

STATUS AND DEMOGRAPHIC RATES OF THE CHRISTMAS SHEARWATER *Puffinus nativitatis* ON KURE ATOLL

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SUMMARY

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The Christmas Shearwater *Puffinus nativitatis* is a small (350 g) Procellariiform seabird that nests on remote islands in the tropical and subtropical Pacific Ocean. Little is known about its demography or conservation needs. We banded and recaptured 1120 Christmas Shearwaters on Kure Atoll, the northwestern-most of the Hawaiian Islands, on 60 occasions during a 20-year period, 1995–2014. To provide demographic information that is lacking for this species, we used robust design mark-recapture models to estimate apparent annual survival, emigration, capture probabilities, and size of the study population. Annual survival of residents was 0.864 SE 0.034, which is typical for seabirds this size. The oldest known bird was at least 17 years and 1 month old. Of birds banded as chicks, the average age of first recapture was 3.9 years. Among birds captured, 11% appeared to be transients. The annual emigration rate was 0.249 SE 0.096. Thirteen shearwaters captured on Kure originally were banded on Midway Atoll; three of were captured multiple times and presumably were breeding on Kure, indicating there is exchange between the colonies on those two islands. The size of the study population averaged 358 birds, with an increasing trend and an estimate of 480 birds in the last two years. The primary reason for the population increase was eradication of Polynesian rats *Rattus exulans* in 1995, which has resulted in a 10-fold increase in shearwater population size since the last estimate in the 1980s. The high survival rate and increasing number of birds indicate that the Kure Christmas Shearwater population is robust.

Key words: Christmas Shearwater, demography, emigration, mark-recapture, population size, *Puffinus nativitatus*, seabirds, survival

INTRODUCTION

The Christmas Shearwater *Puffinus nativitatis* is a small (350 g) Procellariiform seabird of the tropical and subtropical Pacific Ocean. Nesting colonies are located on remote islands, including the Hawaiian, Line, Phoenix, Samoan, Marquesas, Marshall, Tuamotu, and Austral islands in the central Pacific, and on Easter Island and islands off Chile in the eastern Pacific (Seto 2001, USFWS 2005). The global population size is unknown, but the largest colonies of about 3000 pairs each are located on Christmas Island (Schreiber & Schreiber 1989) and the Pitcairn islands (Brooke 1995). In the Hawaiian Islands, the total population is thought to be 2500–3000 pairs, with the largest colonies on Laysan (1500–2000 pairs) and Lisianski (400–600 pairs) islands (Seto 2001, USFWS 2005). The breeding biology of the Christmas Shearwater has been well described (Seto 2001), but little is known about its demography. Survival and emigration rates have never been estimated in this species, and there has been no population estimate for Kure Atoll published since Harrison (1990) reported 20–30 pairs in the 1980s.

Kure Atoll is the oldest (29.8 million years) and most northwestern island in the Hawaiian Archipelago (Price & Clague 2002). Kure, an important seabird breeding site, currently supports over 100000 breeding pairs of at least 18 species (Hawai'i Division of Forestry and Wildlife [DOFAW] unpubl. data). The environment of Kure was drastically altered in 1955 by construction of a radar reflector by the US Navy. The US Coast Guard made further modifications by constructing a runway and several buildings and began to occupy the island in 1960. Numerous alien species have been introduced to

Kure, including the Polynesian rat *Rattus exulans* and a variety of plants, which have negatively affected the native flora and fauna. The Coast Guard abandoned the island in 1992 and demolished most structures in 1993, when management of the island as a State Seabird Sanctuary was transferred to DOFAW. A rat eradication program was implemented immediately, and by 1995 no rats remained. Since 1993, DOFAW staff and volunteers have made annual trips to monitor seabird and plant populations, remove invasive species and marine debris, and conduct other management. Kure is the only island in the Northwestern Hawaiian Islands that is owned and managed by the State of Hawai'i rather than by the US federal government.

The goals of this project were to (1) provide demographic information on Christmas Shearwaters based on long-term banding and recapture data collected at Kure from 1993 to 2014 and (2) help assess whether management actions implemented on Kure by DOFAW since 1993 have benefited the species. Specifically, we used robust-design mark-recapture models to estimate apparent annual survival, emigration, capture probabilities, and population size (Pollock 1982, Kendall *et al.* 1995, 1997). Robust-design models employ a combination of traditional Lincoln-Peterson methods used to estimate capture probability and population size over a short time (Williams *et al.* 2002) and simple mark-recapture methods (sometimes called Cormack-Jolly-Seber models) used to estimate survival over longer time periods (Cormack 1964, Jolly 1965). The study population is assumed to be closed during the shorter sampling periods, meaning the population does not change in size, but during the longer time intervals the population

is allowed to change due to births, deaths, emigration, and immigration. These longer and shorter time periods are respectively called either primary and secondary sampling periods (Kendall *et al.* 1995) or trapping sessions and occasions (White & Burnham 1999). Although robust design models have more specific data requirements and entail more effort, they allow estimation of more demographic parameters and often result in more precise estimates (Kendall *et al.* 1997, 2009).

STUDY AREA AND METHODS

Study site and population

Kure is the northernmost coral atoll in the world and is located at a biogeographic position known as the “Darwin Point” — the northern extent of coral reef development, beyond which cooler ocean temperatures prevent coral growth from keeping pace with the rate of geological subsidence. It is a roughly circular atoll with a reef 9.7 km in diameter enclosing a lagoon with two islets comprising an area of about 81 ha. Green Island, the larger of the two islets, rises 6.1 m above sea level and is located in the southeastern quadrant of the lagoon.

Christmas Shearwaters arrive at nesting colonies in Hawai‘i in February to find a mate and prepare a nest, then leave for 2–3 weeks on a pre-laying exodus, returning to lay a single egg in April and May (Seto 2001). Chicks hatch in June and July, and fledge in late August and September. Both parents incubate the egg in alternating shifts lasting 4–5 d (Seto 2001). Both parents feed the chick daily for the first 4–6 weeks, and feeding frequency declines as the chick develops, with an average feeding frequency of 0.63 per parent over the entire nesting cycle (Amerson & Shelton 1963).

On Kure Atoll, Christmas Shearwaters nest on the ground surface under dense vegetation, primarily the shrub naupaka *Scaevola sericea*. They are difficult to observe at their nests because of the dense naupaka, so we captured adults at night on an adjacent inactive runway that the birds used for takeoff and landing as they departed and arrived at their nests (Fig. 1). Because they were not captured at a nest, it is possible that some birds were not breeding but were pre-breeders or transients that were visiting Kure from another island. Some Christmas Shearwaters nested away from the runway, and those birds probably used other open areas, such as beaches, to take off and land, and thus were not sampled in this study. We estimate that we sampled about 90% of the population (see Discussion). In some years we banded chicks in accessible nests.

Data collection

We captured shearwaters on the ground by hand or with a pole net. We attempted to standardize search effort each night by walking one circuit along the north and south sides of the runway. We did not attempt to determine the sex of birds. We marked unbanded birds with a US Geological Survey Bird Banding Laboratory stainless steel leg band with a unique serial number. If a bird was already banded, we recorded the band number. However, the study was not originally designed for mark-recapture analyses, and the band number of recaptured birds was not recorded on some occasions in the early years of the study (1995, 1996, 1998, 1999, parts of 1997, 2000, and 2001). The number of capture occasions within a year varied among years (mean = 3.0, range 1–5). We captured birds on more than one occasion in all years except 1998. The interval

between capture occasions also varied (mean = 33.0 SE 4.0 d). Beginning in 2004, we recorded information on search effort and environmental conditions on each night when shearwaters were captured, including times when capture effort began and ended, number of observers, moon phase, and wind speed and direction.

Analyses

We created a capture history for each bird, consisting of the date of initial banding (or first recapture) and all subsequent recaptures. For birds originally banded on Midway, their encounter history started on the date we first recaptured them on Kure. We did not attempt to estimate juvenile survival because the sample of chicks was too small, and we excluded chicks from mark-recapture analyses unless they were recaptured as adults, in which case they were added to the data set on the date of first recapture. We also excluded 2014 from analyses because search effort in that year was the lowest of any year, with few birds banded ($n = 10$) or recaptured ($n = 15$), and half of the effort occurred in a month (May) when capture rates typically have been low.

These capture histories resulted in a data set that included 1078 individual birds, consisting of 1056 birds banded as adults on Kure, nine birds banded as chicks on Kure and recaptured as adults, and 13 birds banded on Midway and recaptured on Kure.

We used Huggins robust-design mark-recapture models (Huggins 1991) in Program MARK 6.1 (White & Burnham 1999) to generate maximum-likelihood estimates of apparent annual survival (S), emigration (γ''), remaining outside the study area once emigrated (γ'), initial capture probability (p), recapture probability (c), and population size (N). Transients and pre-breeders can present problems in mark-recapture studies because such birds may remain in the colony for only a short time and thus do not have the same capture probability as resident birds, leading to underestimation of survival rates (Pradel *et al.* 1997, Clucas *et al.* 2008). Pre-breeders, in particular, may prospect for nest sites in more than one location before they settle (Clucas *et al.* 2008). Robust-design models directly estimate the rate of temporary emigration and help to prevent underestimation of the survival of residents (Kendall *et al.* 1997). In addition, we employed another



Fig. 1. Christmas Shearwater study site on Kure Atoll. Shearwaters were captured along a former runway 1.2 km long.

method of dealing with transients, using an age-structured approach in which the survival rate in the first year after capture (S1) is different from the survival rate in all subsequent years (S2+) (Pradel *et al.* 1997). Instead of actual ages, the classes represent the number of years since first capture. Because transient birds are less likely to be recaptured after the first year, the survival estimate in the second and subsequent years is more likely to reflect that of residents. Use of an age-structured approach also allowed us to estimate the proportion of transients in the population using the following equation (Pradel *et al.* 1997):

$$1 - S1/S2+$$

We created a set of candidate models to examine factors of biological interest (Table 1). Model notations followed Lebreton *et al.* (1992), in which subscripts indicate whether parameters differed among years (p_{yr}) or were constant over time, indicated by a dot (p). We started with a complex model, in which capture and recapture probabilities varied among years, and removed terms (backward selected) until the simplest model was reached, in which all parameters were constant over time (Burnham & Anderson 2002). We compared the fit of models with Akaike’s Information Criterion corrected for small sample size (AIC_c), as calculated by Program MARK. We considered the model with the lowest AIC_c value to have the best fit. We were unable to start with the most complex global model, in which all parameters varied among years, because the data were too sparse, resulting in inestimable parameters.

Robust design models require at least two capture occasions within each trapping session, but in 1998 we captured shearwaters on only one night. To allow use of robust design models, we added a “dummy” occasion in 1998, and we fixed the initial capture probability and recapture probability at zero for that occasion. We also fixed the recapture probability at zero for occasions on which the band number of recaptured birds was not recorded. This allowed the initial banding record to be used while accounting for the lack of recapture data. In the Huggins versions of robust design models, the population size is not estimated directly but instead is a derived parameter calculated from the capture probabilities (Cooch & White 2006). Because we had to fix some capture probabilities at zero due to missing data, the population size estimates from those years (1995–2000) were suspect, and we did not report them.

We conducted a goodness-of-fit test using the median \hat{c} approach in MARK to determine whether a global model adequately fit the data and whether assumptions underlying analyses were reasonable.

However, because the median \hat{c} approach is not supported for robust design models in MARK, we conducted the test on a global Cormack-Jolly-Seber model using the same data set. The global model included terms with annual variation in capture and recapture probabilities, but not annual variation in survival or emigration, for the reasons explained above. The value of \hat{c} was 3.21 SE 0.19, indicating that the data were overdispersed, so we adjusted \hat{c} to the estimated value and used the quasi- AIC_c ($QAIC_c$), although adjustment of \hat{c} did not affect model order. Overdispersion often occurs when many individuals have identical encounter histories, and this was true in the Christmas Shearwater data set; many birds were banded on the same night and not encountered again.

We investigated the preferred conditions for capturing shearwaters using a multiple regression analysis, with number of birds captured (including birds newly banded and recaptures) as the dependent variable, and amount of time spent searching, number of observers searching, wind speed, and moon phase (MoonConnection.com) as independent variables. We expressed moon phase as the proportion of days from new moon to full, e.g. six of 14 days = 43% full. We examined seasonal variation in capture rate with a one-way ANOVA, using number of birds captured per hour as the response variable and month as the factor. We lumped months into two-month periods (April–May, June–July, and August–September) for analysis because sample sizes were small in some months.

Although the number of chicks banded was too small to estimate juvenile survival, we used recaptures of birds banded as chicks to measure age at first return to the colony.

RESULTS

We captured and banded 1120 different Christmas Shearwaters on 60 occasions from 1995 to 2014, and we made 763 recaptures of those birds. We captured most birds from June to August, with some birds captured in April, May, and September in some years. Thirteen of the birds originally were banded on Midway Atoll and subsequently recaptured on Kure. Of the 1107 birds banded on Kure, 41 were banded as chicks and 1066 were banded as adults.

The best mark-recapture model was one in which the rates of apparent survival (S), emigration (γ''), and remaining emigrated (γ') were constant across all years, and in which the initial capture and recapture probabilities varied among years (Table 1, first model). Models in which survival and emigration rates varied among years resulted in parameter estimates that were

TABLE 1
Robust design mark-recapture models used to estimate annual survival (S), emigration (γ''), remaining emigrated (γ'), initial capture probability (p), and recapture probability (c) of Christmas Shearwaters on Kure Atoll from 1995 to 2013

Model ^a	Delta AIC_c	$QAIC_c$ weights	Model likelihood	Number of parameters
S1 S2+ γ'' 1 γ'' 2+ γ' 1 γ' 2+ p_{yr} c_{yr}	0.00	0.71	1.00	40
S1 S2+ γ'' 1 γ'' 2+ γ' 1 γ' 2+ p_{yr} c.	1.76	0.29	0.41	26
S1 S2+yr γ'' 1 γ'' 2+ γ' 1 γ' 2+ p_{yr} c_{yr}	23.33	0.00	0.00	57
S1 S2+ γ'' 1 γ'' 2+ γ' 1 γ' 2+ p. c.	39.63	0.00	0.00	8

^a The model with the lowest $QAIC_c$ was judged to have the best fit and indicated that survival and emigration rates were constant across years, and that capture probabilities varied among years. S1 and S2+ are survival rates in the first year after capture and second and subsequent years, respectively.

not realistic in some years, such as survival estimates of 0.0 or 1.0, indicating the data were too sparse to allow investigation of annual variation in those parameters (e.g. Table 1, third model).

Annual survival of Christmas Shearwaters in the first year after initial capture, which likely included transient birds, was 0.765 SE 0.087. Annual survival in the second year and all subsequent years, which likely represented an unbiased estimate for breeding birds, was 0.864 SE 0.034. The proportion of transients in the sampled population was thus $1 - 0.765/0.854 = 0.105$. The estimated annual emigration rate was 0.249 SE 0.096, and the estimated rate of remaining outside the study area once emigrated was 0.833 SE 0.096. The oldest known bird was at least 17 years and 1 month old, banded as an adult on 8 July 1997 and recaptured on 15 August 2014. Four other birds were at least 15 years old, and 21 birds were at least 10 years old.

The estimated size of the Christmas Shearwater study population on Kure averaged 358 SE 21 birds, but it varied over time (Fig. 2). The trend in population size was generally increasing, but the estimates fluctuated and the relationship was not significant ($F_{1,11} = 1.65$, $P = 0.23$). Three of the four highest estimates occurred in the last four years of the study, and the estimate in both 2012 and 2013 was about 480 birds.

Of chicks banded on Kure, the average age of first recapture was 3.9 years (range 1–6 years). Of the 13 birds originally banded on Midway Atoll and recaptured on Kure, five were banded as adults and eight were banded as chicks. Three of those birds were recaptured multiple times on Kure, including two birds banded as chicks and one as an adult, suggesting they probably had emigrated to Kure and were breeding. Of the Midway birds banded as chicks, the age at which they were recaptured on Kure averaged 6.0 years (range 4–8 years), not counting one bird banded as a chick on 27 August 1997 on Midway and recaptured on Kure only 32 d later.

Multiple regression analysis showed that the number of shearwaters captured on a given night varied significantly ($F_{4,24} = 5.12$, $P = 0.006$, $R^2 = 53.2\%$) and that the amount of time spent searching was the most important predictor of the number of birds captured (Table 2; Fig. 3). Capture rate of shearwaters also varied seasonally ($F_{2,25} = 4.77$, $P = 0.018$), with lower capture rates in April and

May and the highest capture rate in August (Fig. 4). Other factors had weaker, non-significant, effects on the number of birds captured. There was a tendency toward lower capture rate when the moon was fuller and the wind speed was higher, but there was substantial variation; sometimes relatively large numbers of birds were captured in such conditions. Surprisingly, the number of people searching had a weak negative relationship with number of birds captured.

DISCUSSION

The Christmas Shearwater demographic estimates produced in this study are useful for helping to determine the status of the species on Kure and worldwide, and for assessing the efficacy of management actions undertaken by DOFAW on Kure since 1993. The survival estimates also can be used as proxies in demographic analyses of related species of similar size for which no survival estimates are available, such as the threatened Newell's Shearwater *Puffinus auricularis newelli* (Ainley *et al.* 1997). Our results show that the number of Christmas Shearwaters on Kure has increased about 10-fold since the previous published estimate of 20–30 pairs in the 1980s (Harrison 1990). The primary reason for this increase was the eradication of Polynesian rats from the atoll in 1993–1995. Most of the increase likely occurred in the years immediately following rat eradication, but there was some indication that the population is still increasing, with the highest estimates of 480 birds in the last two years of the study. Some additional birds occur in parts of the island that we did not sample (perhaps another 30 pairs; DOFAW unpubl.

TABLE 2
Factors affecting the number of Christmas Shearwaters captured each night, based on results of multiple regression analysis

Factor	Regression line slope	t value	P value
Time searching	20.95	3.71	0.002
Number of people searching	-1.32	0.41	0.69
Moon phase	-0.10	0.52	0.61
Wind speed	-0.47	0.36	0.72

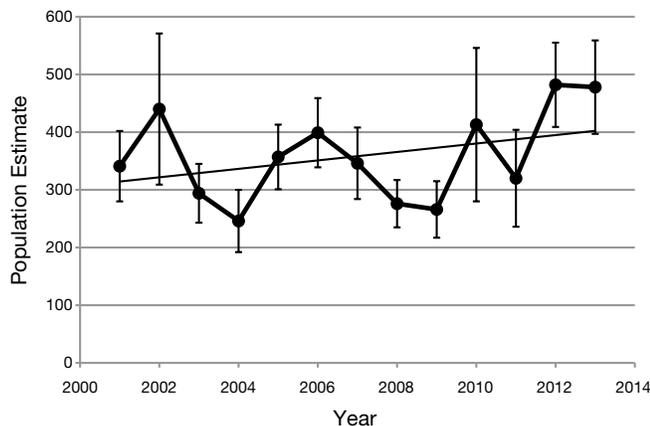


Fig. 2. Christmas Shearwater population size estimates on Kure Atoll by year, based on Huggins robust design mark-recapture analyses, with least squares regression line. Error bars are SE.

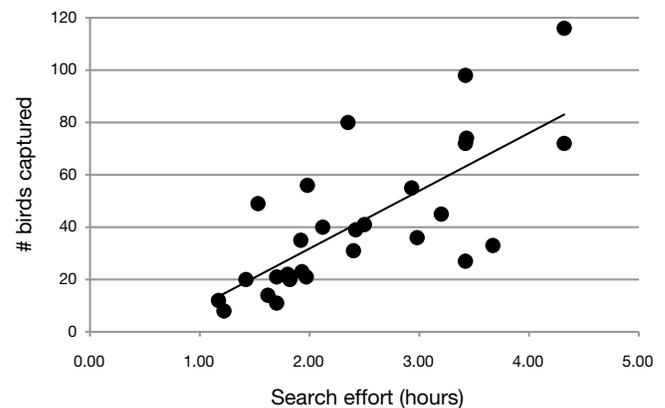


Fig. 3. Relationship between number of shearwaters captured and amount of time searched each night, and trend line. More hours searching resulted in more birds captured.

data), so our estimate represents about 90% of the population. No recent population estimates are available from other islands, but the colony on Kure is now among the largest in the Hawaiian Islands, after Laysan (1500–2000 pairs), Lisianski (400–600 pairs), and Nihoa (200–250 pairs) (Harrison 1990), all of which have never had predators. The number of Christmas Shearwaters on Midway has likely continued to increase from the 200 pairs reported in 1997, shortly after eradication of rats in 1995 (Seto 2001).

Ground-nesting seabirds are highly vulnerable to predation, and for small and medium-sized seabirds like the Christmas Shearwater, rats are one of the most serious non-native predators (Jones *et al.* 2008). Similar increases in shearwater numbers have been documented after eradications of rats from other islands in Hawai'i and elsewhere, including Christmas Shearwaters on Midway (Seto 2001), Wedge-tailed Shearwaters *Puffinus pacificus* on Mokolii (Smith *et al.* 2006) and Mokuauia islets near O'ahu (Marie *et al.* 2014), Cory's Shearwaters *Calonectris diomedea* in the Mediterranean (Iguar *et al.* 2006) and Audubon's Shearwaters *Puffinus lherminieri* on islands near Corsica (Pascal *et al.* 2008). Similarly, after a predator-proof fence successfully excluded black rats *Rattus rattus* from Kaena Point Natural Area Reserve on O'ahu (Young *et al.* 2013), the number of young Wedge-tailed Shearwaters produced in the reserve increased 385% in the first three years (VanderWerf *et al.* 2014).

The annual survival rate of resident adult Christmas Shearwaters estimated in this study, 0.864, is typical for a small Procellariiform seabird. The age of the oldest known bird in this study, 17 years 1 month, was similar to the previous longevity record of 17 years for an individual on Laysan (Seto 2001). Survival rate and lifespan in birds and other animals generally are correlated with body size (Sæther 1989, Ricklefs 2010). Larger seabirds, such as albatrosses, have higher survival rates, with healthy populations typically having an annual survival rate of 0.93 or higher (Véran *et al.* 2007, VanderWerf & Young 2011). In the Sooty Shearwater *Puffinus griseus*, which at 780 g is twice the body size of the Christmas Shearwater, Clucas *et al.* (2008) found that unbiased survival estimates of residents ranged from 0.917 to 0.966 at three sites, and estimates of survival in the first year after capture, which included transients, ranged from 0.398 to 0.734. The larger difference in survival rates in the first year and all subsequent years found by Clucas *et al.* (2008) indicate a much higher proportion of transients or pre-breeders was present in the populations, which likely is related to the much larger size of the Sooty Shearwater populations

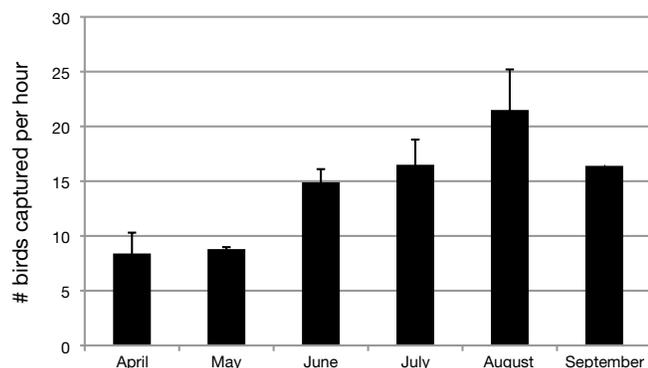


Fig. 4. Number of shearwaters captured per hour by month. Error bars are SE.

studied, up to 2.75 million pairs at one site. In Cory's Shearwater, which is among the largest shearwaters at 800 g, annual survival averaged 0.89 SE 0.02 (Brichetti *et al.* 2000). In smaller species, more similar in size to the Christmas Shearwater, estimates of annual survival have been similar to our estimate, including 0.90 in the Manx Shearwater *P. puffinus* (450 g; Perrins *et al.* 1973) and 0.84 in the Fairy Prion *Pachyptila turtur* (175 g; Croxall 1981). In the Balearic Shearwater *P. mauretanicus* (500 g) in Mallorca, Oro *et al.* (2004) found that annual survival was only 0.78 SE 0.02, unusually low for a Procellariiform seabird and an indication that the population was declining and threatened. By contrast, the high survival rate and increase in number of birds we found for the Christmas Shearwater on Kure following rat eradication indicate that the population is robust.

About 11% of the Christmas Shearwaters encountered on Kure appeared to be transients that visited the island for less than a year and did not breed there. Most of the transients probably returned to their island of origin, but some visitors, such as the three birds from Midway that we recaptured repeatedly, appeared to remain on Kure and become part of the breeding population.

About 25% of the Christmas Shearwaters captured on Kure emigrated at least temporarily each year; almost half of these probably were transients, as described above. Some of the other emigrants from Kure probably were pre-breeders that hatched on Kure and visited colonies on other islands in search of a mate and nest site. Once they had emigrated, most birds (83%) stayed outside the study area; this group presumably consisted of transients that had visited from another island. About 17% of birds that emigrated eventually returned to Kure, and many of those probably were pre-breeders that returned to nest on their natal island. Christmas Shearwaters from the colony on Kure probably interact most often with birds from the colony on Midway — the closest island at 89 km — as evidenced by the 13 birds from Midway recaptured on Kure. However, they also may interact with colonies on more distant islands such as Laysan, 720 km from Kure, which supports a larger colony (Seto 2001).

The average age at which we recaptured birds banded as chicks (3.9 years) agrees with Seto (2001), who reported that four birds were observed breeding for the first time at 4 years of age.

Another important management action on Kure has been to control the alien plant golden crownbeard *Verbesina encelioides*. This highly invasive plant can form dense stands that reduce the amount of breeding habitat for surface-nesting seabirds, particularly albatrosses, and can even entrap chicks among their tough stems (VanderWerf 2013). Christmas Shearwaters are less vulnerable to this plant because they nest under dense shrubs and not in the open, but efforts to control *Verbesina* will benefit Christmas Shearwaters by preventing loss of naupaka breeding habitat. Another alien plant, *Cassitha filiformis*, has spread recently on Kure and killed some naupaka shrubs under which Christmas Shearwaters nest (DOFAW unpubl. data). This alien should be controlled to ensure adequate breeding habitat remains available.

The results from this study may be useful in guiding studies of other ground-nesting seabirds in which nests are difficult to access. Despite our effort to standardize search effort by distance walked, the amount of time required to complete the circuit varied, largely depending on how many birds were captured. We recommend that effort be

standardized by amount of time spent searching and not just by the distance covered. In order to make best use of limited personnel time, capture efforts should be made first in August, July, and June, when shearwaters are feeding chicks, and in other months if workload allows. Christmas Shearwaters incubate eggs in April and May in shifts lasting 4–5 d, resulting in fewer trips away from the nest and less opportunity to catch them. When feeding chicks, they come and go from the nest more often, making them easier to catch. Although the effects of moon phase and wind speed on capture rate were not significant, there was a tendency toward fewer birds being captured when the moon was fuller and the wind was stronger. Capture efforts should be planned for dates with little or no moonlight. Adding observers to increase search effort is not a substitute for more search time. Too many observers actually may decrease capture rate by scaring birds away. A minimum of three people seems sufficient, and up to five is still useful, but more than that may be counter-productive.

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