Plots ranged in size from 165 m^2 to 8387 m^2, and surveying was conducted in areas of varying habitats and proximity to anthropogenic influences in each of the three burrow density areas throughout Sand Island. Occupancy was derived from the number of apparently active burrows containing an egg in relation to the total number of apparently active burrows successfully searched.

Following completion of this survey, breeding population size estimates were derived using the CTBS method, and a method equitable to using a traditional approach. Using the CTBS method, population estimates were calculated separately for low, medium, and high burrow densities. These estimates were derived as the product of mean burrow density, mean occupancy, and the total area encompassed in each of the three different burrow density categories. A total breeding population size estimate using the CTBS was subsequently derived for Sand Island by adding these three estimates together.

Using this same burrow density and occupancy data, a total breeding population size estimate was calculated similar to using traditional methods. The estimate was calculated as the product of mean burrow density and occupancy for all plots sampled, and this value was subsequently multiplied by the total nesting area, as originally mapped.

1.2.3 The Total Population Size of Bonin Petrels, Sand Island

(Mistnetting and Ground Capture Period: 2 February 2008 - 5 March 2008)

For a total of 21 nights, Bonin Petrels were captured using one 7 ft x 18 ft (2.13 m x 5.49 m) mistnet, or taken off the ground from within a 30 m radius (approximately) of the net during the latter stages of their egg-laying period (Seto and O'Daniel 1999). Birds were captured during 2-hour shifts (approximately) immediately following sunset when considerable numbers return en-mass from pelagic feeding grounds (Seto 1994). Six netting sites were established, two in each of the low, medium, and high density colonies (Figure 1.2).

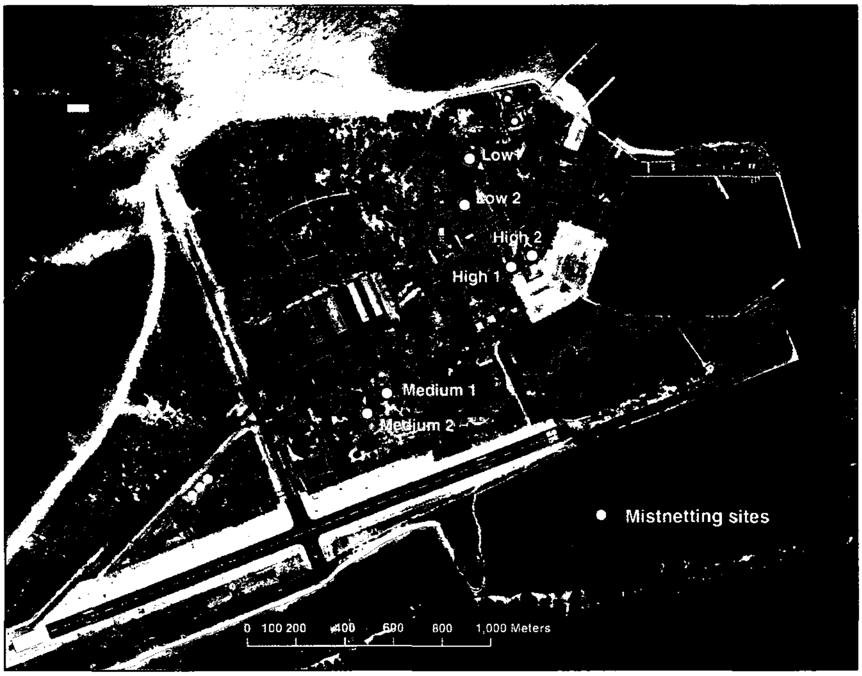

Figure 1.2: Burrow density specific mistnetting sites, Sand Island, Midway Atoll (2008). Source: DigitalGlobe, QuickBird, October 2005.

Colonies were selected on the basis of being sufficiently large, isolated from other colonies of different burrow densities, and easy to access at night. Since breeding Bonin Petrels are more likely to consistently return to the same location as they share in incubation duties than non-breeding individuals, two sites were chosen within each colony to increase the likelihood that each individual, breeding or not, has an equal change of capture. The two sites were positioned approximately 189 m, 114 m and 96 m apart in the low, medium, and high burrow density areas respectively. Mistnets in the low burrow density area were positioned farther apart in an attempt to maximize the likelihood that an equal number of individuals would be using the capture area compared to high density areas. In high density areas, birds are nesting closer together, so the mistnets were positioned closer together.

On average, more than eight days was allowed to pass between netting at the same site to increase the probability of recapturing breeding birds by taking into account their incubating patterns. For example, if a Bonin Petrel was captured and banded and then began incubating, allowing time between capture sessions would increase the likelihood of recapturing this individual. Bonin Petrels were leg-banded (left leg using Bird Banding Laboratory issued incoloy bands), visual observations of brood patches recorded, and the outer lateral edges of each birds cloaca was measured. This was done using digital callipers after the cloaca was lightly sprayed with a 10% alcohol solution. Once sprayed, feathers could be quickly parted clearly revealing the lips of the cloaca thereby increasing accuracy in measurement.

Many species of petrels show no obvious sex-linked dimorphism, but have been successfully sexed based on the differences in cloaca measurements (Serventy 1956; Boersma and Davies 1987; Copestake et al. 1987; Warham 1990; Seto 1994; Seto 1995; O'Dwyer et al. 2006). Research indicates the cloaca can remain enlarged for weeks post-laying, and a study on Gould Petrels (*Pterodroma leucoptera*), another gadfly petrel, proved 96% successful in accurately determining the sex of breeding adults (O'Dwyer et al. 2006). Bonin Petrel eggs represent approximately 22% of their body weight (average fresh-egg mass 39.2 g ± 0.3 SE; Grant et al. 1982), and can be felt when holding the birds. Although molecular sexing studies on Bonin Petrels have not been done, it was used in this study because the method has received continued support from USFWS biologists, it allows comparison of earlier estimates by Seto, and is the only other in-field method available. This study was commenced later in the laying season to maximize the probability that most breeding females would already have laid their egg and could be identified by enlarged cloacae and developed brood patches.

Brood patches were categorized from 0-5 (Figure 1.3) using a method earlier adopted by Seto (1994). A captured bird was determined to be a breeding female if the cloaca measured >10 mm and the brood patch was determined to be 0 or 1, naked or nearly naked with minimal feather coverage, or if the female was carrying an egg, regardless of the cloacal size or brood patch categorization. Birds with a brood patch of 2 were identified by an unbroken lateral line of feathers down the centre of their patch, 3 by this same, unbroken lateral line along with some further partial feather coverage, 4 by nearly complete feather coverage with little exposed skin, and 5 was characterized by the complete lack of a brood patch, fully feathered with no exposed skin. To minimize stress when numerous birds were simultaneously captured, some individuals were banded and did not have either their cloaca or brood patch evaluated (n = 23).

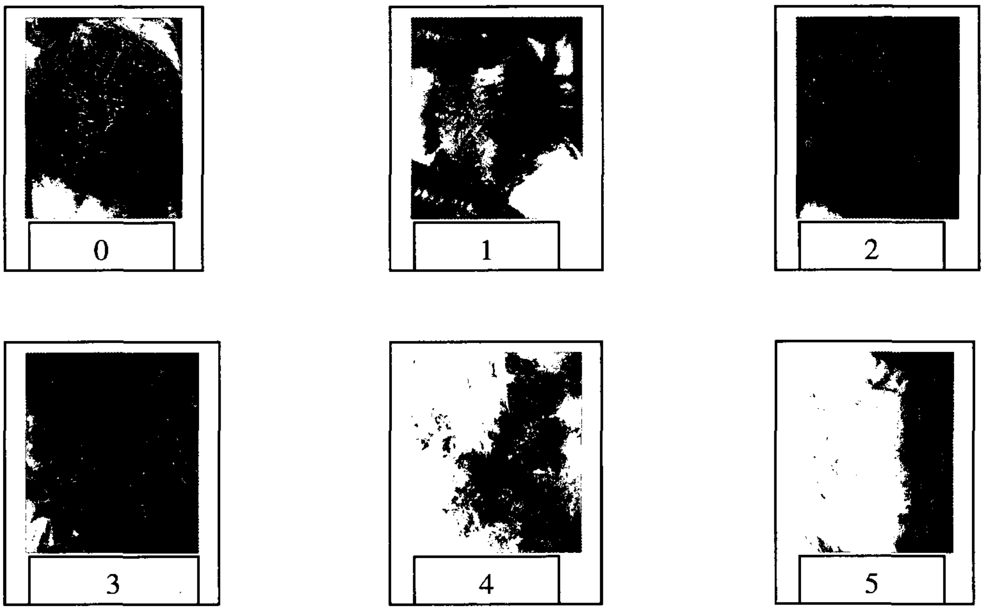

Figure 1.3: Brood patch development in Bonin Petrels showing 0-5 categorizations. A breeding individual was identified as having a brood patch of 0 or 1, and non-breeding from 2-5.

Total population size estimates were latterly derived from the proportion of captured birds exhibiting, and not exhibiting breeding characteristics. More specifically, the breeding population size estimates calculated using the CTBS and traditional methods were assumed to be equal to the proportion of breeding birds captured during mistnetting. The numbers of breeding females captured were determined using combined sexing measures (cloaca size and brood path categorization), and this value was then doubled to include their mate. It was assumed that numbers of both breeding females and males was equal. The proportion of non-breeding individuals was calculated from the remaining proportion of captured birds where combined measures were not met, and both breeding and non-breeding numbers were summed to yield total population size estimates. Two total breeding population size estimates were derived, one specific to the CTBS method, and one related to traditional methods.

The total population size estimate using this method is related to individuals using Sand Island, whereas the total population size estimate(s) produced from modelling (Chapter 2) is related to the entire Atoll. Since just five pairs of Bonin Petrels use Spit Island (USFWS pers. comm.), and very few use Eastern Island (approximately 200 burrows were identified as apparently active during this study), the total population size estimates based on the ground-count methods and from modelling should be similar.

1.3 RESULTS

Apart from marking and mapping burrows and nesting colonies on Eastern Island, research was solely conducted on Sand Island. Population size estimates were calculated for Bonin Petrels nesting on Sand Island only because burrow density and occupancy studies were not undertaken on Eastern Island (Figure 1.4).

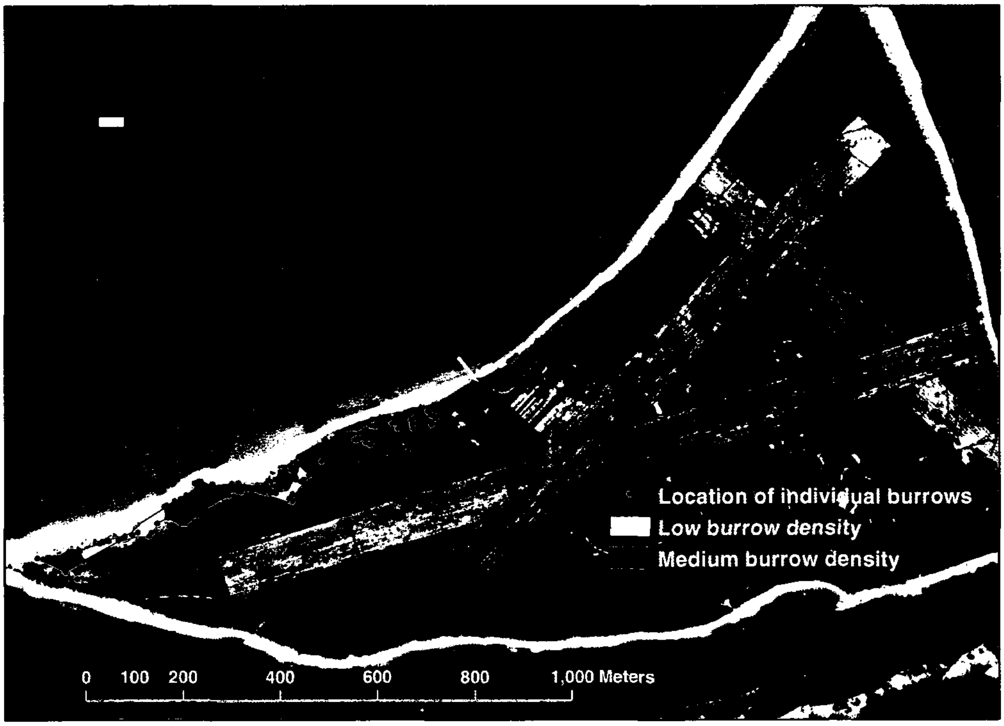

Figure 1.4: Bonin Petrel individual burrows (black dots) and low and medium burrow density nesting areas (polygons), Eastern Island, Midway Atoll (2008). Source: DigitalGlobe, QuickBird, October 2005.

1.3.1 Nesting Area

Results from colonial mapping indicate that a total of 1,538,070 m^2 (154 ha) was occupied by nesting Bonin Petrels on Sand Island within the combined low, medium, and high burrow densities accounting for 31% (467,087 m^2; 46.71 ha), 32% (497,243 m^2; 49.72 ha) and 37% (573,741 m^2; 57.37 ha) of the total area respectively (Figure 1.5).

Figure 1.5: Bonin Petrel nesting areas classified into low, medium, and high burrow densities, Sand Island, Midway Atoll (2008). Source: DigitalGlobe, QuickBird, October 2005.

1.3.2 Burrow Density and Occupancy

A total of 402 (100 m^2) density plots were surveyed. The mean number of apparently active burrows in low, medium, and high density areas as originally mapped were 5.65/100 m^2 (range 0-26, SD 4.97), 11.07/100 m^2 (range 1-33, SD 6.81) and 24.63/100 m^2 (range 3-72, SD 13.69) respectively.

A total of 895 apparently active burrows were burrowscoped, 789 successfully, equating to an 88% success rate. Some burrows could not be scoped because either the camera could not be manipulated around roots or sharp turns, or was not long enough to reach the end of the burrows, which on average are 1.5 m long (Seto 1994), but can be up to 3 m in length (Seto and O'Daniel 1999). Occupancy was similar in all three density categories (Figure 1.6), but was lower with increasing burrow density. Island-wide mean burrow density was 13.78/100 m^2, and occupancy was 62.26%.

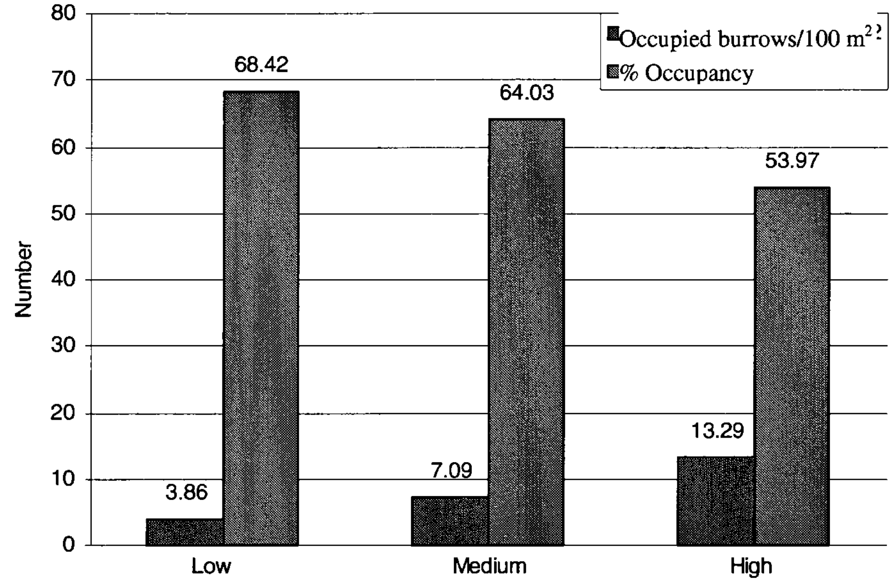

Figure 1.6: The mean number of Bonin Petrels nesting per plot (100 m^2) and occupancy in low (recorded and scoped n = 209), medium (recorded and scoped n = 278), and high (recorded and scoped n = 302) density nesting colonies, Sand Island, Midway Atoll (2008).

1.3.3 Breeding Population Size Estimate: CTBS Method

An estimate of 129,733 breeding pairs was derived from summation of the products of burrow density and occupancy calculated independently in low, medium, and high burrow density nesting areas (Table 1.1).

Table 1.1: CTBS breeding population size estimate for Sand Island, Midway Atoll (2008).

Breeding pairs (CTBS)	95% CI Burrow density	95% CI Occupancy	95% CI Burrow density range	95% CI Occupancy range
129,733	+/-4,516	+/- 9,634	125,216-134,249	120,099-139,367

1.3.4 Breeding Population Size Estimate: Traditional Method

A comparative estimate of 131,954 breeding pairs was derived from the products of mean burrow density, occupancy and total nesting area (Table 1.2). The range of the population size estimate was considerably larger using traditional methods compared to using the CTBS method.

Table 1.2: Traditional breeding population size estimate for Sand Island, Midway Atoll (2008).

Breeding pairs (Mean)	95% CI Burrow density	95% CI Occupancy	95% CI Burrow density range	95% CI Occupancy range
134,954	+/-7,969	+/-15,940	123,985-139,923	116,013-147,894

1.3.5 Total Population Estimate: Capture-Recapture

During the 21 mistnetting sessions, a total of 661 Bonin Petrels were captured, 638 where the cloaca and brood patch were recorded. The mean recapture rate was 5.6%, with 37 birds recaptured. The proportion of recaptures was approximately 3%, 6% and 7% in low, medium, and high burrow density nesting colonies respectively. All recaptured birds from 2008 had originally been banded at the same site.

In addition, there were two recaptured individuals that had originally been banded on Midway in 1996, and one from 1997. Three more recaptures were recorded. The U.S. Bird Banding Laboratory records indicate that two of these individuals, whose bands were recorded during this study, were still in the possession of an unidentified bird bander. The other was incorrectly identified in their records as a Brown Noddy, *Anous stolidus*. Although the recaptured birds had their bands read twice in the field, it is possible that they were recorded incorrectly. Investigation into the origin of banding of these three birds is still underway. If all of these recaptured birds were originally banded on Midway, greater support for using closed-capture models to estimate their total population size would be provided.

The number of breeding females that met the combined measures (cloaca was >10 mm and the brood patch categorized as 0-1) and were not carrying eggs, but presumed to have already laid, was 62. Nineteen other females were carrying eggs, and of these, three did not meet the combined measures criteria (Table 1.3). Thus, the number of breeding females determined using cloaca size and brood patch categorization was increased an additional 15.79%.

Table 1.3: The cloacal measurements and brood patch categorizations of female Bonin Petrels captured during mistnetting that were found carrying eggs, Sand Island, Midway Atoll (2008).

Date female captured carrying an egg	Location	Band #	Cloaca (mm)	Brood patch
04-Feb-08	H1	1483-63617	11.98	1
04-Feb-08	H1	1483-63632	10.66	1
05-Feb-08	M1	1483-63673	14.18	**2**
05-Feb-08	M1	1483-63676	14.08	1
05-Feb-08	M1	1483-63681	10.46	1
05-Feb-08	M1	1483-63684	12.91	0
05-Feb-08	M1	1483-63690	**9.05**	1
07-Feb-08	H2	1483-63743	12.28	0
07-Feb-08	H2	1483-63756	10.84	0
08-Feb-08	M2	1483-63761	10.07	1
08-Feb-08	M2	1483-63765	12.47	1
12-Feb-08	L1	1483-63794	**9.21**	1
12-Feb-08	L1	1483-63816	12.65	0
12-Feb-08	L1	1483-63818	11.77	0
13-Feb-08	H1	1483-63831	12.24	0
15-Feb-08	M1	1483-63851	12.33	0
15-Feb-08	M1	1483-63853	12.91	1
17-Feb-08	L2	1483-63885	11.96	0
24-Feb-08	M1	1483-83037	10.62	0

The total number of breeding females was then doubled to account for their mate, and in low, medium, and high burrow density colonies, represented 17.15%, 45.44%, and

26.26% of the total breeding population respectively. Cloacas measured during this capture study ranged from 4.41 mm to 14.18 mm. The proportion of Bonin Petrels exhibiting the six conspicuous stages of brood patch development was calculated for each of the burrow density categories (Figure 1.7).

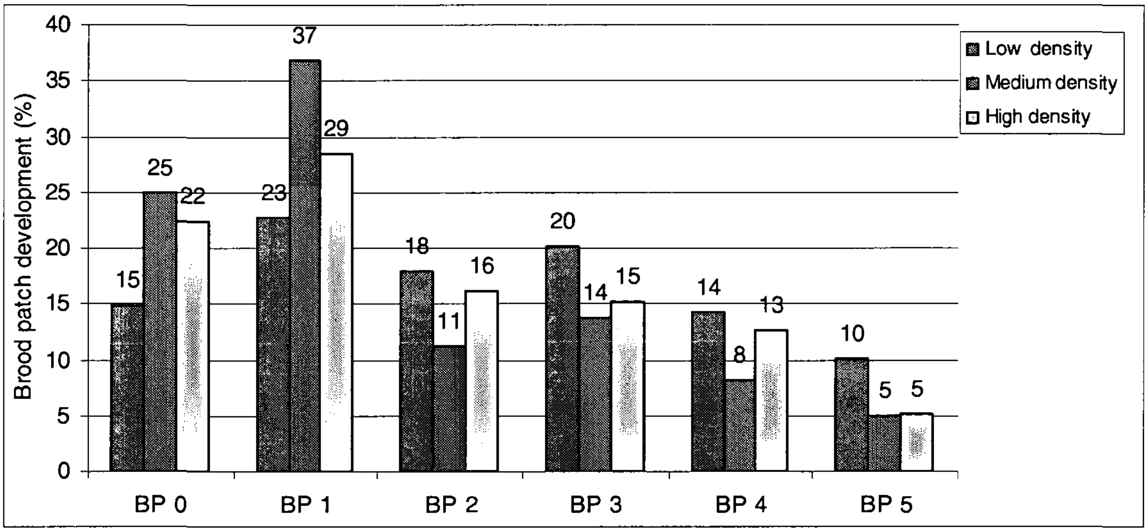

Figure 1.7: The proportionate development of brood patches of Bonin Petrels captured during mistnetting in low, medium, and high burrow density colonies, Sand Island, Midway Atoll (2008).

Two total population size estimates were derived assuming the proportion of breeding birds from this mistnetting study were equal to the number (or proportion) of breeding individuals calculated using both the CTBS and traditional ground-count methods. The remaining proportion of mistnet captured individuals were assumed to be non-breeding birds, and these two values (breeding and non-breeding individuals) were summed to provide total population size estimates unique to the CTBS and traditional methods.

In effect, using the estimates from the three density categories from the CTBS method, three separate non-breeding population estimates were produced for the low, medium, and high burrow density categories. The number of non-breeding individuals was calculated based on the proportion of captured birds not exhibiting breeding characteristics, and is directly correlated to the number (and proportion) of breeding birds calculated using the CTBS. The second total population estimate was similarly achieved, but used the breeding estimate derived using traditional methods. The non-breeding estimate was derived, as above, from the proportion of non-breeding individuals captured during mistnetting.

The total population size based on the CTBS estimate was 947,081 individuals. The percentages of non-breeding birds captured in low, medium, and high burrow density netting areas were 83% (comprising approximately 22% of the total population), 55% (comprising approximately 17% of the total population), and 74% (comprising approximately 61% of the total population) respectively (Figure 1.8). The total population size estimate using the traditional method was 876,059 individuals.

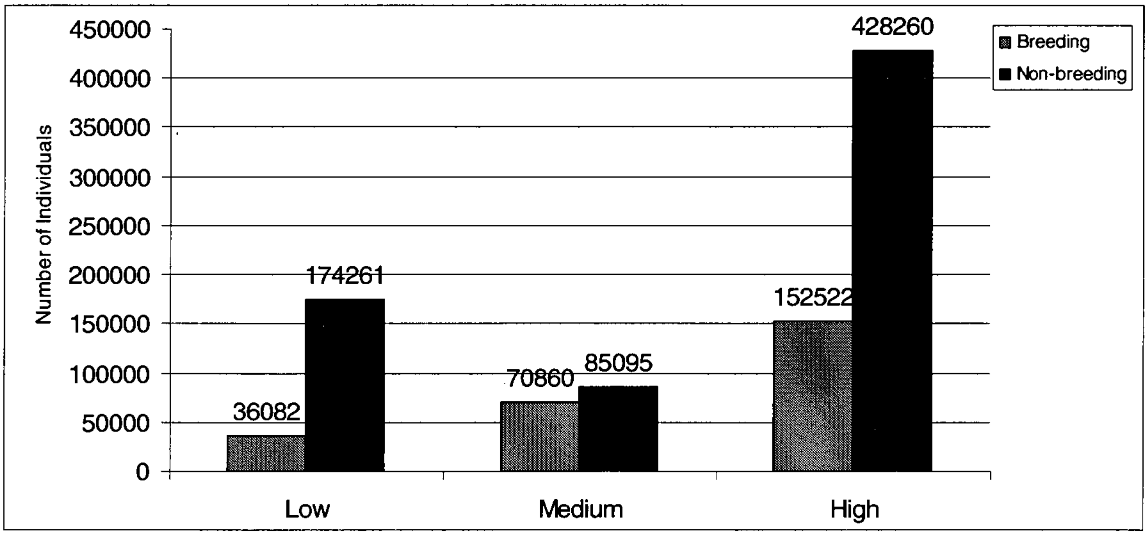

Figure 1.8: Bonin Petrel breeding and non-breeding individuals in low (22%), medium (17%) and high (61%) burrow density colonies calculated using the CTBS, Sand Island, Midway Atoll (2008).

1.4 A REVIEW OF BONIN PETREL DATA COLLECTED BY, OR IN COLLABORATION WITH THE USFWS

1.4.1 Cloacal Size of Bonin Petrels

Cloacal measurements that were taken using digital callipers by USFWS staff in 1998 (by the author) and 1999 from Bonin Petrels breeding within artificial nestboxes (originally constructed and set into the ground on Sand Island by Seto; Seto 1994) were evaluated using paired t-tests, and provides further evidence that the cloacae of breeding females is larger than those of their male partners.

In 1998, 10 pairs had their cloacae measured, and in 1999, 24 pairs were breeding in the artificial boxes and also had their cloacae measured. In 1998, I identified the male and female in each pair, and recorded their band number and cloaca size. In 1999, a sex-based distinction between nesting birds was not documented, so it was assumed that the individual with the larger cloaca was the female, consistent with findings from other studies where breeding female petrels are known to have enlarged cloacae when compared with males (Serventy 1956; Boersma and Davies 1987; Copestake et al. 1987; Warham 1990; Seto 1994; Seto 1995; O'Dwyer et al. 2006). In 1998, the mean size of female and male cloacae were 11.1 mm (SD ± 2.0) and 7.6 mm (SD ± 0.91) respectively, and were significantly different (two-tailed paired t-test, $t = 4.23$, $P = 0.002$, $df = 9$; both datasets passed the D'Agostino and Pearson omnibus normality test). In 1999, the mean size of female and male cloacae were 11.6 mm (SD ± 1.35) and 7.8 mm (SD ± 0.81) respectively, and were also significantly different (two-tailed paired t-test, $t = 12.01$, $P<0.0001$, $df = 23$; both datasets passed the D'Agostino and Pearson omnibus normality test). Although the mean cloacae size of females in 1998 was greater than 10 mm, three of the 10 (30%) females had cloacae measuring less than 10 mm, and would not have been classified as a breeding bird in this study, unless they were found carrying an egg at the time of capture. In 1999, only two of the 24 (8%) females nesting in artificial boxes had cloacae measuring less than 10 mm. In 1999, one of these females had their cloacae re-measured and it had enlarged from 9.08 mm in 1998, to 11.8 mm in 1999. This particular individual re-nested in the same artificial nestbox, and mated with the same partner in both years.

Bonin Petrels nesting in artificial boxes numbered (by Seto) 1, 10, 14, 22, and 27 in 1998, all returned in 1999, mated with the same partner, and laid eggs. The mean cloacae size for these returning females increased from 10.9 mm (SD ± 1.59) to 12.3 mm (SD ± 1.06) in 1998 and 1999 respectively, and this difference is statistically significant (two-tailed paired t-test, $t = 2.86$, $P = 0.046$, $df = 4$). The mean cloacae size for returning males actually decreased from 7.7 mm (SD ± 0.89) to 7.5 mm (SD ± 0.92) during this same time period, but the difference was not statistically significant (two tailed paired t-test, $t = 0.52$, $P = 0.63$, $df = 4$). None of the males had cloacae larger than 10 mm.

1.4.2 Population, Burrow Density, Occupancy, and Age of First Breeding

As expected, the number of breeding Bonin Petrels on Sand Island has significantly increased following extirpation of rats from Midway Atoll. The breeding population has grown between 1994 (Seto 1995) and 2008, as has the total population (Figure 1.9). The percent of breeding birds is fairly similar between these two time periods (22.4%, 1994; 27.4%, 2008) and the area occupied by breeding Bonin Petrels has increased from approximately 280,813 m^2 (28.08 ha) in 1991 (Kirkpatric 1991) to 1,538,070 m^2 (153.81

ha) in 2008.

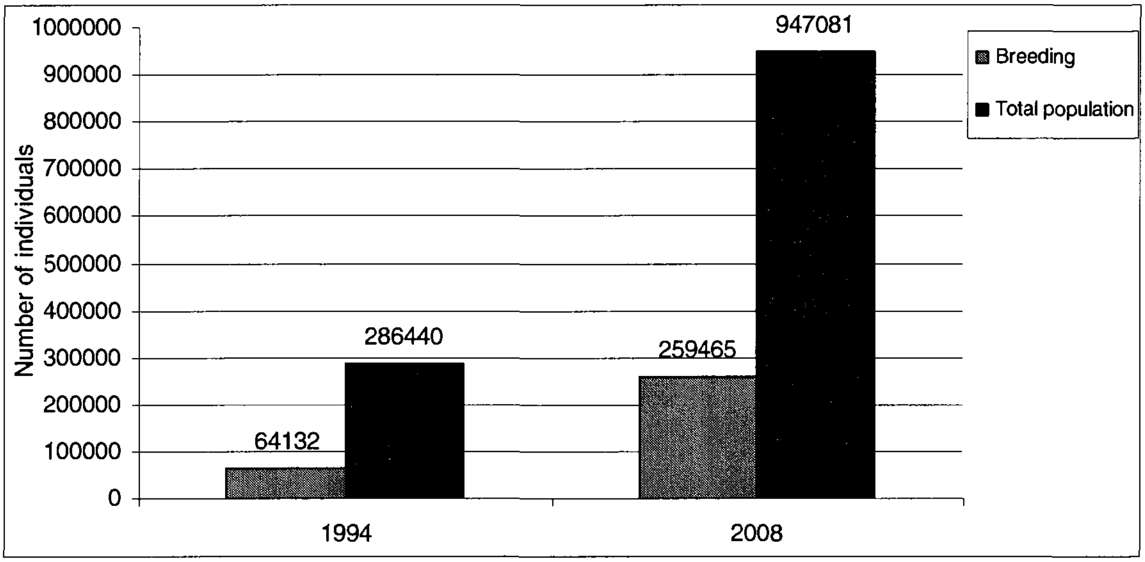

Figure 1.9: Comparison of the breeding and total population size of Bonin Petrels in 1994 and 2008 (CTBS), Sand Island, Midway Atoll.

However, mean burrow densities have declined from 21.20/100 m^2 (USFWS 1998) to 13.78/100 m^2 in 2008, as has the mean occupancy from 74.4% (USFWS 1998) to 62.3% in 2008. To draw conclusions on such declines is challenging, as results may have arisen from inconsistent study designs. In 2008, 402 monitoring plots (totalling 40,200 m^2) were randomly positioned within a variety of nesting habitats and densities throughout Sand Island, whereas in 1998, only 4 plots were monitored (totalling 3149.94 m^2), and it is unlikely that similarly representative nesting habitats and densities were sampled. Also, in the early 1990's, Bonin Petrels did not successfully breed where rats were present, but were successful in areas where rat populations were low, perhaps contributing to the higher densities and occupancies in these areas following the rats' eradication.

In addition, results from USFWS mistnetting efforts in 1999 indicate that Bonin Petrels are a minimum of four years of age prior to breeding. Two individuals were caught and found carrying an egg that had originally been banded as chicks in 1994 and 1995 (Table 1.4).

Table 1.4: Bonin Petrels originally banded as chicks, and subsequently recaptured and found carrying an egg during mistnetting by the USFWS in 1999.

Original band #	Original capture year & status	New band #	Re-capture date	Re-capture location	Cloaca (mm)	Brood patch
1313-78073	1994/chick	Not re-banded	28-Jan-99	AT&T (L1)	11.62	1
1403-15786	1995/chick	1483-27407	03-Feb-99	Chapel 2 (M2)	15.41	0

1.5 DISCUSSION

Prior to this study, population size data related to Bonin Petrels was sparse. Although this seabird was monitored on Midway Atoll to a limited extent in the 1990's, consistent methods to accurately assess abundance and reproductive success permitting longer-term comparisons had not been used. Where wildlife populations occupy limited breeding habitats and are vulnerable to predation, such as the Bonin Petrel, it is particularly important to have reliable information about their population size and the proportion of breeding individuals in order to monitor their population trends and predict its future growth capacity (Calvert and Robertson 2002). As witnessed on Midway, accidentally introduced rats caused a tremendous decline in the total population of Bonin Petrels.

The USFWS have recently improved their seabird conservation plans to include species such as Bonin Petrels; where data related to their population is poorly known, where considerable proportions of their population are found within U.S. management jurisdictions, and where they are particularly vulnerable to threats. Better understanding trends in the abundance of Bonin Petrels on Midway Atoll could serve as an indicator of changes in their distribution, and could also be indicative of other ecological changes occurring in surrounding areas. This research has provided population size data of Bonin Petrels on Midway Atoll, and additional insight of how to improve the accuracy of breeding population size estimates using a modified stratified and random ground-count censusing technique, the CTBS. The CTBS method is transferable to similarly nesting seabirds around the world.

1.5.1 Methods to Identify Breeding Females

Use of combined sex measures proportionately reduces the number of individuals that are classified as breeding, thereby affecting total population size estimates. It is therefore possible that the total population of Bonin Petrels has been overestimated proportionate to the number of breeding females misidentified as non-breeding if the cloaca measured <10 mm and/or the brood patch was identified as >1 and the female was not carrying an egg. However, results from this study indicate that non-breeding birds may develop brood-patches, which is not uncommon in Procellariforms (Dr. Ian Jones, Memorial University, NF pers. comm.). While the proportion of breeding individuals determined in low, medium, and high burrow density colonies using combined cloacal and brood patch measures (and multiplied by two to account for their mate) were 17%, 45% and 26% respectively, the proportion of individuals exhibiting significant feather loss (brood patch categories 0-2) were considerably higher 56%, 73%, and 67% respectively.

Results from the nestbox study in 1998 and 1999 suggest that the probability of misidentifying breeding females as non-breeding is likely very small if cloaca size is used to sex breeding females as presented in this study. Breeding female Bonin Petrels have larger cloacae than males, and they tend to enlarge over time. Cloacae of male Bonin Petrels do not enlarge over time and, from data collected in 1998 and 1999, are never larger than 10 mm. Misidentifying breeding females as non-breeding is therefore likely the highest for first-time breeders, and decreases with age and subsequent breeding efforts. Also, given that all five pairs of Bonin Petrels, where both the male and female birds had their leg band numbers recorded and cloacae re-measured, returned to the same nestboxes to breed in both 1998 and 1999, suggests 100% nest site and pair fidelity.

Another factor which may have contributed to an underestimate of the breeding population size, and consequently an overestimate of the total population size, is the inherently lengthy laying period for Bonin Petrels; which can last for more than six weeks. It is possible that the cloacae of some breeding females may not have been extended to >10 mm if either: they were not expected to lay for several weeks following capture, or had laid their egg several weeks prior to capture. However, it has been demonstrated that the cloaca of other species of female petrels become distended one month prior to laying, and can remain enlarged for up to 35 days (Serventy 1956; Warham 1990). Another, unpublished study of 2625 cloacal determinations of Westland Petrels (*Procellaria westlandica*), reported a 94% success rate with measurements collected within two months of laying (O'Dwyer et al. 2006). The cloaca of breeding female Wilson's storm-petrels (*Oceanites oceanicus*) can also be discriminated from males and non-breeding females for up to one month after laying (Copestake et al. 1987).

Thus, in future, it is suggested that breeding status is determined when an individual is captured and found carrying an egg, or based on cloacae size alone. While it has been shown that measuring cloacae is repeatable to within 0.1 mm for storm-petrels (Boersma and Davies 1987; Samuelsen et al. 2006), digital callipers are sensitive and Bonin Petrel cloacae are also small, so care should be taken when measuring. If brood patch measures are excluded from evaluation, the number of breeding females is adjusted by 10.53%, since two of nineteen individuals captured were found carrying an egg yet their cloacae was < 10 mm. The resultant CTBS total population size estimate is 907,176 individuals.

1.5.2 Advantages of the CTBS

Albeit similarly time-demanding and laborious compared with traditional approaches used to estimate breeding populations of burrow nesting seabirds, this study provides evidence of several advantages in using this new method, the CTBS. Results indicate that 95% confidence limits are considerably narrower, density specific nesting areas are accurately and proportionately mapped and defined, and habitat data can be overlaid onto the density map allowing statistical interpretation of burrow densities and occupancies specific to habitat type, slope, aspect etc.. Alternatively, land cover maps can be superimposed onto the density layer map and be similarly evaluated (Chapter 3). Finally, because sample plots are randomly selected within known nesting areas, little time is spent travelling to or setting up plots in areas where there are no burrows, a common issue when using traditional, systematic methods whereby monitoring for the presence/absence of burrows can be used to locate colonial boundaries themselves (Walsh et al. 1995).

The CTBS provides independent breeding and total population size estimates specific to the areas encompassed by conspicuously different nesting densities, while also providing excellent spatial representation of nesting patterns. Both the CTBS and traditional survey methods likely produce somewhat conservative estimates because occupancy surveys were undertaken mid-incubation and some eggs may have been lost and not identified during scoping, and areas where approximately ten or fewer burrows were found scattered over proportionately large areas, or bounded by impermeable surfaces/structures were discounted.

In this study, two total population size estimates were derived for Sand Island based on the CTBS, one where both brood patch and cloaca size were used to sex breeding females, 947,081 individuals, and the other using cloaca size alone, 907,176 individuals. Another estimate was produced using the same data, but using the mean burrow density and occupancy obtained from random plot sampling, the traditional approach, 876,059 individuals. Since non-breeding Bonin Petrels may develop brood patches, and results from this study indicate that cloaca size alone can be used to distinguish breeding females from males and non-breeding birds, the CTBS result of 907, 176 individuals will be used for comparative purposes to estimates using closed population modelling and Program MARK (Chapter 2).

Using a similar approach and data collected in 1994 by Seto (Seto 1994), derivation of the total population size from 1611 captured individuals based on the proportions of breeding and non-breeding individuals, the total population size estimate ranged from 286,440 to 304,796 individuals (CTBS-traditional). Medium burrow density colonies contributed disproportionately few individuals to the population size in both 2008 (17%) and 1994 (13%). Interestingly, the contributing proportion of breeding individuals to the total population increased from 22.39% in 1994 (USFWS) to 27.4% in 2008 suggesting that the individual replacement rate has declined slightly. Both burrow density and occupancy have declined between 1998 and 2008. It is possible this study provides some insight into the preferred breeding density and occupancy levels of Bonin Petrels on Sand Island in light of the fact rats have not influenced nesting patterns for over 10 years. Further inference regarding contributing proportions between these years is not possible without understanding the unquestionable dynamics between rat densities and proximity to monitoring plots and netting sites in 1994.

1.5.3 Egg Laying Period

The last known published egg-laying date for Bonin Petrels was 11 February in 1981 (Grant et al. 1983), and 2 February in 1993 and 1994 (Seto 1994). Results from this study indicate that either the laying period has extended, or may be starting later in January since 42% (n = 8/19) of females carrying an egg were captured after 11 February, and the final female captured with an egg was 24 February 2008 (Table 1.3). This pattern could possibly be related to changes in the marine environment and linked to prey availability (Furness 1978; Cairns 1987; Montevecchi et al. 1988; Monaghan et al. 1989; Bost and LeMaho 1993; Penteriani et al. 2002; Rejt 2003). Also, younger individuals tend to lay eggs later in the breeding season (De Forest and Gaston 1996; Laaksonen et al. 2002; and Gonzalez-Solis et al. 2004). At present, there are suspected to be more young individuals comprising Midway's Bonin Petrel population than when rats were present. It is therefore possible this younger contributing portion was captured during netting, and may be linked to inherent behaviours making them more prone to capture than older birds. In addition, Seto stopped mistnetting birds on 18 February in 2004, so laying data past such time is not available. Although Seto monitored approximately 119 active burrows throughout the Bonin Petrel breeding cycle in 1994, it is possible that the sample size was too small to capture females laying eggs later in the season. Thus, the sample size and robustness of previous studies may not have been adequate, or lasted long enough to capture the latest breeders.

CHAPTER 2. ESTMATING THE TOTAL POPULATION SIZE OF BONIN PETRELS USING CLOSED POPULATION CAPTURE-RECAPTURE AND MODELLING, SAND ISLAND, MIDWAY ATOLL

2.1 ESTIMATING ABUNDANCE USING CAPTURE-RECAPTURE AND MODELLING: GENERAL INTRODUCTION

Currently, there is no widely adopted method to estimate the total population size of Bonin Petrels (*Pterodroma hypoleuca*) or similarly nesting species. The purpose of this investigation was to establish whether results from a capture-recapture (CR) study and statistical modelling using closed population models in Program MARK (Version 6, Build 6001) (White and Burnham 1999), provide both precise and accurate total population size estimates. To evaluate the precision and accuracy of modeled estimates, the total population size estimate derived from the CTBS ground-count of 907, 176 individuals was used. It would be advantageous to use CR and modelling for similarly nesting seabirds worldwide because these methods can be significantly more cost and labour efficient, and are potentially less harmful to the study species than using ground-count studies for estimating population size. Capturing birds can be done at colony peripheries, thereby eliminating the need to access main colony areas, thus decreasing the habitat destruction that would normally result from burrow censuses (Seto 1995). Long-term banding studies would also provide data on annual recruitment, differential survivorship, lifetime reproductive performance (Seto and O'Daniel 1999), the laying period, and the proportion of breeding to non-breeding individuals allowing insight into population dynamics (e.g., whether the population is likely increasing or declining). In this study, the laying period of Bonin Petrels on Midway Atoll appears to have extended by approximately two weeks (13 days) from earlier published data (Grant et al. 1983;

Seto 1994). However, the sample size and robustness of previous studies may not have been adequate, or lasted long enough to capture the latest breeders.

Ground-count censuses simply provide an estimate of the breeding population size. Therefore, some type of capture study is required to identify the proportions of breeding and non-breeding individuals in order to derive a total population size estimate. Since capture data must be collected to produce estimates of total abundance for burrow and crevice-nesting seabirds anyhow, evaluating the performance of modeled estimates is sensible. Furthermore, total population size estimates based on the proportions of breeding and non-breeding individuals and the ground-count breeding estimate are only specific to the area encompassed by the ground-count. In this study, the total population size estimates based on the ground-count methods only relate to Sand Island, whereas modelled estimates relate to the total population size for the entire Atoll. However, since very few Bonin Petrels (approximately 200 breeding pairs) were found on Eastern Island, and just five breeding pairs are believed to use Spit Island (USFWS pers. comm.), this ground-count based total population size estimate is comparable to the modeled estimates. Considering the on-going statistical advancements of models to produce more precise estimates of abundance by appropriately representing the heterogeneities in the behaviour of wildlife populations, and the growing interest in modelling by wildlife managers where budgets to monitor populations can be restrictive, such efforts are increasingly worthwhile.

Deriving the most accurate estimates of breeding and non-breeding individuals from the ground-count was important, because the ultimate goal was to evaluate the usefulness of estimates produced from modelling. Using modern statistical models to estimate the total population size of burrow-nesting species has received little attention, with few published studies available for reference (Calvert and Robertson 2002). Possible explanations could include: the difficulty of producing accurate estimates with which to compare to model results; models are statistically complex, especially those which account for individual heterogeneity while producing estimates of abundance, so the process of model building and interpreting results can be challenging; and the effort to undertake both ground-count and modelling studies requires significant resources. In addition, models that produce estimates of abundance for closed populations which incorporate individual specific covariates, such as behaviours that lead to unequal capture probabilities, have not been implemented in widely available software such as Programs MARK and CAPTURE.

2.1.1 An Earlier Capture-Recapture Study of Bonin Petrels

In 1995, Seto used modelling based on the results from a CR study of 1611 Bonin Petrels to estimate their total population size on Sand Island, Midway Atoll. Seto used Bailey's modification of the LPI, where $N = r(n+1)/m+1$; and N = total population, r = total number of banded birds, n = total number of captured birds, and m = total number of banded birds at risk of recapture. Seto compared the results from modelling to estimates that were produced from a ground-count. The total population size was derived based on the proportions of breeding and non-breeding birds captured and sexed using combined sex measures of cloacal and brood patch development. Seto found that modeled estimates using the LPI severely underestimated the total population size and concluded that one of the underlying assumptions of this model, that birds captured are a random sample of the population and that each banded individual has an equal chance of recapture, had been violated. Seto suggested that, in future, nets be positioned in more than one location to try and increase the probability that both breeding and non-breeding individuals would have the same likelihood of capture (Seto 1995).

By setting up two mistnets in close proximity to one another and within each nesting classification (low, medium, and high burrow density), this study has, in part, increased the probability of equal catchability for all individuals, regardless of breeding status. In addition, the observed capture histories are more likely representative of a greater cross-section of individuals, and hence behaviours. Coupled with the availability of modern closed population capture-recapture models, which account for unique behavioural responses, time effects, group heterogeneities, and where estimates of abundance (*N*) are possible, the total population size estimates produced in this study should be less biased than those calculated by Seto in 1995. Significant and on-going advancement in model properties and continued methodological testing using common CR case studies has helped to validate their robustness, precision, and accuracy in estimating total population size.

2.1.2 Closed vs. Open Population Modelling and Model Assumptions

Estimates of abundance are possible using either closed or open population models. These classes of models are based on product multinomial distributions and are nearly always estimated using maximum likelihood (Burnham and Anderson 2002). The methods of maximum likelihood were first developed by R. A. Fisher in the early 1900's (Amstrup et al. 2005). Lee and Su (2006) offer the following guidance when determining if closed or open population models should be used. "A closed model is usually valid for data collected in a short-term investigation and assumes that there are no additions (birth or immigration) or losses (death or emigration), and the population size remains constant during the study period. An open model, often used for long-term investigations, allows for additions or losses so that population size varies over time throughout the experiment".

The issue of using closed vs. open population models and their associated model assumptions are particularly noteworthy because the derived estimates of abundance can be significantly different depending on which type is used. While there are commonly used closure tests (Otis et al. 1978; Rextad and Burnham 1991; Stanley and Burnham 1999), these tests are sensitive to behavioural and temporal variation in capture probabilities (Williams et al. 2002) and therefore were not used. Also, there is no behavioural data for this species to identify how breeding and non-breeding Bonin Petrels use Midway Atoll and surrounding environments. However, because sampling was conducted in a relatively short time period (< 1 month), population fluctuation caused from death/emigration and immigration to the sampled population was deemed relatively insignificant. Also, Midway is geographically isolated from other islands where Bonin Petrels breed, and considering their colonial/social behaviours, it is unlikely that a considerable number of individuals would have been present and captured on Midway during this study period, only to leave (permanently) to another locale. So, although there may be some statistical support for estimating abundance using open population models, there is more support for estimating their population using closed population models.

The central relevant closed population model assumption is that each bird has an equal chance of capture and recapture. While there is no published data to support behavioural differences between breeding and non-breeding Bonin Petrels, it is to be expected that both of these groups use Sand Island to varying degrees during the breeding cycle. For example, non-breeding birds are not as likely to consistently return to the same area as breeding individuals. The non-breeding portion of the population may return, but less frequently, to prospect for a potential burrow site and mate, while the breeding birds consistently return to incubate their egg. Conversely, the incubating breeders may not be at equal risk of capture because incubation periods vary. Hence, the capture probabilities both among and between breeding and non-breeding individuals is different. Fortunately, modern closed population models have been developed that relax the assumption of equal catchability thereby minimizing the bias of derived estimates.

2.2 METHODS

2.2.1 Software to Estimate Abundance Using Closed Population Capture-Recapture Models

Presently, there are two widely available, free, computer programs that include statistical models designed to estimate abundance of closed populations from multi-session capture-recapture techniques; Program MARK and CAPTURE. Program MARK (http://welcome.warnercnr.colostate.edu/~gwhite/mark/ mark.htm) uses numerical maximum likelihood techniques to compute estimates of model parameters (e.g., capture, recapture, survival probabilities, and abundance etc.). The number of estimable parameters is used to compute the quasi-likelihood AICc value for the model. Akaike (1974) proposed the information criterion AIC under the assumptions that: (i) a specified parametric family of probability distributions encompasses the true model, and (ii) a model is estimated by the maximum likelihood method (Ando 2007). The divergence of the fitted model from the true model is measured by the Kullback-Leibler (K-L) information, or equivalently by an expected log likelihood $\log f\,(z|\,\hat{\theta})dG(z)$, where $\hat{\theta}$ is the maximum likelihood estimator (Ando 2007). AIC is fundamental to the model selection process and is based on the relationship between the relative expected K-L distance and the maximized log-likelihood (Burnham and Anderson 2002).

Closed population capture-recapture models have been developed to relax the assumption of equal catchability and they consider three sources of variations: time effects, behavioural response, and individual heterogeneity (Amstrup et al. 2005). Time effects refer to environmental variabilities such as temperature, rainfall, and humidity which can influence capturability between netting events. Behavioural responses are those associated with trap shyness, or the avoidance of mistnets, and may not be an attribute of the individual, but of the study configuration (White 2008). Individual heterogeneity can be due both to observable or unobservable inherent factors such as age, breeding status, sex and incubation patterns. More sophisticated models can be fitted that both estimate total population size and provide insight into the capture process by incorporating covariates (Amstrup et al. 2005), such as those more recently developed by Pledger (2000) which have been used in this study.

Program MARK was selected because it includes all of the closed population likelihood models in CAPTURE, and includes additional models that allow comparisons between groups, and the incorporation of time-specific and/or group-specific covariates. Models developed by Pledger (2000) which use mixtures of p values (probability of capture) to model individual (by group) heterogeneity are also unique to MARK. These models are particularly useful for this study because they allow consideration of the different capture probabilities between breeding and non-breeding groups. At present, closed population capture-recapture models in Program MARK can only model p

(capture) and *c* (recapture) probabilities by attribute groups (i.e., breeding vs. non-breeding, incubating vs. non-incubating, males vs. females etc.), as a function of time, but not as a function of individual-specific covariates. This is the main limitation of MARK, since this type of model which allows for individual as opposed to group-specific covariates, such as unequal capture probabilities, have not been implemented (White and Burnham 1999). These types of models may produce more accurate estimates of abundance.

Program CAPTURE can also be run through MARK. One particularly useful tool within CAPTURE is the "appropriate model" function which uses the capture histories to provide an estimate of abundance (excluding model M_{tbh}) once the most appropriate generating model has been identified. This provided both a secondary method to confirm whether candidate models using Program MARK provided reasonable estimates of abundance, and also provided an alternate means to select candidate models based on the support reported when CAPTURE is run (refer to Results). Closed population capture-recpature models are also available in CAPTURE that are not based on maximum likelihood, but are based on other statistical methods, such as the jackknife, which have also received widespread support from wildlife biologists.

2.2.2 Closed Population Capture-Recapture Models and Program MARK

Program MARK supports twelve different closed population capture-recapture models with different data types classified within a hierarchy of dichotomous divisions (Cooch and White 2008), six of which are used in this study to estimate abundance. The remaining six data types consider situations where individuals can inadvertently be misidentified. These models were not appropriate for this study because birds were permanently marked using leg bands, and it was unlikely that any birds were misidentified.

The most obvious split between the six chosen data types are between models that estimate abundance (*N*) in the likelihood (Otis et al. 1978) and those with abundance conditioned out of the likelihood (Huggins 1989). Models where *N* is conditioned out of the likelihood are not compatible using AIC selection methods to those that estimate abundance in the likelihood, and need to be modeled separately. The other differences result from constraints on different parameters (i.e., capture/recapture). Estimates of survival are not computed because closed population capture-recapture data assumes that survival is equal to one during the short period of study.

2.2.3 Parameter Estimates and Program MARK

Parameter estimates are obtained using statistical methods of maximum likelihood. This method of estimation provides the "most likely" parameter value given the observed data thereby linking the data, unknown model parameters, and assumptions, which subsequently allows for rigorous, statistical inference (White et al. 2006). Program MARK computes the log (likelihood) based on the encounter histories:

Log (likelihood) =

$$\sum_{1}^{\text{No.Unique Enc.Hist.}} \text{log[Pr(Observing this Encounter History)] x No. Of Animals with this Encounter History}$$

(White and Burnham 1999)

The input data for Program MARK are the encounter histories from CR studies. Files (.inp) are created with 0 representing "not encountered", following original capture and marking, and 1 representing "recaptured". From these files, the log-likelihood is built for each animal because of the structure of the multinomial distribution (White et al. 2006). White et al. (2006), describe the process of parameter estimation and the strategy used in Program MARK:

"Because of the properties of the log-likelihood function derived from the multinomial distribution, the log-likelihood for all the animals is proportional to the sum of the numbers of animals with a specific encounter history times the log of the probability of that encounter history. For k encounter histories of those first captured in period 2, each with n animals observed with that history, the symbolic log-likelihood is

$$\log L\,(\Phi_2, p_3, \Phi_3, p_4, \Phi_4,\ p_5\,|\,n_i, Xi,\ i = 1, \ldots, k)$$

$$\infty \sum_{i=1}^{1} n_i \log[\Pr(Xi)],$$ (Cooch and White 2008)

the log of the likelihood of the parameters $\Phi_2, p_3, \Phi_3, p_4, \Phi_4,$ and p_5, given n_i animals with encounter history Xi for the k observed encounter histories, is proportional to the sum of the encounter history frequency times the log of the probability of this history for all k encounter histories. The strategy used in Program MARK to obtain the estimates of the unknown parameters ($\Phi_2, p_3, \Phi_3, p_4, \Phi_4,$ and p_5) is to numerically maximize the log-likelihood function by adjusting the values of the unknown parameters until the log-likelihood reaches a maximum (i.e. no matter how the parameters change, a value of the log-likelihood cannot be obtained that is greater than the current maximum)".

2.2.4 Parameter Index Matrices and Design Matrices

Fortunately, building models to manipulate parameter indices is relatively easy using the parameter index matrices (PIMs) in Program MARK. For example, capture and recapture probabilities can be equated so that a single estimate is used by changing the PIMs where p (capture probability) = c (recapture probability). This is particularly important where p and c are modeled as functions of one another in closed population capture-recapture models. For example, capture probabilities may be allowed to vary through time, but in changing $p = c$ in the PIMs, the recapture probability is constrained to this same probability which makes intuitive sense. The concept of a PIM derives from the program SURGE (Lebreton et al. 1992; Pradel and Lebreton 1993), with graphical manipulation of the PIM first demonstrated by Program SURPH (Smith et al. 1994; White and Burnham 1999).

PIM's must be constructed prior to the design matrix. The concept of a design matrix comes from general linear models (GLM) (McCullagh and Nelder 1989) and for use with capture-recapture studies from Program SURGE (Pradel and Lebreton 1993; White and Burnham 1999). The design matrix ($\underline{X}$) is multiplied by the parameter vector ($\underline{\beta}$) to produce the original parameters (i.e., p, c, and N etc.) via a link function (White and Burnham 1999). In essence, the design matrix function allows further manipulation of model structures so estimation of parameters can be functions of temporal and attribute group covariates. In this study, for example, models were built using the design matrix so that capture and recapture probabilities were allowed to vary through time, but constrained to be different by an additive constant on the logit scale. More complex models were subsequently constructed representing capture probability varying through time with additive differences between mixture groups which represent the two covariates/groups, breeding and non-breeding individuals. Behavioural responses were also added to these models using the design matrix, and in doing so, models were developed allowing for time variation, behavioural variation and individual variation in capture probability between breeding and non-breeding groups.

2.2.5 *Model Selection*

Goodness of fit testing for closed population capture-recapture MLE models is not currently possible within program MARK. This is because there is no unique way to compute a saturated model (where the number of parameters equals the number of data points so the fit of the model is effectively ‘perfect’), and with models incorporating heterogeneity, there is an infinite set of possible models (Cooch and White 2008). To overcome this problem of model fitting, several other methods are available using the numeric outputs generated for each model using Program MARK.

Candidate models, or the best approximating models, were selected, in part, based on Akaike’s information criterion (reported as AICc) where those ranked highest, or closest to 1, were assumed to be the most appropriate. When $\hat{c}$ is equal to 1, MARK uses AICc for model selection:

$$\mathrm{AICc} = -2\log(L(\hat{\beta}) + \frac{2K(K+1)}{n-K-1}$$ (Burnham and Anderson 1998)

where $\log(L(\hat{\beta})$ is the log of the likelihood of the parameters (β) given the data, K is the number of parameters estimated, and n is the finite sample size. $\hat{c}$ is used as a measure of lack of model fit caused by extra binomial variation where values of 1 or less represent models that appropriately fit the data and values > 2 (over dispersion) indicating that the model may not appropriately fit the data.

$\hat{c} = \chi 2/\mathrm{df}$ (Cooch and White 2008)

where the difference in fit (deviance) between the saturated model and any model is asymptotically $\chi 2$ distributed. In Program MARK, the deviance is defined as the difference in $-2 \log(L)$ of the current model and the saturated model. However, a known and reported problem of Program MARK is that the deviance for the closed captures model divided by its degrees of freedom is not a valid estimate of ĉ. This problem likely exists because closed population capture-recapture models are not in the exponential family, and this type of estimate of ĉ is only valid for models in the exponential family (refer to the Program MARK homepage http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm). Although ĉ can be adjusted within MARK to act as a variance inflation factor to correct the estimates of sampling variances and covariances (White et al. 1999), given the above and following communication with Gary White (who developed Program MARK), ĉ was not adjusted, but kept equal to 1. Fortunately, the actual estimates of *N* often remain unbiased in the presence of over-dispersion (McCullagh and Nelder 1989). Where ĉ < 1, it is generally suggested to use a value of 1 and not make any adjustments, and accordingly, ĉ was always kept equal to 1, regardless of its value.

The normalized Akaike weights (AICc weight) provide an index of 'relative plausibility' (likelihood) for each model (Cooch and White 2008). Dividing the weight assigned to the top ranked or candidate model by the approximating model provides an indication of model support. For example, if the weight of the candidate model is 0.56 and the next approximating model is 0.33, then the candidate model is supported 1.7

times (0.56/0.33) more than the approximating model. This feature is particularly useful because the relative importance of one parameter vs. another can be calculated using their weights. In this sense, the relative importance of time vs. the influences of heterogeneity can be determined from the weights produced when either time or heterogeneity is included in the model structure. These weights (w_i) are calculated for each approximating model (i) in the candidate model set as:

$$w_i = \exp \frac{(-\Delta AIC)}{(\ 2\ )} \div \sum \left\{ \exp \frac{(-\Delta AIC)}{(\ 2\ )} \right\} \qquad \text{(Cooch and White 2008)}$$

The ΔAICc values were also used to identify support between models. Burnham and Anderson (2002), as a general rule of thumb, suggest that where $\Delta AICc < 2$, both models have equal weight. Where $2 < \Delta AICc < 7$ there is considerable support for differences between models, and where $\Delta AICc > 7$ there is strong evidence that the higher ranked model is more appropriate given the input data/capture history.

Although actual estimates of *N* for these more complex models of Pledger (2000) are not available using CAPTURE, this program does still provide an alternate method of establishing model support, outside MARK, and provides a secondary system to confirm that models selected within MARK are most likely appropriate given the input data. This function was especially helpful in situations where the best approximating model(s) was derived using MARK's PIMs and design matrices, and were more complex to include group (covariate) differences in time, behaviour and heterogeneities. However, Stanley and Burnham (1998) reported that the existing model selection process in CAPTURE usually selects an inappropriate model in simulations, so model averaging was also used to account for model uncertainty and provide more stabilized inferences of *N* (Burnham and Anderson 2002).

2.2.6 Model Uncertainty

Model Averaging

Essentially, all models are wrong, but some are useful (Box and Draper 1987). This study aims to provide valid inferences about the total population size of Bonin Petrels on Midway Atoll from models that were selected because they most appropriately represented the data (the capture histories from a short-term capture-recapture study) and study species, by incorporating models which include group differences in behaviour between breeding and non-breeding individuals. Given there is no objective method to selecting a model from the various heterogeneous models (Amstrup et al. 2005), model averaging was used to overcome some of the uncertainty inherent in selecting candidate models. Once the best approximating models were selected, models were averaged, either within MARK where models were nested, or based on the same likelihood (Figure 2.1), or outside MARK if models were not based on the same likelihood. Averaging within Program MARK is advantageous because the outcome is a weighted estimate according to the assigned AICc weights given the dataset.

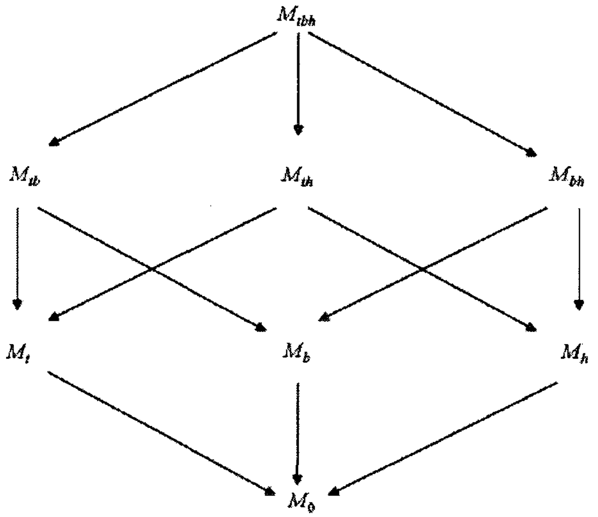

Figure 2.1: Models pointed to by arrows are nested in the above model. Source: White 2008.

Although the confidence intervals for models averaged within MARK are automatically generated, Cooch and White (2008) suggest calculating these by hand to avoid error (refer to Appendix B).

Study Design

Heterogeneity is omnipresent in animal populations (White and Anderson 2004). While capture probabilities differ between breeding individuals because of unique incubation patterns, the difference in capture probabilities between breeding and non-breeding individuals is likely even more significant. While it is unfortunate that models to include individual covariates are not presently available in Program MARK, models were selected to include two mixtures which represented breeding and non-breeding groups (covariates) in this study. To compensate for the inherent unequal capture probabilities of breeding individuals, where individual incubation periods vary, more than eight days were allowed to elapse between capture sessions at any given site. In addition, six capture locations were chosen, two in each of the low, medium, and high burrow density colonies to ensure that capture histories more likely represented the population than if only one site in each density area had been used.

The bias in *N* associated with model selection and associated with the assumption of equal capturability inherent in closed population capture-recapture models will have been effectively minimized by: stratifying the capture study, choosing two capture sites in each density area and pooling the data; allowing more than eight days to pass between capture events to increase the probability of recapturing an individual that was captured and subsequently began incubating; and selecting models that incorporated group heterogeneities and averaging the results of candidate models. However, severe heterogeneity in capture probabilities and/or very small capture probabilities will still result in an underestimation of abundance (Coull and Agretsi 1999; Hwang and Huggins 2005; Pledger 2005).

2.2.7 Model Building and Program MARK

Capture Histories and Data Pooling

In total, twenty-four models were built using the six data types for two combined capture histories, one for each of the medium and high burrow density areas where birds were captured using mistnets. A "combined capture history" dataset is derived from pooling the results from both of the mistnet sites which were positioned within each of three burrow density classifications. Because the Huggins models did not produce valid estimates of *N* for the medium and high combined history datasets, these twelve models were not used for any other datasets. The models of Huggins (1989) are useful in situations where the variation in capture probability among individuals is closely associated with easily measured covariates, such as sex, or size. However, since there are no obvious and measurable characteristics for individual Bonin Petrels which could be linked to their capturability, this information could not be incorporated into the Huggins models. Accordingly, just twelve models were constructed for the combined capture history in the low density area, and another twelve for both low density Sites 1 and 2 histories. Another twelve models were built for a combined dataset that included information from the first three capture session's at all six locations.

The capture history files were created based on the numbers of individuals captured and recaptured at each of the netting locations, where 1 denotes an individual was captured and recaptured, and 0 representing this individual was not recaptured during a particular netting session. The first three capture history files were created by pooling the data from the two sites located in each of the burrow density areas (low, medium, and high) to create more robust datasets. The two capture sites in the high burrow density area were each sampled four times, and the two sites in the medium density area were each sampled three times, so combining the data was straightforward. However, while Site 1 in the low burrow density area was sampled four times, Site 2 was sampled just three times. In order to pool the data, the last capture history (occasion) was dropped from Site 1, and unfortunately, this meant that two of the five recaptures were dropped resulting in a very low recapture rate (1.9%) for this combined dataset. To determine if derived estimates of N were appreciably affected by the reduced rate of recapture caused from data pooling, models were also constructed independently for both Sites 1 and 2 in the low density area where recapture rates were higher, 2.24% and 3.64% respectively. Recapture rates for the medium and high density sites were 5.1% and 7.47% respectively.

Model Notation and Link Functions

The theories and methods used in Program MARK including the model structures and/or references for these structures can be found at http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm. The results presented in this study include the notation developed by Otis et al. (1978) followed by an expanded description as follows:

M_0 $\{N, p(.) = c(.)\}$ which denotes constant p and c

M_t $\{N, p(t) = c(t)\}$ time varying p and c

M_b $\{N, p(.), c(.)\}$ behavioural response where $p \neq c$

M_h $\{N, p_a(.) = c_a(.), p_b(.) = c_b(.), \pi\}$ heterogeneous p where $p_a \neq p_b$

General models, M_0, models that were designed to incorporate time (M_t), behavioural (M_b) and heterogeneity effects (M_h) of capture probability, as well as combinations of these effects (i.e., M_{th}, M_{tb}, M_h, M_{tbh} etc.), were constructed. Some of these models were simply generated by running the six standard data types available using Program MARK, and some were custom built using the PIMs and design matrices (refer to Results and Appendix C). These custom models allowed p and c to be modeled as functions of one another and allowed variations in time, behaviour and heterogeneity in capture probability based on two mixtures which represented the breeding and non-breeding groups in this study (from the models of Pledger 2000).

Parameters were estimated using the default SIN link function when the six standard data types were used. Practically speaking, the SIN link can only be used where the (identity) design matrices have only a single '1' in any given column (monotonic relationships). In some instances, more than a single '1' was used to derive estimates where changes were made to the identity matrices to construct models M_{tb} (independent) $\{N, p(t) = c(t) + b\}$, M_{tbh} (mixture) $\{N, p_a(t), c_a(t) = p_b(t) + \mathrm{b}, c_b(t) + \mathrm{b}\}$ and M_{tbh} (full) $\{N, p_a(t) = c_a(t) + \mathrm{b} = p_b(t) + z = c_b(t) + z + b, \pi\}$, representing additive effects. In these situations, the logit link was used. From White and Burnham (1999) the SIN link is the best link function to enforce parameter values in the [0, 1] interval and yet obtain correct estimates of the number of parameters estimated, mainly because the parameter value does reflect around the interval boundary. In contrast, the logit link allows the parameter value to asymptotically approach the boundary, and is better for non-identity design matrices. Generally speaking, these link functions will provide slightly biased estimates of the mean value of N (White et al. 1999). However, standard errors of the estimates normally dominate so that these link-associated biases are normally ignored (White et al. 1999).

Models to Estimate Abundance

Firstly, the models of Otis et al. (1978) and Huggins (1989) called "Closed Captures" and "Huggins Closed Captures" respectively were run, and models M_0 $\{N, p(.) = c(.)\}$ and M_b $\{N, p(.), c(.)\}$ were built using the PIMs. Models of Otis et al. (1978) are based on the full likelihood parameterization with three types of parameters p_i (probability of first capture), c_i (probability of recapture) and N. The Huggins models contain only p_i and c_i with N estimated as a derived parameter because the likelihood is conditioned on the number of animals detected and therefore N drops out of the likelihood. Second, using the PIMs, p was made equal to c and the overlap function was used to delete the remaining redundant values. This common model structure M_t $\{N, p(t)$

$= c(t)\}$ allows the capture probability to vary through time, but forces the recapture value to equal the capture probability since both are equally and interchangeably related to capturing birds (Cooch and White 2008). These latter two model structures were further altered to allow both p and c to independently vary through time, generating model structure M_{tb} (constant) $\{N, p(t), c(t)\}$. However, this particular model structure is not valid because there is no constraint placed on the final recapture. Thus, it was altered using the design matrix to generate an alternate model, M_{tb} (independent) $\{N, p(t) = c(t) + b\}$. This also allowed both p and c to vary through time, yet the recaptures were constrained to be different by an additive constant on the logit scale, thus statistically linking recapture with the capture likelihood.

Next, "Closed Captures with Heterogeneity" and "Huggins Heterogeneity" models were run without any changes. The first data structure incorporates a finite mixture represented by π, the probability that an individual belongs to mixture a, for one or more mixtures (M_h). This structure is a simplification of the models of Pledger (Pledger 2000) where $p = c$ and is fixed as a constant across time. "Huggins Heterogeneity" represents Huggins' models generalized with finite mixtures with p constant with mixture (M_h). Both have the same expanded descriptions $\{N, p_a(.) = c_a(.), p_b(.) = c_b(.), \pi\}$ and provided two additional estimates of N.

The "Full Closed Captures with Heterogeneity" and "Huggins Full Heterogeneity" were subsequently run, without alteration, thus generating an additional two estimates for model M_{tbh} (general) where $\{N, p_a(t), c_a(t), p_b(t), c_b(t), \pi\}$. Models M_{tbh} allow for variation in time (for both p's and both c's) and behaviour and individual heterogeneity in capture probability. Since a final constraint was not used for the final recapture, this model did not produce valid estimates of N. However, since this model structure includes two mixtures that correspond to the breeding and non-breeding groups of Bonin Petrels, represented by the letters a and b, the design matrix was used to create two additional and valid $\mathrm{M_{tbh}}$ model structures, $\mathrm{M_{tbh}}$ (mixture) and $\mathrm{M_{tbh}}$ (full) $\{N, p_a(t), c_a(t) = p_b(t) + \mathrm{b}, c_b(t) + \mathrm{b}, \pi\}$ and $\{N, p_a(t) = c_a(t) + \mathrm{b} = p_b(t) + z = c_b(t) + z + b, \pi\}$ respectively. The mixture model represents two groups, breeding and non-breeding Bonin Petrels, where their capture and recapture probabilities independently vary through time, but with an additive and constant difference between the two groups. Thus, while each of the capture and recapture probabilities of one group are unique and vary through time, both are independently linked with a second group's capture and recapture probabilities by an additive constant. The full $\mathrm{M_{tbh}}$ model statistically links both capture and recapture for each of the breeding and non-breeding groups, and then links one group to another by an additive constant. This latter structure provides the greatest statistical commonality of capture and recapture both within each group, and between the two groups. Another six estimates of N were produced from models $\mathrm{M_{th}}$ $\{N, p_a(t) = c_a(t), p_b(t) = c_b(\mathrm{t}), \pi\}$, $\mathrm{M_{bh}}$ $\{N, p_a(.), c_a(.), p_b(.), c_b(.), \pi\}$ and $\mathrm{M_h}$ $\{N, p_a(.) = c_a(.), p_b(.) = c_b(.), \pi\}$, providing a total of twelve estimates using these data types. Model $\mathrm{M_h}$ constructed using "Closed Captures with Heterogeneity" and "Huggins Heterogeneity" both expectedly produced the same result. Producing estimates with the same model, but based on different likelihoods, increased the probability that candidate models could be weighted and averaged within Program MARK.

As noted above, models where N is conditioned out of the likelihood are not compatible using AIC selection methods to those that estimate abundance in the likelihood, and hence, need to be modeled separately. However, the estimates produced using the Huggins' models were not valid, so models were run and saved in single database files where AICc ranking, shown as model likelihood, was commensurate (Appendix C). Where candidate models are based on the same likelihood and nested, models were averaged within Program MARK thereby producing a weighted average estimate of N. The confidence intervals (CIs) for models averaged within MARK should be calculated by hand. The formulas required for these calculations can be found in Appendix B. Otherwise, the CIs are generated from the information matrix.

2.2.8 *Nesting Area Equated with Abundance Estimates*

Modeled estimates of N were assumed to represent an area equivalent to 2827 m^2. This is the approximate area where birds were opportunistically taken from the ground at each of the mistnetting sites (when no birds were being processed or caught in the net), and equates to a 30 m^2 radius around the mistnet. No birds banded in 2008 were recaptured at any other site than originally captured, and the shortest distance between capture sites was approximately 96 m in the high density area. The final population size estimates were derived from the product of the estimate by the total nesting area specific to the density category modelled (i.e., low, medium or high) $\div$ 2827 m^2.

2.3 RESULTS

Table 2.1 provides density specific and total population size estimates derived from the proportion of mistnetted birds identified as breeding and non-breeding using cloacal size alone, and based on the ground-count breeding population size estimate using the CTBS method. These are the numbers that modelled estimates were compared against.

Table 2.1: The total population size of Bonin Petrels derived based on the CTBS ground-count method and the proportions of breeding and non-breeding individuals captured, Sand Island, Midway Atoll (2008).

	Individuals	Confidence interval*	Range (individuals)
Low nesting density	192,815	9804	183,011-202,618
Medium nesting density	140,690	7764	132,926-148-454
High nesting density	573,671	11334	562,337-585,005
Total population	907,176	9634	897,542-916,810

*Confidence intervals are based on occupancy and were calculated specific to each nesting density. The mean confidence interval was used to provide the total population size range.

Only candidate models and those selected for averaging have been included in the results below. Refer to Appendix C for the output tables of results for all models built using Program MARK for each of the density classifications and below-mentioned scenarios. In some instances, models were excluded from the candidate set even though they were well supported. Excluded model(s) were those providing the same estimate as another well supported and approximating (candidate) model(s), but where this selected alternate model could be averaged with another nested model within Program MARK. Averaging within MARK is advantageous because the outcome is a weighted estimate according to the assigned AICc weights given the dataset. Model averaging helps to both reduce model selection uncertainty and bias associated with estimates of *N* (Burnham and Anderson 2002; Pledger 2005).

2.3.1 High Density Combined Capture History (Mistnet Sites 1 and 2) Models and Estimates

Table 2.2: High burrow density combined history models, support, and population estimates.

High Density Combined History Models	Δ AICc	AICc Weights	Model Likelihood	Population Size Estimate	95% CI Low	95% CI High
Full closed captures with heterogeneity M_{th}	0.00	0.56	1.00	1532.46	945.98	2658.06
Closed captures M_t	1.07	0.33	0.59	1647.51	1158.65	2417.33
Full closed captures with heterogeneity M_{tbh} (mixture)	3.08	0.12	0.21	1647.51	1158.65	2417.33

Based on four capture sessions and a recapture rate of 7.47%.

Table 2.3: High burrow density combined history model ranking using Program CAPTURE.

CAPTURE "appropriate" model

Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	0.76	0.85	0.05	0.00	0.04	0.24	0.39	1.00

Appropriate model probably is M(tbh), estimate of *N* is unavailable

Table 2.4: High burrow density combined history model averaged population estimates.

Model Averaging - MARK	Population Size Estimate	95% CI Low	95% CI High
M_{th} and M_{tbh} (mixture)	1552.73	542.64	2632.54
M_t	1647.51	1158.65	2417.33
Mean	1600.12	850.64	2524.93

Although support for model M_{tbh} (mixture) was not as strong (ΔAICc > 2) when compared to models M_{th} and M_t, it was included because it produced a similar abundance estimate and was selected as the most appropriate model using program CAPTURE. Models M_{th} and M_{tbh} (mixture) are based on the same likelihood, so these estimates were averaged within MARK. This resultant estimate was then combined with that of model M_t, and these values were subsequently averaged outside of Program MARK. The mean of these two estimates was 1600.12 and therefore, the total number of individuals occupying the high density nesting areas of Sand Island was 324,696 (range 172,612 -

512,358 individuals). This estimate is considerably lower than that produced using the CTBS (573,671 individuals).

2.3.2 Medium Density Combined Capture History (Mistnet Sites 1 and 2) Models and Estimates

Table 2.5: Medium burrow density combined history models, support, and population estimates.

Medium Density Combined History Models	Δ AICc	AICc Weights	Model Likelihood	Population Size Estimate	95% CI Low	95% CI High
Full closed captures with heterogeneity M_{th}	0.00	0.58	1.00	483.41	294.45	932.17
Full closed captures with heterogeneity M_h	1.90	0.22	0.39	1202.56	636.51	2436.82
Closed captures M_0	2.09	0.20	0.35	992.92	573.60	1834.30

Based on three capture sessions and a recapture rate of 5.1%.

Table 2.6: Medium burrow density combined history model ranking using Program CAPTURE.

CAPTURE "appropriate" model

Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	1.00	0.74	0.25	0.59	0.00	0.40	0.26	0.61

Appropriate model probably is M(o), where *N*=992
SE=305.16, low=575, high=1828

Table 2.7: Medium burrow density combined history model averaged population estimates.

Model Averaging - MARK	Population Size Estimate	95% CI Low	95% CI High
M_{th} and M_h	683.77	421.43	726.96
M_0	992.92	573.60	1834.30
Mean	838.34	497.51	1280.63

The estimate produced from model M_0 was used because it was relatively well supported and received support as "likely the best model" using Program CAPTURE. Models M_{th} and M_h were averaged within Program MARK, and CIs calculated by hand (Appendix B). Averaging models M_{th} and M_h within MARK was particularly valuable in this case, because the estimates were very different. The resultant mean of the two estimates from M_0 and combined models M_{th} and M_h was 838.34, and therefore, the total number of individuals occupying the medium density nesting areas of Sand Island was 147,434 (range 87,494 - 225,216 individuals). The modeled estimate is very similar to that produced using the CTBS (140,690 individuals).

2.3.3 Low Density Combined Capture History (Mistnet Sites 1 and 2) Models and Estimates

Table 2.8: Low burrow density combined history models, support, and population estimates.

Low Density Combined History Models	Δ AICc	AICc Weights	Model Likelihood	Population Size Estimate	95% CI Low	95% CI High
Closed captures M_t	0.00	0.50	1.00	2734.86	1031.70	7758.09
Closed captures M_{tb} (independent)	0.89	0.32	0.64	178.98	159.60	433.13
Full closed captures with heterogeneity M_{tbh} (mixture)	2.04	0.18	0.36	2734.39	1032.08	7752.02

Based on three capture sessions and a recapture rate of 1.9%.

Table 2.9: Low burrow density combined history model ranking using Program CAPTURE.

CAPTURE "appropriate" model

Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	0.82	0.91	0.13	0.13	0.00	0.28	0.41	1.00

Appropriate model probably is M(tbh), estimate of N is unavailable

Table 2.10: Low burrow density combined history model averaged population estimates.

Model Averaging - MARK	Population Size Estimate	95% CI Low	95% CI High
M_t and M_{tb} (independent)	1738.03	733.75	2946.38
M_{tbh} (mixture)	2734.39	1032.08	7752.02
Mean	2236.21	882.92	5349.20

Each of the candidate models M_t, M_{tb} (independent), and M_{tbh} (mixture) were well supported, with model M_{tbh} selected as the most likely model using Program CAPTURE. Model averaging was particularly helpful in this scenario, where one of the population size estimates (M_{tb} independent) was considerably different than the others. Model M_{th}

was also well supported, however the estimate was the same as that produced from model M_{tbh} (mixture), so model M_{th} was excluded. Although just three capture sessions were undertaken and a minimum of four occasions is desirable when using models incorporating heterogeneity, model M_{tbh} was used because it was both well supported, and provided an equitable estimate to the top ranked model M_t.

The mean of the two estimates was 2236.21, and therefore the total number of individuals occupying the low density nesting areas of Sand Island was 369,418 (range 145,856 - 883,677 individuals). This modeled estimate is considerably greater than that produced using the CTBS (192,815 individuals).

To provide valid inferences about population size from modelling, a minimum recapture rate of 5% has been suggested (J. Rotella, ecology Professor and population modeller from Montana State University pers. comm. to the USFWS). This higher than expected abundance estimate could therefore have resulted from the very low recapture rate of 1.9%. The low recapture rate likely resulted from a proportionately greater number of non-breeders being present in this low density area (83%), where young birds are oftentimes marginalized and forced to breed in less favourable habitats (Curio 1983; Forslund and Part 1995; Ferrer and Bisson 2003), compared to the other density classifications (medium density = 55%, high density = 74%), coupled having with only three capture sessions. Even though the high density nesting areas also had a relatively high proportion of non-breeding birds, the recapture rate was 7.47%. Four capture sessions were undertaken in the high density netting area which may have contributed to the higher recapture rate, especially considering there are more breeding birds in the immediate vicinity of capture sites, and Bonin Petrels tend to fly low only in close proximity to their burrows, making these individuals more prone to subseqent recapture.

Table 2.11 provides the total population size derived from summation of the three modeled estimates for the low, medium, and high combined history datasets as detailed in Sections 2.3.3, 2.3.2 and 2.3.1 respectively. Notably, the modeled estimate is similar to those produced using ground-count methods.

Table 2.11: The total population size of Bonin Petrels derived using combined history datasets in the low, medium, and high burrow density classifications and using the closed population capture-recapture models in Program MARK, Midway Atoll (2008).

Combined Histories	*N*	95% CI Low	95% CI High
Low	369418	145856	883677
Medium	147434	87494	225216
High	324696	172612	512358
Total population	**841548**	405962	1621251

2.3.4 *Low Density Mistnet Site 1 Capture History Models and Estimates*

As noted above, models were constructed independently for Sites 1 and 2 capture histories in the low density nesting area only. The purpose was to determine if pooling the data, and omitting the last capture session from Site 1 which resulted in a lower recapture rate, greatly influenced estimates of *N*. Since the Huggins' models did not produce valid estimates, only the remaining three data types were used.

Table 2.12: Low burrow density Site 1 history models, support, and population estimates.

Low Density Site 1 Models	Δ AICc	AICc Weights	Model Likelihood	Population Size Estimate	95% CI Low	95% CI High
Full closed captures with heterogeneity M_{tbh} (full)	0.00	0.35	1.00	137.61	134.27	181.71
Closed captures M_{tb} (independent)	0.54	0.27	0.77	139.48	134.44	202.20
Full closed captures with heterogeneity M_{tbh} (mixture)	1.08	0.20	0.58	2563.71	950.41	7365.04
Closed captures M_t	1.39	0.18	0.50	2206.93	834.70	6266.50

Based on four capture sessions and a recapture rate of 2.24%.

Table 2.13: Low burrow density Site 1 history model ranking using Program CAPTURE.

CAPTURE "appropriate" model								
Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	0.79	0.90	0.16	0.13	0.00	0.29	0.43	1.00
Appropriate model probably is M(tbh), estimate of *N* is unavailable								

Table 2.14: Low burrow density Site 1 history model averaged population estimates.

Model Averaging - MARK	Population Size Estimate	95% CI Low	95% CI High
M_{tb} (independent) and M_t	956.32	219.79	1121.20
M_{tbh} (full) and M_{tbh} (mixture)	1029.57	271.85	1525.78
Mean	992.94	245.82	1323.49

All of the above candidate models were well supported, however the estimates were considerably different between models M_{tbh} (full)/M_{tb} (independent) and models M_{tbh} (mixture)/ M_t. Again, using the weighted MARK averaged estimates helps to both reduce model selection uncertainty and the variability associated with the estimates produced.

The mean of the two MARK averaged estimates was 992.94 and therefore, the total number of individuals occupying the low density nesting areas of Sand Island using the Site 1 capture history was 164,032 individuals (range 40,608 - 218,638 individuals). This estimate is relatively similar to that produced using the CTBS (192,815 individuals) and could be due, in part, to using a dataset with four capture sessions instead of three, and having a slightly higher recapture rate while maintaining a reasonably robust dataset (based on 134 marked individuals).

2.3.5 Low Density Mistnet Site 2 Capture History Models and Estimates

Table 2.15: Low burrow density Site 2 history models, support, and population estimates.

Low Density Site 2 Models	Δ AICc	AICc Weights	Model Likelihood	Population Size Estimate	95% CI Low	95% CI High
Closed captures M_0	0	0.62	1.00	521.18	180.43	1787.64
Closed captures M_b	1.02	0.38	0.60	118.78	66.01	424.44

Based on three capture histories and a recapture rate of 3.64%.

Table 2.16: Low burrow density Site 2 history model ranking using Program CAPTURE.

CAPTURE "appropriate" model

Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	1.00	0.84	0.43	0.76	0.00	0.48	0.37	0.82

Appropriate model probably is M(o), where *N*=521
SE=346.26, low=183, high=1764

Table 2.17: Low burrow density Site 2 history model averaged population estimates.

Model Averaging - MARK	Population Size Estimate	95% CI Low	95% CI High
M_0 and M_b	370.07	204.42	719.38

The estimates produced from models M_0 and M_b were very different. Model averaging helped to reduce the biases associated with model selection uncertainty. Estimates for models M_h and M_{bh}, incorporating heterogeneities, were the same as produced by models M_0 and M_b respectively. Given that such models should be used where there are a minimum of four capture sessions, models M_0 and M_b were based on the same likelihood and could be averaged within Program MARK, and Program CAPTURE selected model M_0 as the most appropriate model given the data, M_h and M_{bh} were excluded from the set of candidate models.

The mean of the two MARK averaged estimates was just 370.07, and therefore, the total number of individuals occupying the low density nesting areas of Sand Island using the Site 2 capture history was 61,135 (range 33,770 - 118,841 individuals).

Although the recapture rate for this site (3.64%) was higher than that of the low density combined histories (1.9%), the dataset was based on only three capture sessions and the histories of just 55 individuals, and was perhaps too small to allow a valid inference of *N*.

2.3.6 Combined Capture History (Low, medium, and high) Models and Estimates

While the total population size estimate derived from summation of the three estimates calculated independently for the low, medium, and high combined datasets is the preferred approach, another estimate was produced using the first three capture histories for all of the capture sites combined. By combining the histories, an even more robust data set was produced, but the recapture rate was subsequently lower and the dataset is comprised of just three capture occasions. Modeled estimates produced using the unique capture histories for low density Sites 1 and 2 were different than when these datasets were combined. This particular approach was subsequently taken to provide insight into the relative importance of a more robust dataset, the number of capture sessions, and the recapture rate when comparing modeled estimates to those produced using the CTBS methods. Since the Huggins' models did not produce valid estimates, only the remaining three data types were used.

Table 2.18: Low, medium, and high burrow density combined history models, support, and population estimates.

Low, Medium and High Density Combined History Models	Δ AICc	AICc Weights	Model Likelihood	Population Size Estimate	95% CI Low	95% CI High
Full closed captures with heterogeneity M_{th}	0.00	0.61	1.00	4647.22	3180.42	6928.84
Full closed captures with heterogeneity M_{tbh} (mixture)	0.87	0.39	0.65	4952.81	3233.38	7769.91

Based on three capture histories and a recapture rate of 3.9%.

Table 2.19: Low, medium, and high burrow density combined history model ranking using Program CAPTURE.

CAPTURE "appropriate" model

Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	0.76	0.82	0.04	0.00	0.20	0.39	0.42	1.00

Appropriate model probably is M(tbh), estimate of N is unavailable

Table 2.20: Low, medium, and high burrow density combined history model averaged population estimates.

Model Averaging - MARK	Population Size Estimate	95% CI Low	95% CI High
M_{th} and M_{tbh} (mixture)	4767.32	4537.73	5010.11

Both candidate models were well supported. Model M_t was excluded since the estimate was the same as that for model M_{th}, and the preferred approach is to average the model estimates within Program MARK. The total population size estimate for Sand Island using the combined capture histories was 2,593,333 individuals (range 2,468,438 - 2,725,403 individuals), and is considerably higher copared to the CTBS estimate produced.

2.4 DISCUSSION

2.4.1 Comparing Modeled Population Estimates to the CTBS Ground-Count Estimates

Consistent with methods used to estimate the breeding population size using the CTBS, the three total population size estimates for the low, medium, and high burrow density areas, where capture histories from the two mistnet sites positioned within each of the density categories had been combined, were summed to derive a total population size of 841,548 individuals (Table 2.11) for Midway Atoll. This estimate is similar to the total population size estimate derived for Sand Island from the proportion of breeding and non-breeding individuals captured, and using the CTBS ground-count method of 907,176 individuals.

For both high and medium combined datasets, capture histories were best represented by a model incorporating both time and heterogeneities. Individual heterogeneity can be caused by such factors as breeding status and incubation patterns. The low combined dataset was best represented by model M_t, where time, and hence environmental variabilities (e.g., weather conditions), were most influential to the model structure and most closely matched the observed capture patterns.

The behaviours between breeding and non-breeding Bonin Petrels are different. Both male and female breeding Bonin Petrels consistently return to their burrows and share in incubation duties. Non-breeding birds are not as attached to the colony, and are not as likely to consistently return to the exact same location. Non-breeding individuals may also return to a nesting colony less frequently. Proportionately more non-breeding birds use low (83%) density nesting colonies compared to medium (55%) and high (74%) burrow density areas. Thus, one possible interpretation is that environmental variability is more influential to non-breeding compared to breeding Bonin Petrels in determining whether to return to their breeding colony or not. Another reason is that non-breeders return less consistently and frequently which would also contribute to greater variability in their patterns of capture compared to breeding individuals. Thus, models incorporating time effects may inherently be most representative of the observed capture histories in low density areas.

The models developed by Pledger (Pledger 2000) which incorporate heterogeneity performed well. The models of Pledger used in this study considered behavioural variability for two groups. This suggests that two patterns of observed capture histories would best be represented using this type of model structure, breeding vs. non-breeding individuals, and provided rationale for their use. It is reasonable to assume that where there are equal numbers of breeding and non-breeding Bonin Petrels that these two different behaviours could be statistically differentiated from their unique capture histories. Expectedly, models incorporating heterogeneity were the top two ranked models for the medium density site, where the proportions of breeding and non-breeding Bonin Petrels were most similar. Time effects were in both the top two ranked models for both the low and high density areas, where the proportions of non-breeding individuals are much higher.

In the low density area, model M_{tb} (independent) was also well supported. This corresponds to either a response to the type of capture method used, and if some individuals were "trap happy" or "trap shy", and/or may be related to the study design. During this study, there was evidence that Bonin Petrels purposefully avoided the mistnets, particularly on clear and bright nights. However, this trap shy behaviour was not commonly observed. It could also be related to study design and where the mistnets were positioned. In low density areas, nets were positioned farthest apart, and what appeared to be the most exposed location compared to the other, higher density colonies where mistnets were positioned.

Although recapture rates were > 5% (the recommended rate) for both the high and medium combined history datasets, resulting estimates of total population size were lower in these two categories than those produced using the CTBS methods. Recently, Hwang and Huggins (2005) have demonstrated analytically that ignoring heterogeneous probabilities of capture leads to an underestimate of the population size. Although Pledgers' latent-class finite-mixture models were built that used different capture probabilities for two groups, breeding vs. non-breeding, they are still assumed to be homogeneous within these two groups. The main limitation of Program MARK is that models which account for individual heterogeneity are not yet available, and these types of models may produce more accurate estimates for similarly behaving burrow-nesting seabirds.

Furthermore, following simulations using recaptures of snowshoe hares to estimate abundance (based on the assumption of closure) and to counts of bird species to estimate species richness, Dozario and Royale (2003) found that in situations where animals have widely varying rates of capture, estimates of *N* obtained by fitting latent-class finite models (used in this study) were considerably more biased than those obtained by fitting beta-binomial or logistic-normal models. These continuous models are not available in Program MARK. The reason provided is that the discrete distribution specified in the finite-mixture does not adequately approximate the latent distribution of capture rates. Whereas models that specify individual variation in capture rates hierarchically using continuous distributions, such as a beta distribution of latent capture probabilities (Burnham 1972) or a normal distribution of their logits (Coull and Agresti 1999; Fienberg et al. 1999), are practically advantageous because the number of model parameters needed to specify heterogeneity in individual capture does not increase with *N*, thus ensuring model parameters are well identified (Dozario and Royale 2003). Continuous mixtures are also more appropriate than finite mixtures for approximating the differences in detectability among species caused from behavioural differences (Dozario and Royale 2003).

Intuitively, one would assume that the total population size estimate in the low density nesting areas should be less than both the medium and high density areas.

However, the modeled total population size estimate in the low (369,418 individuals) density area was considerably higher than that produced using the CTBS methods (192,815 individuals), and higher than both the high (324,696 individuals) and medium (147,434 individuals) burrow density combined history modeled estimates. The most obvious reason for this overestimate was the low recapture rate (1.9%) in this area. Even though the low combined capture history dataset is relatively robust, where there were 158 banded individuals, the recapture rate was too low, and additional capture sessions may not help to increase this rate. For example, Site 1, with four capture sessions, had a lower recapture rate (2.24%) than Site 2 (3.64%), with just three capture sessions.

However, the low density Site 1 dataset did produce a similar estimate (164,032 individuals) compared with the density specific CTBS estimate, so the actual number of individuals captured, and hence capture sessions, is also likely important. Models incorporating heterogeneity perform best when there are a minimum of four capture sessions (White pers. comm.). If we exclude models incorporating heterogeneity from the low and medium combined capture histories, where there were 3 capture sessions, the estimates are 1738 and 993 individuals respectively, yielding density specific total population size estimates of 287,119 and 174,618 individuals respectively. Both of these values are higher to those produced using the CTBS methods (192,815 and 140,690 individuals respectively), and were expected, again because of the low recapture rates observed for these sites, which leads to over-estimates of *N*. Conversely, the modeled total population size estimate in the high density area, where the recapture rate was much higher (7.47%) yielded a considerably lower estimate, 324,696 individuals, compared with those derived using the CTBS, 573,671 individuals. This may have resulted from variations in capture probability which tend to underestimate population size, coupled with higher than expected recapture rates which is related to the study design and species specific behaviours where breeding individuals tend to fly lowest, or near the mistnets, when close to their burrows.

The total population size estimate (2,593,333 individuals) derived from pooling the data from the first three capture sessions of all sites was more than 2.5 times higher compared to the CTBS estimate. Regardless of whether models incorporating heterogeneity are included or not, the estimate is approximately the same. This provides further evidence that more than three recapture sessions are required to provide valid estimates of population size if the closed population models in Program MARK are used. Independently modelling Sites 1 and 2 from the low density area further provided insight into the relative importance of the number of capture sessions and the robustness of the dataset. Low density Site 1, with four capture sessions and 134 marked individuals, produced the most equitable estimate (164,032 individuals) compared to ground-count methods (192,815 individuals). Low density Site 2 used capture data from just 55 individuals, and both the low density combined history and Site 2 datasets used capture histories from just three sessions, with both datasets producing less equitable population size estimates (369,418 and 61,135 individuals respectively). And as expected, the LPI (Bailey's modification) significantly underestimated the total population, 548,088 individuals, similar to that reported in Seto's previous study (1995), where the assumption of equal catchability is violated (Appendix D).

2.5 CONCLUSIONS AND RECOMMENDATIONS

Results from this study indicate that using the closed population capture-recapture models available in Program MARK and model averaging can yield reasonable total population size estimates compared to ground-count methods provided: results are pooled if more than one capture location is used, results are independently modeled for each of the nesting density classifications, and the dataset is relatively robust. A recapture rate of greater than 5%, alongside a minimum of four, but preferably six (White pers. comm.) capture sessions is also desirable when using closed population capture-recapture models in Program MARK, particularly those incorporating heterogeneity. When models incorporating heterogeneity are excluded from the low and medium combined history datasets, modeled estimates are relatively similar to those based on ground-count methods used in this study. However, a considerable difference existed between the modeled total population size estimate in the high density category compared to that resulting from ground-count methods. Also, the population size range associated with the modelled total population size estimate, 405,962 – 1,621,251 individuals, is considerably greater than that produced using the CTBS ground-count and capture method, 897,542 – 916,810 individuals. The CTBS range was calculated using the confidence intervals derived from occupancy plot sampling (Table 1.1).

A combination of factors led to the downward and upward population biases from modelling. Low recapture rates (< 5%) tend to result in overestimations, and may be challenging to accommodate using any different capture strategy in the low density nesting areas where there are proportionately more non-breeding individuals. There are also proportionately fewer individuals at risk of recapture in the low density nesting areas.

One solution would be to position two mistnets in closer proximity than used in this study, for example, separating nets by approximately 50 m, and moving the nets randomly within this fixed zone on each separate capture occasion. This may result in higher recapture rates of young, prospecting and non-breeding birds, because these birds are less likely to consistently return to the exact same location as compared with breeding birds that are incubating eggs. Given that the proportion of non-breeding birds is highest in low density nesting colonies, increasing the likelihood of re-capturing these non-breeding birds seem particularly important in these areas. Moving the capture locations closer together would also help to provide further rationale for the actual area each of the estimates is related to. For example, if a significant number of individuals are captured in both nets positioned 50 m apart, greater support for the related area associated with the estimates would result.

Biases associated with underestimation, as documented in the high density nesting areas, could be managed by using other classes of models, such as beta-binomial and/or logistic-normal models. Alternatively, moving the nets within a 50 m radius on each capture occasion, as noted above, may also help to minimize the probability of recapturing breeding birds in these high density nesting colonies. Although this appears contradictory to the abovementioned, the difference is reflected by which group of birds are being targeted, breeding vs. non-breeding. In low density areas, to increase the probability of recapturing non-breeding birds (thereby decreasing population size estimates) requires a strategy that broadens the general area where birds could potentially be captured within. Conversely, by moving the nets, even within a relatively narrow zone, the likelihood of recapturing the same breeding birds likely decreases, because this group of individuals consistently return to the exact same site to relieve their partners and begin incubating.

If Program MARK is used, and a capture study is designed to include a minimum of four to six sessions, pooling the data from all of the capture locations, regardless of where they are located, may help to reduce the biases associated with high and low recapture rates which are related both to study design and the behaviours of Bonin Petrels. If the mean recapture rate is used, population size estimates may be more consistent with ground-count estimates, and would also provide greater insight into the usefulness of models available using Program MARK, which is widely available to wildlife managers. We need further examination of the situations in which various models perform well (Pledger 2005). While there is support that the closed population capture-recapture models in Program MARK can provide precise estimates of population size, future capture studies should include a minimum of four capture sessions, and nets be randomly moved within a fixed, approximately 50 m zone. It may also be worthwhile to use beta-binomial and/or logistic-normal models. If user-friendly software is available, which includes beta-binomial and/or logistic-normal models, the results from these population size estimates could be compared to those produced using Program MARK and provide evidence of which models perform best. This would, however, require an intensive ground-count census, such as the one detailed in this study, to ensure comparable estimates are available and accurate.

Estimating the population size of Bonin Petrels is challenging. This study provides valuable information about how to design a capture study to obtain useful estimates of abundance from the closed population capture-recapture models available in Program MARK, and additionally, what other classes of models may perform better considering the unique behaviours of this burrow-nesting, and undoubtedly other similarly nesting seabirds. Using Bonin Petrels on Midway Atoll facilitated comparison of total population size estimates based on ground-count methods and closed population capture-recapture modeled estimates because it is a relatively isolated population, and the central model assumption requiring population closure could reasonably be met. However, to ensure that model assumptions relating to closure are definitively met; behavioural studies that investigate how Bonin Petrels use Midway Atoll are still required. Alternatively, intense mist-netting efforts at the three main NWHI nesting areas, Laysan and Lisianski Islands and Midway Atoll, would help to quantify movements within and among them (Seto and O'Daniel 1999). As with many seabirds, information on the feeding grounds and the non-breeding range of Bonin Petrels is generally lacking, and this information is needed for successful management of this species (Seto and O'Daniel 1999). Thus, while radar methods to estimate the total population size of Bonin Petrels is worth investigating, capturing birds would provide additional and valuable information, such as annual recruitment, differential survivorship, and lifetime reproductive performance.

Bonin Petrel Populations and Present-Day Management Practices

Under management of the USFWS, Midway's wildlife is afforded a high level of legislated protection. However, four current and on-going practices may continue to impact their survivorship and are detailed below.

1. The USFWS conduct an annual albatross breeding pair census on Midway Atoll. Approximately 18 volunteers count every albatross nest on the Atoll in December

of each year, and many Bonin Petrel burrows are collapsed (USFWS pers. comm.). In December, Bonin Petrels are actively digging and preparing their burrows and nest sites with their egg laying period commencing in early January (Seto and O'Daniel 1999). Considering that many burrows are collapsed during each census, it would be sensible to collect information that would permit quantification of the impacts on the reproductive success of Bonin Petrels caused by the census.

2. The USFWS has incurred great expense attempting to eradicate a particularly invasive non-native plant, *Verbesina*, or Golden crown-beard. This plant presently occupies considerable portions of available nesting habitat on Midway Atoll (Chapter 3). While *Verbesina* itself may negatively impact seabird productivity, damage caused by its removal is conspicuous to petrel colonies (considerable numbers of burrows were found collapsed in managed areas) and, in the short-term, will impact productivity. Where *Verbesina* has been hand-pulled, considerable numbers of burrows have collapsed because root structures themselves had once formed part of the burrows. Simply walking through colonies threatens burrow integrity and causes collapse, and can be especially damaging in areas of medium and high density nesting which account for approximately 70% (107 ha) of the total nesting area. Any large-scale disturbance to colonies could impact breeding success, especially considering the site tenacious behaviours of Bonin Petrels (100% site/pair fidelity, this study; and 25% re-occupancy, Seto 1995) in subsequent years.

Results from this study do, however, provide evidence that the breeding and total population size of Bonin Petrels has grown considerably since rats were eradicated, even with the abovementioned *Verbesina* management. In the longer-term, removal of

Verbesina would improve nesting conditions for seabirds using the Atoll. Control work could be restricted to when Bonin Petrels are not nesting.

3. AquaMaster Herbicide (active ingredient; glyphosate isopropylamine salt) is presently being applied to extensive areas of Sand Island to control *Verbesina* (Monsanto; http://www.monsanto.com/monsanto/ag_products/pdf/labels_msds/aqua_master_msds.pdf). While the product is listed as non-hazardous under the United States Occupational Health and Safety Act and has been identified as non-toxic to some aquatic species, it has been found slightly toxic to avian species from results of 5 day LC (lethal concentration) ingestion studies (Bobwhite quail, *Colinus virginianus*; Mallard duck, *Anas platyrhynchos*) (U.S. Environmental Protection Agency 2002; Wilhelms et al. 2006). While AquaMaster has a half life of < 7 days in aquatic environments, it strongly binds with soil and has a half-life of 2-174 days. It is therefore possible that continued, longer-term use over extensive portions of Bonin Petrel nesting habitats, that reproductive success and survivorship may be affected, especially considering the site tenacious behaviours of Bonin Petrels. Collecting productivity and reproductive success data in sample plots positioned throughout the range of available habitats on Midway Atoll would provide insight into the impact of both *Verbesina*, and *Verbesina* management practices, to Bonin Petrels.

4. The USFWS has continued to collect valuable population and productivity data of Laysan albatrosses (*Phoebastria immutabilis*), Black-footed albatrosses (*P. nigripes*) and Red-tailed Tropicbirds (*Phaethon rubricauda*) from long-established study plots. Populations of Bonin Petrels have significantly rebounded following eradication of the rat in 1997, and some of these long-term study plots now contain high numbers of

nesting petrels. Care should be taken during monitoring to minimize disturbance to Bonin Petrels and their burrows.

Recommendations

1. Initiation of a ground-count monitoring and mapping program equitable to this study and undertaken every 3-5 years would provide valuable information about trends in Bonin Petrel breeding population sizes on Midway Atoll. Burrow densities and occupancy could be linked to habitat and anthropogenic influences. Considering Midway is now open for tourism, and the on-going commitment to eradicate *Verbesina* and control ironwood tree densities and distribution, another non-native species where a considerable proportion of Bonin Petrels prefer to nest, understanding nesting patterns and preferences is particularly important. Fieldwork would require about an eight week commitment by two persons, two GPS units and mapping software. At present, volunteer commitments average three months in length, some possessing MSc. degrees, and both hardware and software are available. Further commitment to produce population size estimates and a detailed report would likely be required.

2. Monitoring seabird productivity, or breeding success, is also important to detect or reflect changes in environmental conditions. Yearly productivity monitoring, conducted within plots randomly positioned within representative habitats for example, would provide insight into immediate threats from reduced prey species availability that wider-scale, less frequent population censusing may not alone reveal (Walsh et al. 1995). Techniques to establish a successful plot-based productivity study and methods to

statistically analyse the data is available in "The Seabird Monitoring Assessment for Haswai'i and the Pacific Islands" (Citta et al. 2007).

While a plot-based study is encouraged, the scope of this type of study should be broadened to permit quantification of the impacts caused from *Verbesina*, *Verbesina* and ironwood management practices, yearly albatross counts, and buried solid waste. For example, Bonin Petrel reproductive success study plots could be established in areas of: varying albatross densities; varying densities of *Verbesina*, ironwood trees, and land covers; in areas subject to varying levels of herbicide use and subject to other *Verbesina* management, and in areas where waste is buried, particularly in areas where they may be concern about its toxicity. If a plot(s) were established in areas where Bonin Petrels are breeding both in nestboxes and in natural burrows, quantification of the impacts from the yearly albatross census and where *Verbesina* is increasingly becoming more dominant, or conversely being managed, may provide useful data to help better manage this seabird species.

3. Establishing a mistnetting program would allow among-year comparison of the proportion of breeding and non-breeding birds if sampling protocols are consistently followed. If a ground-count was completed, the total population size could be calculated from the abovementioned breeding and non-breeding proportions, and CR modelling could be undertaken. Mistnetting would also provide additional information about their breeding cycle and egg laying dates, and estimates of survivorship, lifetime reproductive performance, and annual recruitment would be possible. A minimum of three to four individuals, one possessing a U.S. migratory bird banding permit, would be required for a period of two hours per night for approximately 24 sessions if CR is

considered. Appreciably fewer sample sessions are necessary if simply the proportion of breeding to non-breeding individuals is sought.

4. A total of 43 artificial (plastic) Bonin Petrel nestboxes were buried in 2005 and are ready for occupancy on Sand and Eastern Islands (Laniawe 2005). Long-term data could be collected pertaining to incubation shifts, feeding rates, survivorship, site tenacity, age at first breeding and longevity. Poor hatch success in nestboxes has been documented in previous USFWS studies (mean success of 35% in wood/plastic boxes combined compared to a natural burrow hatch success of 80%, unpublished by author, 1998). Although temperature may not be impacting hatch success (Seto pers. comm.), the reason for such failures are worth investigating. Commitment from one individual for a couple of hours each day from the beginning of January (commencement of egg laying) through to the end of June when chicks will have fledged would likely be required. If nestboxes on Eastern Island are checked, additional time would be required.

CHAPTER 3. THE IMPORTANCE OF LOCAL ECOLOGICAL CONDITIONS TO NESTING PATTERNS OF BONIN PETRELS ON SAND ISLAND, MIDWAY ATOLL

3.1 LOCAL ECOLOGICAL CONDITIONS: GENERAL INTRODUCTION

Nest site characteristics of Bonin Petrels are not well known, and there is no documented or quantified evidence that associates nesting patterns with local conditions (habitat and anthropogenic influences) on Midway Atoll, or elsewhere. The primary goal of this Chapter was to quantify the relative importance of land cover with nesting patterns of Bonin Petrels on Sand Island. Bonin Petrel nesting colonies were originally mapped into areas of low, medium, and high burrow densities (in order to quantify the total nesting area and produce breeding and total population size estimates) which allowed quantification of the relative importance of land cover with nesting patterns based on the proportionate overlap of these two layers. A second goal was to identify how nesting patterns of Bonin Petrels relate to two particularly invasive species on Midway Atoll, *Verbesina* and ironwood trees. Much of the discussion pertaining to nesting patterns and relationships between Bonin Petrels, albatrosses, *Verbesina* and stands of ironwood trees is anecdotal, however it has been included because there appears to be a conspicuous knowledge gap in this area. No published studies have quantified the impact *Verbesina* has on nesting bird habitats (Feenstra and Clements 2008).

Midway Atoll is a highly disturbed system, stemming from a long history of human occupation and war. Over the years, more than 200 non-native plant species have been purposefully or accidentally introduced. The most common and invasive/noxious, introduced taxa to Midway Atoll include *Verbesina*, ironwood trees, wild poinsettia (*Euphorbia cyanospora*), haole koa (*Leucaena leucocephala*), sweet alyssum (*Lobularia* *maritima*), buffalo grass (*Stenotaphrum secundatum*), peppergrass (*Lepidium virginicum*), and bermuda grass (*Cynodon dactylon*). *Verbesina* is now found on all of the main Hawaiian Islands, except Ni'ihau, and is becoming more dominant on Midway Atoll, where it out competes all 20 of the extant native plant species (Feenstra and Clements 2008). On Sand Island, *Verbesina* stands composed 18.2 ha in 1991, whereas in 2004, they comprised 60 ha, an increase of 330% (Laniawe 2004). Based on the land cover identified in the Land Cover map (2007), *Verbesina* presently occupies approximately 140 ha on Sand Island, an increase of 770% since 1991.

Verbesina appears to lower the quality of habitat to indigenous birds by creating a physical barrier to nesting birds, lowering nest density, and shading out native plants (Feenstra and Clements 2008). *Verbesina* is a sunflower-like herbaceous annual plant, ranging in height from 0.3 m to 1.7 m, with yellow flowers. It is a highly invasive species, mainly due to its high seed production (300 - 350 seeds per flower and multiple flowers per plant), seed dormancy, ability to tolerate dry conditions, and possible allelopathic effects (Feenstra and Clements 2008). In 1997, the Midway Atoll USFWS Refuge received funding to control/eradicate *Verbesina*, and have been using various herbicides, limited mowing (in the 1990's), and pulling it by hand (http://www.fws.gov/midway/management.html). Efforts to control *Verbesina* will likely extend beyond a decade (USFWS pers. comm.). Its removal will alter the present-day landscape of Sand Island and impact the breeding success of Bonin Petrels; through burrow collapse as control technicians walk through fragile nesting colonies, and from loss of structural integrity when root systems are pulled, or die as a result of herbicidal treatments. Therefore, identifying those areas that both support high numbers of breeding pairs of Bonin Petrels, and characterizing aspects of their preferred nesting habitats, are particularly important. Stands of ironwood trees also appear to negatively impact the quality of habitat for nesting seabirds, particularly albatrosses (USFWS pers. comm.). Ironwoods have known allelopathic effects, and needle litter in the understory also suppresses germination of other plant species. On Midway Atoll, efforts to control the number and density of ironwood trees are also ongoing. All ironwood trees have been cut down on Eastern Island, and at the time of this study, trees were actively being felled on Sand Island. The Atoll has also recently re-opened its doors to tourism, so understanding the relative importance of the various habitats throughout Sand Island to nesting Bonin Petrels is critical, particularly if any restorative works are planned for buildings in areas of high Bonin Petrel nesting densities.

3.2 METHODS

In 2007, a Land Cover map was created and published for the USFWS which details local ecological conditions, based on land cover, for Sand Island (Figure 3.1), Eastern and Spit Islands (Midway Atoll).

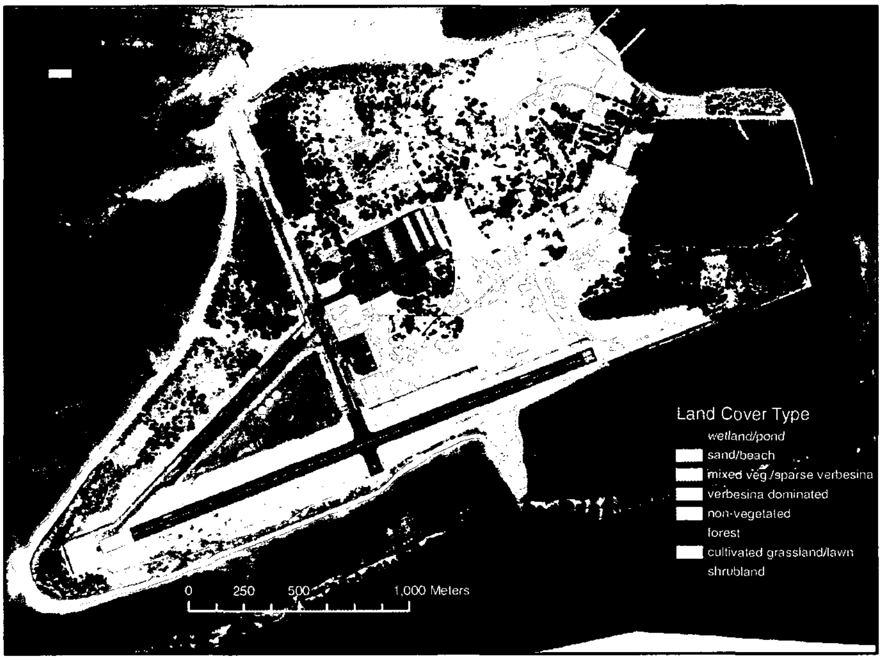

Figure 3.1: Land Cover map (USFWS), Sand Island, Midway Atoll (2007). Source: DigitalGlobe, QuickBird, October 2005 and the USFWS Midway_07_LandCover (shapefile).

This map was produced using satellite images and the following land covers were identified: sand/beach, wetland/pond, sparse *Verbesina*/mixed vegetation, *Verbesina* dominated, shrubland (primarily native Naupaka), managed grassland (e.g., lawns), forest (primarily ironwood trees), and non-vegetated (e.g., areas covered by roads and buildings etc.). Bonin Petrels prefer to nest in sandy environments with native bunch grass (*Eragrostis variabilis)* (Seto 1994). Unfortunately, the methods used to create the Land Cover map could not provide the level of detail required to classify different grasses, or vegetation beneath the forest canopies. In addition, vegetation surveys on Midway Atoll were not undertaken to ground-truth the map when it was created, and accordingly, the classifications are inherently broad.

Bonin Petrel nesting colonies on Sand Island were originally marked (using GPS units) and mapped (ArcGIS) using colour-coded polygons unique to areas of low, medium, and high burrow density colonies, and then uploaded onto a geo-referenced satellite image of Midway Atoll (Figure 1.5, Chapter 1). This map layer was subsequently joined with the Land Cover map of Sand Island using the "union" feature in ArcMAP. This allowed quantification of the relative importance of land cover to nesting category, based on the amount of overlap (m^2), of low, medium, and high density colonies with land cover type. For example, the greater the overlap (m^2) of nesting colonies within the "*Verbesina* dominated" land cover, the greater the importance of this particular habitat to Bonin Petrels compared to the other land covers. The population size estimates produced in Chapter 1 are also used to illustrate the relative importance of land cover type to population size.

Because the land cover classifications were originally created to encompass all three islands of Midway Atoll (Sand, Eastern and Spit), this map was altered to solely include Sand Island. Therefore the relative importance of each land cover to nesting patterns and preferences of Bonin Petrels is specific to Sand Island. Otherwise, the relative importance of land cover to nesting patterns and preferences would be skewed relative to the land covers which are dominant or absent on Eastern (e.g., *Verbesina* and ironwood trees respectively) and Spit Islands. Airplane runways, staging areas (e.g., cargo loading and unloading zones) and the (historic) seaplane hanger zone were not included as part of the "non-vegetated" land cover types, whereas areas occupied by houses and other buildings or considerably smaller areas with impermeable surfaces have been included. Accordingly, the relative proportions for all land covers are marginally greater than if these areas (e.g., airplane runways etc.) had been included. The total area covered by the land cover classifications is approximately 312 ha (3,120,000 m^2), whereas the actual area of Sand Island is 485 ha (4,850,000 m^2). The land covers also did not extend to the outer edges (predominated by "sand/beach" environments) of Sand Island, which also contributes to a slight deviation in the proportions each land cover classification is associated with. One obvious benefit of excluding airplane runways and the sandy fringes of Sand Island, are that the areas (m^2) that each land cover proportionately represents, is more related to the actual land area available to nesting Bonin Petrels, therefore providing greater support for the findings presented in this Chapter.

3.3 RESULTS

Thirteen nesting colonies, or portions thereof, were marked that lie beyond the boundary of the Land Cover map. Bonin Petrel breeding colonies also overlapped with "wetland/pond" and "non-vegetated" land covers; areas not suitable for burrow-nesting birds. Because the Land Cover map was created using a satellite image and was based on the observed variations in patterns and colours, and was not ground-truthed, some margin of error is expected.

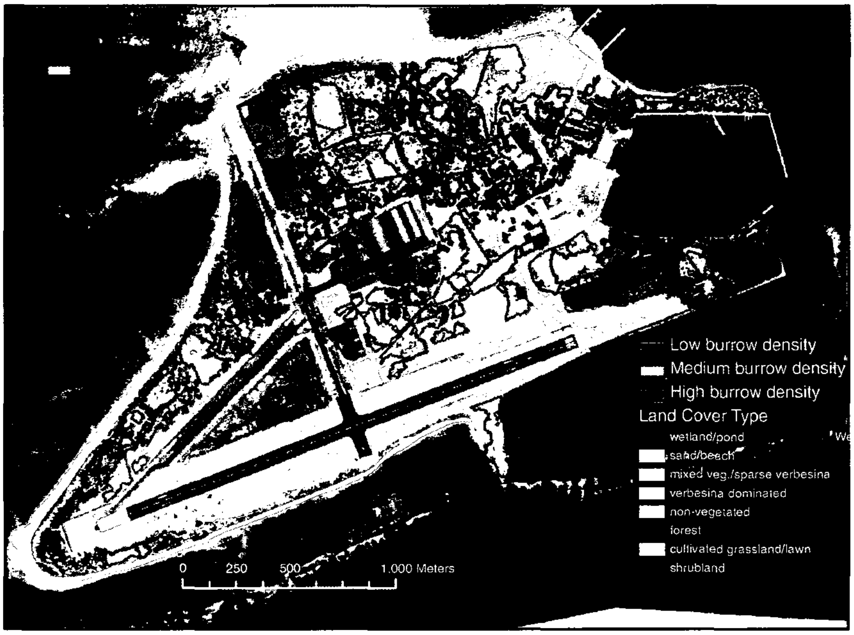

Figure 3.2: Bonin Petrel low, medium, and high density nesting colonies overlain onto a Land Cover map (2007) of Sand Island, Midway Atoll (2008). Source: DigitalGlobe, QuickBird, October 2005 and the USFWS Midway_07_LandCover (shapefile).

Table 3.1: The total area, and the total area occupied by nesting Bonin Petrels within the land cover types of Sand Island, Midway Atoll (2008).

Land Cover Type	Total area (m^2)	Total area with nesting colonies (m^2)	Proportion of total area (%)	Proportion of total area with nesting colonies (%)
Outside the classification boundary	-	3043	0.0	0.2
Wetland/pond	1715	94	0.1	0.0
Sand/beach	56506	24106	1.8	1.6
Mixed vegetation/sparse verbesina	445014	176330	14.3	11.5
Verbesina dominated	952210	507093	30.5	33.0
Non-vegetated	465860	116945	14.9	7.6
Forest	799187	522436	25.6	34.0
Cultivated grassland/lawn	120184	63259	3.9	4.1
Shrubland	279518	124764	9.0	8.1
Total	3120195	1538069	100	100

The "*Verbesina* dominated" category comprised the greatest area (95.22 ha; 952,210 m^2), closely followed by "forested" areas (79.92 ha; 799,187 m^2). If land covers with *Verbesina* are combined ("*Verbesina* dominated" and "mixed vegetation/sparse *Verbesina*"), this invasive species occupies approximately 1,397,224 m^2 or 139.72 ha (45% of the total area relative to the areas classified), and 45% of nesting Bonin Petrels are also found here. "Forest(ed)" areas occupy approximately 26% of Sand Islands total land area (relative to the area covered by the land cover classifications), and 34% of the Bonin Petrel nesting colonies are located within this land cover. Although proportionately greater land area is "*Verbesina* dominated" (31%) compared to "forested" (26%), the forested areas are relatively more important (more preferred) to nesting Bonin Petrels. Approximately 33% of the Bonin Petrel nesting colonies (by area) are located within "*Verbesina* dominated" areas, compared to 34% in "forest(ed)" areas. Excluding the unsuitable land covers for burrowing species, such as "wetlands/ponds" and "non-vegetated" classifications, "mixed vegetation/sparse *Verbesina*" is the least preferred land cover by breeding Bonin Petrels.

Table 3.2: Population size estimates (using the CTBS, cloacal size only) of Bonin Petrels (individuals) unique to burrow density and within the land cover types of Sand Island, Midway Atoll (2008).

Land Cover Type	Low density total population	Medium density total population	High density total population	Total population (combined)	Proportion (%) of total population (combined)
Outside the classification boundary	56	337	1716	2109	0.2
Wetland/pond	0	27	0	27	0.0
Sand/beach	3435	2529	6847	12811	1.4
Mixed vegetation/sparse verbesina	18701	14925	78270	111896	12.3
Verbesina dominated	88681	46570	127659	262910	29.0
Non-vegetated	12573	15676	31079	59328	6.5
Forest	44812	41303	267872	353986	39.0
Cultivated grassland/lawn	10431	4595	21747	36773	4.1
Shrubland	14127	14728	38482	67337	7.4
Total	192815	140690	573671	907176	100

Proportionately more Bonin Petrels use forested areas (353,986 individuals; 39%) than areas dominated by *Verbesina* (262,910 individuals; 29%). If "mixed vegetation/sparse *Verbesina*" is combined with the "*Verbesina* dominated" land cover, the relative importance of *Verbesina* occupied environments to Bonin Petrel populations on Sand Island increases (374,806 individuals; 41%), and is similar to forested areas. However, one conspicuous and large forested area where Bonin Petrels have not colonized, in the south-eastern region of Sand Island, contains an inland pond which was originally occupied by ocean waters, but was filled in when the U.S. Navy constructed protective seawalls along the edges of Sand Island in this particular area. The water table is very close to the ground surface in this region making the habitat unsuitable for burrow-nesting species.

This area was also historically used as a landfill site, but was filled and covered by the U.S. Navy, thus may be less suitable for burrowing birds.

3.4 DISCUSSION

Bonin Petrels prefer dry, sandy environments in which to build burrows and nests, as opposed to areas with more densely packed soils (i.e., greater proportions of organic matter), or areas prone to flooding and/or increased moisture levels. Sandier environments facilitate burrow excavation, allow rainwater to drain from nest sites more quickly and efficiently (Bonin Petrels nest during the winter months, when rainfall is highest), and may also help to keep carbon dioxide and oxygen levels more consistent. Interestingly, the "sand/beach" land cover does not support significant numbers of Bonin Petrels (13,482 individuals), possibly because a considerable portion of these areas identified on the Land Cover map are found adjacent to the high tide line, areas exposed and prone to flooding, and do not support grasses or other vegetation where root systems help to increase burrow strength and integrity. The coral sands along the outer edges of Sand Island may also be finer or coarser than further inland, and may not provide the structural support necessary for their burrows and nests. Considerable numbers of ghost crabs (*Ocypode spp.*) were also found along these beaches, which may influence nest site selection of Bonin Petrels since ghost crabs are known to actively predate on other bird species' eggs and turtle eggs (Wolcott and Wolcott 1999; and Barton and Roth 2008).

Where non-native vegetation such as *Verbesina* has persisted, the underlying substrate is becoming increasingly more compact, and in some areas, the soils are loosely "ribboned" when rolled between the index finger and thumb, indicative of sandy loam soils. In contrast, the underlying substrate in forested areas was sandier, less compact, and more exposed. While conducting the burrow density and occupancy survey (Chapter 1), more burrows collapsed underfoot in forested areas, irrespective of the burrow density classification, than in areas dominated by *Verbesina.*

Figure 3.3: Albatrosses nesting in a monoculture stand of *Verbesina*, Sand Island, Midway Atoll (2008). Note the ironwood forest in the background where *Verbesina* is absent, albatrosses are less prevalent, and sandy soils are exposed beneath the canopy.

Ironwoods are conifers and permit considerable light penetration.

The under-story in these forested areas was generally open, was sparsely populated by other non-native plant species, but importantly, in some areas, was predominated by native bunchgrass. Bunchgrass thrives in well-drained sandy environments, is out-competed by *Verbesina*, and appears to be a preferred nesting habitat of Bonin Petrels. In contrast, *Verbesina* grows in dense, thick monoculture stands, generally out-competes other plant species, is present in sandy to more loamy soils on Sand Island, and can tolerate dry conditions (Feenstra and Clements 2008). The accumulation of organic matter in *Verbesina* dominated areas is faster compared to forested areas, primarily because of the sheer density of *Verbesina*, its composition (less acidic than the needles of ironwood trees, which are slow to decompose), its fast growth rate, annual growth cycle, and high seed production. The importance of forested areas to Bonin Petrel populations can therefore be attributed to, in part, their sandier, well drained, less compact soils, and the presence of native grasses where permanent root structures help to increase burrow support and integrity. The root structures of *Verbesina* are temporary, because it is an annual species with yearly dies offs. Bonin Petrels also use the needles of ironwood trees and grasses to build their nest cups (Seto 1994), whereas other materials, apart from their own feathers, have not been documented for use in nest construction.

Furthermore, (and anecdotally), there appears to be an inverse, negative relationship between nesting Bonin Petrels and nesting albatrosses. In Bonin Petrel colonies of high burrow density, proportionately fewer albatrosses were found nesting, and vice versa. This relationship is conspicuous in forested areas, where there are relatively few nesting albatrosses.

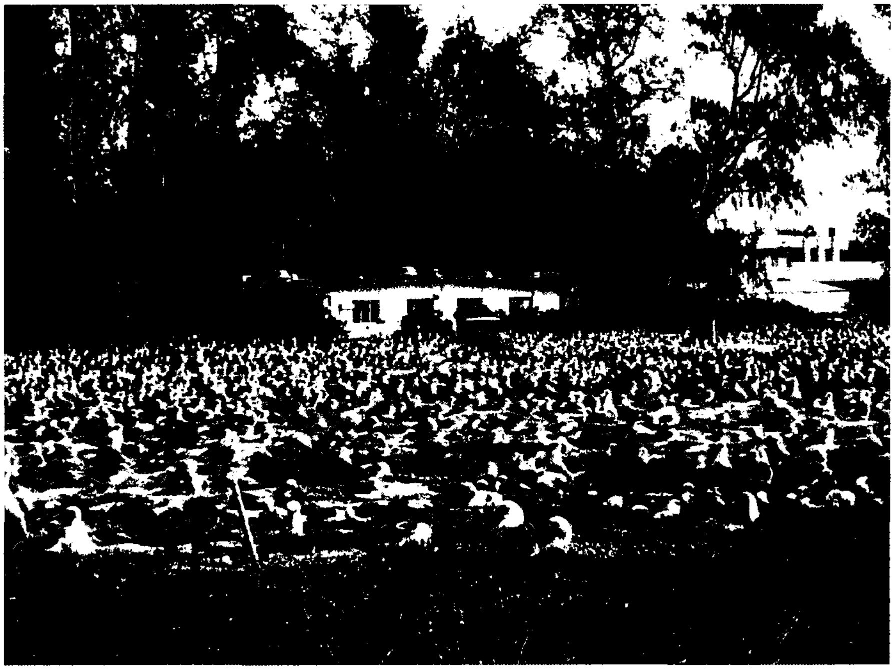

Figure 3.4: A high density nesting colony of Laysan albatrosses in an area historically subject to mowing, and where densities of nesting Bonin Petrels are low, Sand Island, Midway Atoll (2008).

Figure 3.5: A low density nesting colony of Laysan albatrosses and a high density nesting colony of Bonin Petrels. The soils are primarily sandy and exposed with some native grasses growing, Sand Island, Midway Atoll (2008).

Because of their size and structure, albatrosses have difficulty navigating within forested areas, and are prone to strike ironwood trees, particularly in dense stands. Several adults were found dead, impaled and hanging in treetops during this study, which may account for their nesting preference, areas without trees. Bonin Petrel burrows were also prone to collapse under the weight of albatrosses and their nests. On several occasions, Bonin Petrel burrows were found collapsed on return site visits. It appeared most likely that the weight of albatrosses and their nests had caused their collapse. Bonin Petrel nestlings were also found, on several occasions, either half-buried or completely exposed following the collapse of an albatross chick and its nest into their burrows.

The USFWS are expending considerable efforts to control non-native plant species such as *Verbesina*, and are cutting down ironwood trees on Sand Island. Thus, consideration of the relative importance of this land cover to Bonin Petrel populations is prudent. Although ironwood trees negatively impact albatross reproductive success through death by collisions, when trees fall during wind storms (one fallen tree can kill up to eight adults and many trees fall per year season, particularly in winter and during peak albatross presence), and by reducing the available nesting habitat, these forested areas do not support dense stands of *Verbesina*. *Verbesina* also negatively impacts albatross reproductive success by reducing the nesting habitat available to breeding birds, and are the most important to Bonin Petrel populations relative to the amount of land occupied. Albatrosses appear to most heavily populate flat areas that were/are mowed, and/or areas dominated by sand and low lying ground-cover (cultivated lawns and the more natural landscapes on Sand Island). They appear to selectively breed on sturdy, well supported ground (i.e., areas not heavily used by burrowing Bonin Petrels). In contrast, Bonin Petrels prefer undisturbed environments, in part, because their burrows are sensitive to collapse. They also prefer sandy environments that support native grasses, because their root structures help to provide continued long-term support of their burrows. Physiologically it is costly to have to re-dig and maintain burrows during the breeding season, and can result in reduced reproductive success if eggs are lost and birds die as a result of burrow collapse.

3.5 CONCLUSIONS AND RECOMMENDATIONS

To correlate the relative *significance* (as opposed to importance) of land cover to nesting patterns of Bonin Petrels, albatrosses and other indigenous species, the Land Cover map should be ground-truthed. If vegetation data were collected in randomly selected plots, island-wide (Appendix A1), this information could be used to provide evidence that the land covers identified in the Land Cover map both appropriately, and proportionately, represent the actual conditions on Sand Island. Otherwise, adjustments could be made to improve the accuracy of the map where necessary. If albatross nesting patterns were marked and mapped using methods similar to those used in this study for Bonin Petrels, correlation between albatross nesting and land cover would be possible. This map could also be layered with the Bonin Petrel nesting map that was produced as part of this study (Figure 1.5, Chapter 1), and could be used to correlate the patterns of nesting between these two species to better understand if an inverse and negative nesting relationship does exist as hypothesised. Understanding the relative importance/significance of land cover to nesting preferences of albatrosses and Bonin Petrels allows wildlife managers to more appropriately target areas for invasive species control that would be less likely to impact reproductive success of the indigenous breeding colonies.

As stated in the Seabird Monitoring Assessment for Hawaii and the Pacific Islands (Citta et al. 2007), a primary goal of the USFWS is to support conservation strategies in the U.S. Pacific Islands by "detect(ing) and understand(ing) changes in the status and trends of seabird populations…". Four objectives were outlined specific to this goal: (1) monitor trends of seabird populations, (2) understand causes of population change, (3) determine conservation status of seabird populations, incorporating abundance, distribution, trends, and threats to seabird populations, and (4) collaborate with partners to achieve and advance all objectives. Given that "no (population monitoring) data" for Bonin Petrels was available to the collaborators when preparing this report, this study has provided critical information about the abundance and distribution of Bonin Petrels on Midway Atoll (objective 3). Information pertaining to the preferred land cover(s) for breeding Bonin Petrels has also been presented, and could be used, in future, to provide insight into objectives 2 and 3. While going beyond the objectives of the abovementioned report, habitat use and selection are also important variables that influence the population size and distribution of seabirds. Collecting baseline data pertaining to nesting preferences with land cover, and nesting patterns between avifauna, is particularly important where local landscapes have been significantly altered from anthropogenic activities and the introduction of invasive, non-native species. Understanding the relative importance of local conditions to nesting patterns is critical where invasive species have appreciably altered local conditions, and where control efforts will be long-lasting and require the use of herbicides, such as on Midway Atoll.

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APPENDIX A

1) Vegetation data was collected in each of the 402 (100 m^2) plots surveyed for burrow density. Only conspicuous species comprising the majority of land cover were documented. This data has been entered into a MS Excel spreadsheet, but has not been peer reviewed. If the original data are sought, please contact me directly (petrelpeeper@hotmail.com).

2) A report titled "Seabird Monitoring Assessment for Hawaii and the Pacific Islands" (Citta et al. 2007) was prepared at the request of the USFWS to statistically quantify and qualify the most appropriate and practical methods to monitor long-term abundance and success of Bonin Petrel populations on Midway Atoll. The methods used in this study are both comparative and complementary to the monitoring protocols suggested.

3) A request for data pertaining to the latest recorded egg laying dates from the USFWS and Dr. Ian Jones, Memorial University, NF (who studies Bonin Petrels on Tern Island, also forming part of the Northwest Hawaiian Islands chain) was made, but at the time this report was released, no information had been obtained. It is possible that additional information is not available.

APPENDIX B

To estimate the confidence intervals (CIs) for models averaged within Program MARK, the following calculations were necessary (Chapter 14, Cooch and White 2008).

The lower and upper CI bounds for N are given by,

$$\left[M_{t+1} + \left(\hat{f}_0 / C\right), M_{t+1} + \left(\hat{f}_0 \times C\right)\right]$$

where $f_0 = N - M_{t+1}$, f_0 refers to the number of animals not caught, M_{t+1} refers to the number of individuals captured/banded, and based on the assumption that this quantity follows a log-normal distribution.

Then,

$$\hat{f}_0 = \hat{N} - M_{t+1} \quad \text{and} \quad C = \exp\left\{1.96\left[\ln\left(1+\frac{\widehat{\text{var}}\left(\hat{N}\right)}{\hat{f}_0^2}\right)\right]^{1/2}\right\}$$

Since $\hat{N} = M_{t+1} + f_0$, then $\widehat{\text{var}(\hat{N})}$ is the same as the variance of f_0 because M_{t+1} is a known constant. As such,

$$\frac{\widehat{\text{var}}\left(\hat{N}\right)}{\hat{f}_0^2} = \frac{\widehat{\text{var}}\left(\hat{f}_0\right)}{\hat{f}_0^2} = \widehat{\text{CV}}\left(f_0\right)^2$$

The estimated unconditional (model averaged) variance $\text{var}(\hat{\theta})$, calculated over models $\{M_1, M_2, \ldots M_i\}$ is given as

$$\widehat{\text{var}}\left(\hat{\bar{\theta}}\right) = \left[\sum_{i=1}^{R} \hat{w}_i \sqrt{\widehat{\text{var}}(\hat{\theta}_i | M_i) + (\hat{\theta}_i - \hat{\theta}_a)^2}\right]^2$$

where

$$\hat{\theta}_a = \sum_{i=1}^{R} \hat{w}_i \hat{\theta}_i$$

and the w_i are the Akaike weights (Δ_i) scaled to sum to 1. The subscript i refers to the i^{th} model. The value θ_a is a weighted average of the estimated parameter θ over R models ($i = 1, 2, \ldots R$). This estimator of the unconditional variance is the sum of 2 components: (i) the conditional sampling variance $\text{var}(\hat{\theta}_i | M_i)$ (i.e., conditional on model M_i), and (ii) a

APPENDIX B con't

term for the variation in the estimates across the *R* models $(\hat{\theta}_i - \hat{\theta}_a)^2$. The square-root of these terms is then weighted by the Akaike weights w_i. Thus, the unconditional standard error is given as

$$\widehat{\mathrm{SE}}\left(\widehat{\bar{\theta}}\right) = \sqrt{\widehat{\mathrm{var}}\left(\hat{\bar{\theta}}\right)}$$

APPENDIX C

Model results via an output spreadsheet exported from Program MARK for:

i) High density combined capture history models
ii) Medium density combined capture history models
iii) Low density combined capture history models
iv) Low density Site 1 capture history models
v) Low density Site 2 capture history models
vi) Combined capture history models (low, medium, and high sites)

Each table shows the unique models built for each of the abovementioned scenarios. Candidate models which were reported in the Results from Chapter 2 are bolded. Candidate models were selected because they were well supported and were reasonable (the value of *N* was similar to the top-ranked model). Not all models yielding reasonable estimates were well supported. In addition, some models had high standard errors and/or $\hat{c}$'s, and were therefore not chosen as candidate models. Note, models M_{tb} (1 and 2) are not valid structures, but were kept and have been reported because other models were subsequently built using this original structure. The model(s) are not valid because a recapture likelihood is used for the first capture occasion, whereas in reality, a recapture value is not possible until the second capture occasion, when previously marked individuals could be recaptured.

The following numeric classifications are taken from Program MARK. They denote the classes/structures of models used to produce each estimate, and their origins:

1. Closed captures (models of Otis et al. 1978)
2. Huggins closed captures (Huggins 1989)
3. Closed captures with heterogeneity (simplified models of Pledger 2000)
4. Full closed captures with heterogeneity (Pledger 2000)
5. Huggins heterogeneity (Huggins 1989)
6. Huggins full heterogeneity (Huggins 1989)

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High Burrow Density Combined History Models (inclusive)	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	Estimate (individuals)	Candidate Model
{1 Mtb constant}	-1928.524	0	0.55122	1	7	12.8552	308	No
{4 Mtbh, no changes}	-1926.498	2.0262	0.20014	0.3631	8	12.8552	308	No
{4 Mth, p=c}	-1925.328	3.1963	0.1115	0.2023	10	9.9628	1532.4589	Yes
{1 Mt, p=c}	-1924.263	4.2613	0.06546	0.1188	5	21.159	1647.5142	Yes
{1 Mtb independent}	-1922.249	6.2754	0.02391	0.0434	6	21.1535	1242.1263	No
{4 Mtbh full}	-1922.249	6.2754	0.02391	0.0434	6	21.1535	1242.0983	No
{4 Mtbh mixture}	-1922.243	6.281	0.02385	0.0433	6	21.159	1647.5118	Yes
{4 Mbh}	-1878.379	50.145	0	0	5	67.0428	521211.77	No
{1 Mb}	-1874.38	54.144	0	0	2	77.0809	227543.94	No
{1 Mo}	-1872.169	56.3547	0	0	2	79.2916	1723.1229	No
{3 Mh}	-1870.16	58.3644	0	0	3	79.2916	1723.1232	No
{4 Mh}	-1870.16	58.3644	0	0	3	79.2916	1723.1232	No
{6 Mth, p=c}	986.6041	2915.128	0	0	9	2923.928	0.0101698	No
{2 Mtb independent}	987.5258	2916.05	0	0	4	2934.964	0.0566354	No
{2 Mt, p=c}	987.6689	2916.193	0	0	4	2935.107	0.0580265	No
{6 Mtbh mixture}	987.6689	2916.193	0	0	4	2935.107	0.0488921	No
{6 Mtbh, no changes}	988.655	2917.179	0	0	11	2921.909	0.010101	No
{2 Mtb constant}	990.763	2919.287	0	0	6	2934.165	0.0577778	No
{6 Mtbh full}	993.5879	2922.112	0	0	7	2934.967	0.0566718	No
{2 Mb}	1039.352	2967.876	0	0	2	2990.813	0.0513393	No
{2 Mo, p.=c.}	1039.762	2968.286	0	0	1	2993.23	0.0478312	No
{6 Mbh}	1041.364	2969.888	0	0	3	2990.815	0.051396	No
{5 Mh}	1041.769	2970.293	0	0	2	2993.23	0.0478312	No
{6 Mh}	1041.769	2970.293	0	0	2	2993.23	0.0478312	No

Where M(t+1)=308

Medium Burrow Density Combined History Models (inclusive)	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	Estimate (individuals)	Candidate Model
{4 Mtbh, no changes}	-866.1937	0	0.48989	1	4	2.1721	157	No
{1 Mtb constant}	-866.1937	0	0.48989	1	4	2.1721	157	No
{4 Mth, p=c}	-857.6423	8.5514	0.00681	0.0139	5	8.6803	483.41395	Yes
{1 Mb}	-855.972	10.2217	0.00295	0.006	2	16.454	85329.727	No
{3 Mh}	-855.7395	10.4542	0.00263	0.0054	3	14.6608	1202.5552	No
{4 Mh}	-855.7395	10.4542	0.00263	0.0054	3	14.6608	1202.5552	Yes
{1 Mo}	-855.5554	10.6383	0.0024	0.0049	2	16.8706	992.916	Yes
{4 Mtbh mixture}	-853.9453	12.2484	0.00107	0.0022	5	12.3773	1194.987	No
{1 Mt, p=c}	-853.7657	12.428	0.00098	0.002	4	14.6001	986.68771	No
{1 Mtb independent}	-851.9653	14.2284	0.0004	0.0008	5	14.3573	749584.44	No
{4 Mtbh full}	-850.68	15.5137	0.00021	0.0004	7	11.5297	47500.108	No
{4 Mbh}	-849.8688	16.3249	0.00014	0.0003	5	16.4538	72664.731	No
{2 Mtb constant}	414.3627	1280.556	0	0	4	1282.729	0.0306122	No
{2 Mo, p.=c.}	416.2599	1282.454	0	0	1	1290.703	0.0552338	No
{6 Mtbh, no changes}	416.2858	1282.48	0	0	6	1280.556	0.0078679	No
{6 Mth, p=c}	416.2858	1282.48	0	0	6	1280.556	4.72E-04	No
{2 Mb}	417.6887	1283.882	0	0	2	1290.115	0.0581507	No
{6 Mtbh mixture}	417.8128	1284.007	0	0	4	1286.179	0.4130048	No
{2 Mt, p=c}	418.0335	1284.227	0	0	3	1288.434	0.0622756	No
{5 Mh}	418.0609	1284.255	0	0	3	1288.461	0.0280331	No
{6 Mh}	418.0609	1284.255	0	0	3	1288.461	0.0280331	No
{2 Mtb independent}	419.652	1285.846	0	0	4	1288.018	0.062609	No
{6 Mtbh full}	420.9198	1287.114	0	0	6	1285.19	0.3091867	No
{6 Mbh}	422.3293	1288.523	0	0	5	1288.652	0.0467365	No

Where M(t+1)=157

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Low Burrow Density Combined History Models (inclusive)	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	Estimate (individuals)	Candidate Model
{4 Mtbh, no changes}	-915.7733	0	0.47911	1	5	0.0286	158	No
{1 Mtb constant}	-915.5232	0.2501	0.42279	0.8825	5	0.2787	158	No
{1 Mt, p=c}	-910.715	5.0583	0.0382	0.0797	4	7.1298	2734.8578	Yes
{1 Mtb independent}	-909.8205	5.9528	0.02442	0.051	5	5.9813	178.98494	Yes
{4 Mth}	-908.672	7.1013	0.01375	0.0287	5	7.1298	2734.9814	No
{4 Mtbh mixture}	-908.672	7.1013	0.01375	0.0287	5	7.1298	2734.394	Yes
{4 Mtbh full}	-906.4427	9.3306	0.00451	0.0094	7	5.247	168.9933	No
{1 Mb}	-903.5054	12.2679	0.00104	0.0022	2	18.3992	186601.07	No
{1 Mo}	-902.8853	12.888	0.00076	0.0016	2	19.0193	2835.6096	No
{3 Mh}	-902.8853	12.888	0.00076	0.0016	2	19.0193	2835.1797	No
{4 Mh}	-902.8853	12.888	0.00076	0.0016	2	19.0193	2835.1797	No
{4 Mbh}	-899.4504	16.3229	0.00014	0.0003	4	18.3944	496190.51	No

Where M(t+1)=158

Low Burrow Density Site 1 Models	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	Estimate (individuals)	Candidate Model
{4 Mtbh, no changes}	-658.5484	0	0.82747	1	6	0.5489	134	No
{1 Mtb constant}	-653.9493	4.5991	0.083	0.1003	7	3.0947	134	No
{4 Mtbh full}	-651.8843	6.6641	0.02956	0.0357	7	5.1596	137.60557	Yes
{1 Mtb independent}	-651.3492	7.1992	0.02262	0.0273	6	7.7482	139.47632	Yes
{4 Mtbh mixture}	-650.7997	7.7487	0.01718	0.0208	5	10.3432	2563.7148	Yes
{1 Mt, p=c}	-650.4973	8.0511	0.01477	0.0178	5	10.6456	2206.9313	Yes
{4 Mth}	-648.4518	10.0966	0.00531	0.0064	6	10.6456	2206.9037	No
{1 Mb}	-638.4173	20.1311	0.00004	0	2	28.8163	182383.24	No
{1 Mo}	-637.9108	20.6376	0.00003	0	2	29.3228	2300.5913	No
{3 Mh}	-635.8882	22.6602	0.00001	0	3	29.3228	2300.6268	No
{4 Mh}	-635.8882	22.6602	0.00001	0	3	29.3228	2300.6268	No
{4 Mbh}	-634.3696	24.1788	0	0	4	28.8112	16886639	No

Where M(t+1)=134

Low Burrow Density Site 2 Models	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	Estimate (individuals)	Candidate Model
{4 Mtbh, no changes}	-193.4152	0	0.50661	1	4	0	55	No
{1 Mtb constant}	-191.8479	1.5673	0.23139	0.4567	4	1.5673	55	No
{1 Mo}	-188.763	4.6522	0.04948	0.0977	2	8.8281	521.17774	Yes
{3 Mh}	-188.763	4.6522	0.04948	0.0977	2	8.8281	521.1705	No
{4 Mh}	-188.763	4.6522	0.04948	0.0977	2	8.8281	521.1705	No
{1 Mb}	-187.7457	5.6695	0.02976	0.0587	3	7.7704	118.77998	Yes
{4 Mbh}	-187.7457	5.6695	0.02976	0.0587	3	7.7704	118.78007	No
{1 Mt, p=c}	-186.0497	7.3655	0.01274	0.0251	4	7.3655	514.84836	No
{4 Mtbh mixture}	-186.0497	7.3655	0.01274	0.0251	4	7.3655	514.85186	No
{4 Mth}	-185.6465	7.7687	0.01042	0.0206	5	5.6413	281.64249	No
{4 Mtbh full}	-185.4772	7.938	0.00957	0.0189	6	3.6564	56.736593	No
{1 Mtb independent}	-185.2539	8.1613	0.00856	0.0169	5	6.0339	59.149793	No

Where M(t+1)=55

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Combined Capture History Models (low, medium, and high burrow density sites, 3 capture occassions)	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance	Estimate (individuals)	Candidate Model
{1 Mtb constant}	-4363.394	0	0.6388	1	4	2.0707	540	
{4 Mtbh, no changes}	-4362.208	1.1863	0.35299	0.5526	5	1.2446	540	No
{1 Mtb independent}	-4352.221	11.1736	0.00239	0.0037	4	13.2443	354329.26	No
{1 Mt, p=c}	-4351.974	11.4198	0.00212	0.0033	4	13.4906	4647.2039	No
{4 Mth}	-4351.974	11.4198	0.00212	0.0033	4	13.4906	4647.217	Yes
{4 Mtbh mixture}	-4351.105	12.289	0.00137	0.0021	5	12.3473	4952.8085	Yes
{4 Mtbh full}	-4347.235	16.1597	0.0002	0.0003	7	12.1857	894127.65	No
{1 Mb}	-4340.157	23.2373	0.00001	0	3	27.3179	2105702.3	No
{1 Mo}	-4339.987	23.4069	0.00001	0	2	29.4951	4709.7982	No
{4 Mbh}	-4338.736	24.6578	0	0	4	26.7286	2854493.2	No
{3 Mh}	-4337.09	26.3039	0	0	4	28.3747	5020.7001	No
{4 Mh}	-4337.09	26.3039	0	0	4	28.3747	5020.7001	No

Where M(t+1)=540

APPENDIX D

The total population size of Bonin Petrels, Sand Island, Midway Atoll (2008) calculated using Bailey's modification of the Lincoln-Peterson Index N = r(n+1)/(m+1); where total captured (n) = newly banded birds and recaptured birds, # at risk of recapture [r] = total # of banded birds, and N = total population size.

Low density Site 1

Capture date	Total captured (n)	Total recaptured [m]	# at risk of recapture [r]	*N*
02-Feb-08	16	0	0	
12-Feb-08	49	0	65	3250.00
22-Feb-08	39	1	103	2060.00
02-Mar-08	33	2	134	1518.67
Total	189			

Low density Site 2

Capture date	Total captured (n)	Total recaptured [m]	# at risk of recapture [r]	*N*
06-Feb-08	20	0	0	
17-Feb-08	22	1	41	471.50
26-Feb-08	15	1	55	440.00

Medium density Site 1

Capture date	Total captured (n)	Total recaptured [m]	# at risk of recapture [r]	*N*
05-Feb-08	37	0	0	
15-Feb-08	19	3	53	265
24-Feb-08	39	2	90	1200
Total	157			

Medium density Site 2

Capture date	Total captured (n)	Total recaptured [m]	# at risk of recapture [r]	*N*
08-Feb-08	20	0	0	
19-Feb-08	28	3	45	326.25
29-Feb-08	23	1	67	804.00

High density Site 1

Capture date	Total captured (n)	Total recaptured [m]	# at risk of recapture [r]	*N*
04-Feb-08	63	0	0	
13-Feb-08	19	0	82	1640.00
23-Feb-08	52	5	129	1139.50
03-Mar-08	43	5	167	1224.67
Total	308			

High density Site 2

Capture date	Total captured (n)	Total recaptured [m]	# at risk of recapture [r]	*N*
07-Feb-08	35	0	0	
18-Feb-08	11	3	43	129
27-Feb-08	55	2	96	1792
05-Mar-08	53	8	141	846

Burrow density	Site 1	Site 2	Mean (Sites 1 & 2)	Total nesting area (m^2)	*N*
Low	1518.67	440.00	979.33	165.20	161784.06
Medium	1200.00	804.00	1002.00	175.86	176215.33
High	1224.67	846.00	1035.33	202.92	210089.10
Total population size					**548088.49**

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