The Condor 100:438–447

STATUS AND TRENDS OF THE ASHY STORM-PETREL ON SOUTHEAST FARALLON ISLAND, CALIFORNIA, BASED UPON CAPTURE-RECAPTURE ANALYSES[1]

WILLIAM J. SYDEMAN, NADAV NUR, ELIZABETH B. MCLAREN[2] AND GERARD J. MCCHESNEY[3]
Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970

Abstract. We conducted a capture-recapture study on the population size and trends of the Ashy Storm-petrel (*Oceanodroma homochroa*) on Southeast Farallon Island (SEFI), California, based upon data collected in 1971, 1972, and 1992. From March through August, birds were lured to fixed-site sampling locations using taped vocalization playback. Using program JOLLY, we estimated population size and evaluated statistical models using goodness-of-fit and Likelihood Ratio tests. On the southwestern slope of Lighthouse Hill, amidst prime breeding habitat, numbers of breeding birds decreased from 1,271 ± 140 ($\bar{x}$ ± SE) in 1972 to 710 ± 117 in 1992, a decline of 44% (approximate 95% CI = 22–66% decline; $\lambda = -2.8\%$ per annum); for a variety of reasons, we consider this to be the most reliable indicator of population change. In 1971, on a portion of SEFI relatively disjunct from the sampling area in 1972, 2,131 ± 322 breeding birds were estimated. To produce an overall early 1970s estimate with which to compare to 1992, we summed population estimates from 1971 and 1972. An overall value of 6,461 birds, of which 3,402 (53%) were breeders, was obtained for the early period. In 1992, the overall population in roughly the same area was estimated at 4,284 ± 409 birds, of which 1,990 ± 408 (46%) were presumed breeders. These results, encompassing peripheral as well as more centrally located storm-petrel habitat, indicate an overall population decline of 34% and a comparable decline in breeding birds of 42% over the past two decades. However, oceanographic conditions varied between 1971–1972 and 1992, and reduced food availability in 1992 may have influenced colony attendance and breeding effort. Nonetheless, the apparent population decline over the past 20 years suggests that the species warrants management and/or additional protective status.

Key words: Ashy Storm-petrel, capture-recapture analyses, conservation, Oceanodroma homochroa, *population estimation, Southeast Farallon Island.*

INTRODUCTION

The Ashy Storm-petrel (*Oceanodroma homochroa*) breeds primarily on islands off the coast of central and southern California. A few small colonies also occur in Baja California and northern California (Ainley 1995). Population size is poorly known, but over half of the population is believed to breed on Southeast Farallon Island (SEFI; 37°42'N, 123°00'W), California (Ainley et al. 1990, Carter et al. 1992). On SEFI and elsewhere, Ashy Storm-petrels breed in rock crevices, often deep beneath the surface of talus slopes, under boulders and in rock walls. Birds are nocturnal at breeding colonies, possibly as an adaptation to minimize predation by gulls (Ainley et al. 1974). As such, representative direct population counts are almost impossible to obtain. Instead, storm-petrel populations are often surveyed using capture-recapture techniques (e.g., Ainley and Lewis 1974, Furness and Bailee 1981, Furness 1984).

Using the Lincoln-Peterson model modified by an estimate of the extent of habitat surveyed, Ainley and Lewis (1974) estimated 4,000 breeding Ashy Storm-petrels on SEFI in 1972–1973. Sowls et al. (1980) estimated that this number represented 77% of the entire breeding population for this species. Ainley et al. (1990) later speculated that as many as 7,000 birds (including breeders and nonbreeders) were associated with the South Farallon Island (SFI) group, including SEFI and adjacent West End Island. They based this conclusion on large concentrations (~7,000 birds) in Monterey Bay each fall (Ainley 1976), although it is unknown what proportion of the Monterey Bay flocks come from the Farallon population. In 1991, an estimate of 3,100 breeding birds (Carter et al. 1992), a substantially larger population than was previously

[1] Received 29 May 1997. Accepted 27 March 1998.
[2] Present address: San Francisco Bay National Wildlife Refuge, P.O. Box 524, Newark, CA 94560.
[3] Present address: U.S. Geological Survey, Biological Resources Division, 6924 Tremont Road, Dixon, CA 95620.

reported (Hunt et al. 1979), was obtained for the southern California Channel Islands. Including sub-adults, the entire population from Baja California to the Oregon border is probably < 10,000 individuals (Ainley 1995). The species' status is uncertain as it faces a diversity of threats including predation by expanded populations of Western Gulls (*Larus occidentalis*), introduced house mice (*Mus musculus*), and physical and chemical pollutants (Coulter and Risebrough 1973, Sievert and Sileo 1993). Most significantly, the population is threatened by oil pollution, as one major spill near oceanic concentrations could extirpate much of the population. Concern for the species resulted in listing by the U.S. Fish and Wildlife Service as a Category 2 Candidate Species under the Endangered Species Act in 1994 (USFWS 1994). It is now considered a Species of Management Concern by both federal and state (California Department of Fish and Game) regulatory agencies.

To investigate the present status and trends of the Ashy Storm-petrel population on SEFI, we conducted an intensive capture-recapture study in 1992. Our study was similar in design to earlier capture-recapture field-work on this population (Ainley and Lewis 1974), but previous researchers did not focus on population estimation and did not use Jolly-Seber analytical techniques (Pollock et al. 1990). Our specific objectives were to: (1) estimate the population size of Ashy Storm-petrels on SEFI in the early 1990s and (2) assess trends in the population between the early 1970s and early 1990s. To meet the second objective, we reanalyzed data from 1971–1972 using modern techniques of population estimation, based on the Jolly-Seber method.

METHODS

SAMPLING LOCATIONS

From February 1971 through May 1973, biologists from Point Reyes Bird Observatory (PRBO) attempted to capture at least 30 birds every 5 days throughout the year (see Ainley et al. 1974, 1976). In 1971, sampling was concentrated on the southeastern edges of SEFI where many storm-petrels apparently make landfall. These locations are referred to as the Carpenter Shop (CS) and Domes (DO) sites (Fig. 1a). In 1972, netting was concentrated at four closely-spaced sites on a talus slope on the southwestern side of Lighthouse Hill (LHH), where breeding birds appeared prevalent. In 1992, storm-petrels were captured at LHH (2 sites), CS, and DO sampling sites. A new site, North Landing (NL), on the northeastern side of SEFI (Fig. 1a), also was sampled in 1992.

TECHNIQUES TO ATTRACT AND CAPTURE BIRDS

In 1971–1972, taped vocalizations of Leach's Storm-petrel (*Oceanodroma leucorhoa*) were used to attract storm-petrels to sampling sites (Ainley et al. 1974). In 1992, we used Ashy Storm-petrel vocalizations exclusively (recorded in 1971 by D. G. Ainley; see sonogram in Ainley 1995). Tape experiments conducted in 1990 indicated that substantially higher capture rates were achieved when vocalizations of target species were played (McChesney, unpubl. data). Birds attracted to sampling sites were caught in mist nets. We are unsure of the distance from which birds were attracted by tape-luring. During moonlit evenings storm-petrel activity on SEFI is greatly reduced (Ainley et al. 1990); winds also reduce capture efficiency because birds bounce out of mist nets more frequently. Therefore, to minimize time-dependent capture heterogeneity (Pollock et al. 1990), we did not attempt to capture storm-petrels under moonlit conditions nor when winds exceeded 10–15 km hr^{-1}.

FREQUENCY AND DURATION OF CAPTURES

During 1971 and 1972, an attempt was made to capture 30 birds every five days. Consequently, the frequency and duration of netting was inconsistent, dependent upon how quickly this objective was reached (although often > 30 birds were captured) and other factors. There also was no attempt to standardize netting hours during these years. Sampling was conducted on 36 nights in 1971: March, 2 nights; April, 6; May, 5; June, 10; July, 10; and August, 3. Sampling was conducted on 67 nights in 1972: March, 12 nights; April, 7; May, 11; June, 11; July, 10; and August, 16.

In 1992, we attempted to sample each capture location as many times as possible (weather and moonlight permitting) over the course of the breeding season, but within certain parameters. Sites were not sampled in adjacent evenings to minimize the potential of "trap shyness" which may have been caused by habituation to tape-vocalization playback. We also standardized the

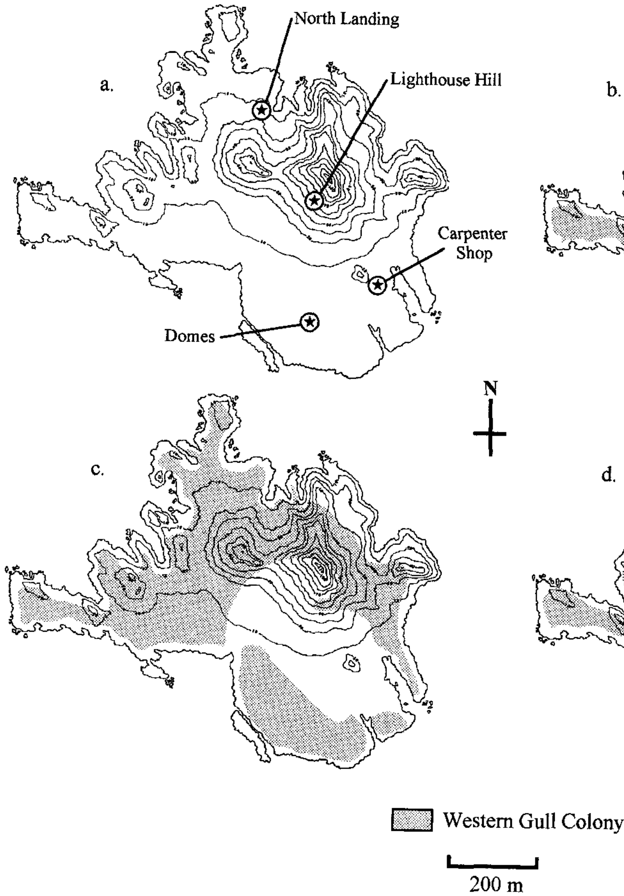

FIGURE 1. Map of Southeast Farallon Island (SEFI), California, showing (a) fixed site sampling locations in 1971, 1972, and 1992, and the distribution of the Western Gull colony in (b) 1959 (after Bowman 1961), (c) 1972 (after Ainley and Lewis 1974), and (d) 1992.

amount of time spent luring and capturing birds to 3 hr/sampling site/night. Sampling was conducted on 20 nights in 1992: March, 3 nights; April, 2; May, 3; June, 8; July, 4; no sampling was conducted in August. On almost all of these evenings, two sites were sampled simultaneously. Sampling was not equal at all sites. Numbers of sampling nights were: CARP, 12; LHH, 14; DO, 7, and NL, 5.

MARKING AND MORPHOMETRICS

Each storm-petrel captured was marked with a numbered metal band authorized by U.S. Fish and Wildlife Service. In 1971–1972, birds were banded with stainless steel "monel" bands, which we discovered (in the late 1970s) opened after long-term exposure to the marine environment. During 1971 and 1972, band loss was assumed to be zero. During most of 1992, we marked birds with incoloy bands made by Lambourne's Inc., Durham, United Kingdom. Starting in mid June 1992 and continuing in 1993, however, we used alloy rings, also made by Lambourne's. Unfortunately, we later (in 1993–1995) found that a few numbers etched in alloy bands became unreadable by the following year, presumably due to exposure to marine conditions. Luckily, this had no effect on our 1992 capture-recapture analyses because all alloy bands were readable throughout the 1992 capture-recapture period. Therefore, band loss also was assumed to be zero in 1992.

After banding, we assessed the condition of each bird's incubation patch in order to determine probable breeding status. Incubation patches were scored as defeathering (i.e., patch forming), bare, bare and vascularized, re-feathering (patch receding), or downy (i.e., no incubation patch evident). Birds with downy incubation patches were considered to be nonbreeders. It is possible that some nonbreeders may develop incubation patches (Ainley et al. 1974, Love 1978, Warham 1990). Consequently, breeding population estimates may be slightly biased high for that reason. We also measured wing chord length to aid in separating the dark-rumped morph of the Leach's Storm-petrel from the similar-looking Ashy Storm-petrel. It is not possible to sex Ashy Storm-petrels from external characteristics.

DATA ANALYSIS

We summarized capture-recapture histories for each month from March through August each year; pooling data by month was necessary to generate sufficient numbers of recaptures for statistical analyses (Table 1). The presumed breeding status of individuals was classified according to whether or not they were observed with positive incubation patch characteristics (i.e., anything other than downy) at least once during their capture-recapture history. We used open population models based on the Jolly-Seber method, utilizing program JOLLY (Seber 1982, Pollock et al. 1990), to estimate breeding and total population size each year. Open populations models are those in which immigration (including births) and/or emigration (including mortality) are assumed to occur between sampling occasions (Pollock et al. 1990). For analyses of population size, analyses were completed on between-month capture-recapture histories. Recruitment during our study was zero because fledging does not begin until late August or early September (Ainley et al. 1990). Therefore, within each season new individuals could enter the population only by immigration. Monthly survival probabilities estimated using program JOLLY, varied from $\phi = 0.654$ to 0.989, with 12 of 29 estimates exceeding 0.90. We note that capture-recapture analyses cannot distinguish between permanent emigration and mortality, unless other sites also are monitored.

Although some aspects of capture methodology differed between the 1970s and 1990s, it is valid to compare results between decades because capture-recapture analyses do not assume constant effort or, in general, that recapture probabilities remain constant through time. In fact, a distinct advantage of capture-recapture analyses is that one can test for significant variability in recapture probabilities between capture occasions and estimate population size accordingly (see below). Therefore, even though capture methodology changed somewhat through time, comparative analysis of the data using capture-recapture models is appropriate.

We estimated the population size ($\pm$ SE) for 1971, 1972, and 1992 using various statistical models which assume different parameter structure. Annual population estimates presented were generated using program JOLLY. In JOLLY, Model A is the standard Jolly-Seber model where survival and recapture probabilities are assumed to vary by capture period; this is the least parsimonious (i.e., most complex) model examined. Model A′ reflects a mortality-only model, assuming no immigration or recruitment during the capture-recapture periods, but is otherwise similar to Model A. Model B assumes constant survival probabilities and variable recapture probabilities between capture periods. Model D assumes constant survival and capture probabilities by capture period. We evaluated fit of each model to the data using goodness-of-fit tests (Pollock et al. 1990). In some cases, data were insufficient to allow goodness-of-fit testing. Models A′, B, and D also were evaluated by testing their underlying assumptions against Model A. For example, using a Likelihood Ratio (LR) test, Model B can be compared to Model A to test whether survival does (Model A) or does not (Model B) vary with time. Specifically, we evaluated the significance of immigration during the capture-recapture period within years by comparing Model A′ with Model A. Results from models which failed to produce estimates (failure of convergence), or models which could be rejected on statistical grounds as described above are not reported. To estimate the variance in population change, we used the following formula for the variance of a ratio (Mood et al. 1973):

$$\mathrm{var}\,(X/Y) = [E(X/Y)]^2\,[V_X/(\mu_X)^2 + V_Y/(\mu_Y)^2] \tag{1}$$

where X = population size in 1992, Y = population size in 1972, μ_X = mean of X and V_X = variance of X; same for μ_Y and V_Y. We then used the standard error of [X/Y] (i.e., variance $[X/Y]^{0.5}$) to construct approximate 95% confi-

TABLE 1. New captures (u_i = unmarked) and recaptures (m_i = previously marked) by month (March–August) of Ashy Storm-petrels on Southeast Farallon Island, California in 1971, 1972, and 1992. Birds marked in previous years (n = 41 from 1972 and n = 31 in 1992) are included as new captures. Recaptures in the month of original marking are excluded, as are multiple captures of the same bird within a single month.

	1971		1972		1992	
Month	u_i	m_i	u_i	m_i	u_i	m_i
March	14	0	103	0	28	0
April	61	1	75	1	128	4
May	104	1	114	10	181	7
June	539	37	252	21	397	84
July	191	45	160	37	258	85
August	14	6	133	69		
Total	923	90	837	138	992	180

dence intervals for the change in population size from 1972 to 1992.

RESULTS

CHARACTERISTICS OF THE DATASET

Captures totaled 1,013, 975, and 1,172 in 1971, 1972, and 1992, respectively (Table 1). Of these totals, 8.9%, 14.2%, and 15.4%, respectively, represented recaptures within each month (excluding birds caught in the month of initial capture and multiple recaptures within months). In 1971, 58.8% of the captured birds had incubation patch characteristics indicative of breeding. In 1972, 67.6% of the captured birds were presumed breeders. In 1992, 54.5% of the captures were of presumed breeders. These differences were statistically significant ($\chi^2_2 = 29.48$, $P < 0.001$); however, the proportion of breeding birds did not differ between 1971 and 1972 ($\chi^2_1 = 0.24$, $P > 0.6$).

ANNUAL ESTIMATES OF POPULATION SIZE

Population estimates for 1971, 1972, and 1992 are presented in Table 2. In 1971, when birds were mist-netted at CS and DO sites, mean (± SE) estimates including both breeders and nonbreeders ranged from 3,498 ± 1,808 to 4,232 ± 604. Estimates of only breeding birds ranged from 1,718 ± 880 to 2,131 ± 322. The breeding population was roughly half that of the total population. Model D failed to produce an estimate (failure to converge). Notably, Model A′ resulted in estimates with the smallest standard error, most reliable goodness-of-fit (breeders: $\chi^2_1 = 0.00$, $P > 0.9$; all birds: $\chi^2_1 = 0.01$, $P > 0.9$), and largest population estimates. Our assumption of no immigration between the sampling period was supported (all birds and breeders: LR test, both $P > 0.4$), confirming the validity of Model A′. Ainley et al. (1974) also indicated that most birds have arrived by May. Therefore, we conclude that Model A′ (no immigration between sampling periods, variable survival probabilities, and constant recapture probabilities) provides a reasonable fit to the data and the most valid representation of Ashy Storm-petrel population size in 1971.

In 1972, when most captures occurred on LHH, estimates of the total population ranged from 2,137 ± 756 to 2,369 ± 1098 birds; Model A was rejected due to lack of fit. The number

TABLE 2. Site-specific estimates of population size (arithmetic means ± SE) based on capture-recapture analysis using program JOLLY. Rejected estimates were those with either significant lack of fit or models whose assumptions were tested and rejected using Likelihood Ratio tests (e.g., $P < 0.05$). See text (or Pollock et al. 1990) for a description of models.

Year	Months	Criteria	Area[a]	Model A	Model A′	Model B	Model D
1971	May–July	breeders	CS/DO	1,718 ± 880	2,131 ± 322	1,765 ± 1,223	failed
1971	May–July	all birds	CS/DO	3,498 ± 1,808	4,232 ± 604	3,673 ± 2,586	rejected
1972	May–Aug.	breeders	LHH	948 ± 239	1,271 ± 140	1,079 ± 459	1,050 ± 369
1972	May–Aug.	all birds	LHH	2,300 ± 660*	2,229 ± 234*	2,369 ± 1,098	2,137 ± 756
1972	April–July	breeders	CS	418 ± 364	rejected	rejected	516 ± 412
1992	April–July	all birds	CS	660 ± 423*	rejected	1,013 ± 937	rejected
1992	April–July	breeders	LHH	684 ± 341	710 ± 117	786 ± 671	587 ± 268
1992	April–July	all birds	LHH	1,542 ± 535	1,595 ± 201	1,701 ± 961	1,543 ± 699
1992	April–July	breeders	all**	1,896 ± 665	1,990 ± 408	failed	failed
1992	April–July	all birds	all**	3,331 ± 875*	4,284 ± 409	3,268 ± 1,621	rejected

* Indicates an estimate with marginal goodness-of-fit (χ^2 with $0.10 > P > 0.05$).
** Indicates data from all sites illustrated in Figure 1a in 1992.
[a] CS = Carpenter Shop; DO = Domes; LHH = Lighthouse Hill; all includes CS, DO, LHH, and NL (= North Landing).

of breeding birds ranged from 948 ± 239 to 1,271 ± 140. The breeding population estimate was again roughly half that of the total population estimate. For breeding birds, each model produced remarkably similar estimates of population size. Model A′ resulted in estimates with the smallest standard error, most reliable goodness-of-fit (breeders: $\chi^2_5 = 6.72$, $P = 0.24$; all birds: $\chi^2_4 = 7.86$, $P = 0.09$), and largest population size. The assumption of no immigration during the capture-recapture sessions was supported (LR tests, $P > 0.20$ for all birds and breeding birds only). Therefore for 1972, Model A′ was the preferred model.

In 1992, three separate estimates were obtained: one for CS, one for LHH, and one for all areas combined. At the CS sampling site, results were difficult to interpret. The total population estimates ranged from 660 ± 423 to 1,013 ± 937, but the lower estimate was based on a model with marginal fit ($P = 0.08$) and inconsistent population estimates for each month. Moreover, all estimates had very large standard errors relative to the mean. The breeding bird population estimate was no more reliable, ranging from 418 ± 364 (Model A) to 516 ± 412 (Model D). Notably, Model A′, the preferred model from 1971 and 1972 analyses, was rejected (LR test against Model A).

The total population estimates at LHH ranged from 1,542 ± 535 to 1,701 ± 961 birds. Results on breeding birds at LHH ranged from 587 ± 268 to 786 ± 671. Whether investigating either breeding bird or total population size, Model A′ provided estimates with the smallest standard error and most reliable goodness-of-fit (all birds: $\chi^2_3 = 2.44$, $P = 0.49$; breeders: $\chi^2_2 = 1.08$, $P = 0.58$). The assumption of no new immigration also was supported ($P > 0.6$ for both total and breeders).

Combining sampling locations in 1992 resulted in a range of 3,268 ± 1621 to 4,284 ± 409 birds, and a range of 1,896 ± 665 to 1,990 ± 408 breeding birds. Model A′ provided the most reliable goodness-of-fit (all birds: $\chi^2_4 = 5.48$, $P = 0.24$; breeders: $\chi^2_4 = 4.26$, $P = 0.37$). The assumption of no immigration was supported (LR tests, both $P > 0.25$). Models B and D were rejected or failed in our analyses of all sites.

POPULATION CHANGE

We examined population change by comparing results obtained using Model A′ and by focusing primarily on LHH, an area centrally located on SEFI, encompassing prime storm-petrel nesting habitat, and including extensive sampling in both 1972 and 1992. Moreover, population estimates for this sampling area were characterized by consistent month-to-month population size estimates (as produced by JOLLY), narrow standard errors of final JOLLY population estimates, similar JOLLY population estimates based on different model structures, and considerable goodness-of-fit (Table 2). Thus, we consider data from LHH to be most reliable with respect to population size and population change. For LHH, breeding birds declined 44% (approximate 95% CI = 22–66% decline) from 1,270 in 1972 to 710 in 1992. The total population declined 28% (approximate 95% CI = 5–51% decline) from 2,230 in 1972 to 1,600 in 1992. The breeding bird population change reflects an annual rate of decline of 2.8% per year.

To assess population change on a broader spatial scale, we considered population estimates from both 1971 and 1972 and compared these values with an overall estimate produced by an analysis of all sites in 1992. In 1971, population estimates reflect capture efforts at the CS and DO sampling sites only (Fig. 1a). In 1972, estimates reflect efforts almost entirely on LHH. In 1992, we sampled the CS, DO, and LHH sites, as well as a new site, NL, on the eastern side of SEFI. Within 1971, there was little evidence of movements between the CS and DO sampling sites: including 90 recaptures of birds originally marked in 1971, only 8 (8.8%) reflected movement between sampling sites. Between 1971 and 1972, recaptures also were limited, with only 41 individuals (< 5%) of the total population marked in 1971 recaptured in 1972. Therefore, there is some justification in believing that capture-recapture surveys in 1971 and 1972 included relatively separate storm-petrel habitat and populations (see also Ainley and Lewis 1974). Consequently, to produce an early 1970s population estimate, we summed results of 1971 and 1972 to obtain an overall estimate of total and breeding bird population size for the early 1970s. Estimates for this period for total and breeding population size were 6,461 and 3,402, respectively.

In contrast, the estimate in 1992 for total and breeding population size based on all sampling sites was 4,280 and 1,990, respectively. Although an additional sampling site was included in 1992, these results indicate a 34% decline in the total population and a 42% decrease in breeding birds between the early 1970s and 1992. However, in contrast to the above results for 1971, of 190 recaptures in 1992 (including multiple recaptures within a month), 66.3% recaptures reflected movement between the site of original marking and the site of recapture. Movement between sites also was significantly related to the site of original capture in 1992 (χ^2_3 = 10.03, P = 0.018): 56% of the recaptures of birds originally marked at LHH involved movement, whereas 71%, 69%, and 94% of the recaptures from birds originally marked at the CS, DO, and NL sites, respectively, reflected movement. These results bear upon our assessment of population change in two ways. First, they again highlight the relative importance of the LHH sampling area. Second, they suggest that our analyses of all 1992 sites may provide a reasonable whole-colony population estimate, even though all available habitat probably was not surveyed (see below).

DISCUSSION

POPULATION ESTIMATION

Estimating population size using capture-recapture analyses can be difficult (Pollock et al. 1990). Previous storm-petrel capture-recapture studies have met with mixed success primarily due to difficulties in obtaining adequate sample sizes of recaptures and meeting model assumptions. In particular, the wandering nature of failed and nonbreeders and uncertainty in separating breeders from nonbreeders are potential problems (Love 1978, Furness and Baillie 1981). We experienced a few problems with the analysis of data, including failure of the modeling process to produce estimates (i.e., failure to converge) and relatively poor goodness-of-fit in some cases. But, our study also resulted in many reasonable estimates, especially those associated with Model A′ and the LHH sampling site. Notably, even if survival probabilities are biased, we feel that survival estimates for LHH in 1972 and 1992 are similarly biased (and survival estimates are similar), such that assessment of population change is possible.

However, numbers of birds, i.e., estimates of breeding and total population size, should be interpreted more cautiously. A whole-colony population estimate is presently unavailable because surveys in both 1971–1972 and 1992 covered only a portion of SEFI and none of adjacent West End Island and surrounding sea-stacks. Although habitat availability on West End and the islets does not appear as favorable as sampled areas on SEFI (Sydeman, pers. observ.), some birds undoubtedly occur there. Moreover, even for SEFI, we cannot be confident that we obtained thorough coverage of all habitat. Whereas luring storm-petrels via tape vocalization playback may be an effective means of capturing and recapturing relatively large numbers of birds, the amount of habitat surveyed is generally unknown and without this information it is impossible to derive a whole-colony population estimate. Assessing the distance from which birds are lured, a difficult task indeed, as well as general movement patterns of birds around the colony (see below), is an important aspect of storm-petrel population estimation, and should be included in all capture-recapture studies.

Of all the estimates produced, we are particularly concerned with those for the CS sampling site in 1992. Although Models A, B, and D provided relatively adequate fit (largest P = 0.08), month-to-month population estimates were inconsistent and all final estimates had large standard errors. Model A′ was rejected by LR test, indicating possible immigration during the capture-recapture period. In considering these analyses, large standard errors by themselves simply portray the level of uncertainty in estimates (J. Nichols, pers. comm.), so we were not misled by the analysis technique *per se*. The rejection of Model A′ and lack of fit for most models may have been related to heterogeneity in recapture probabilities caused by nonbreeders and/or large numbers of transients at the CS site. Ainley et al. (1974) also suggested that transient birds may be found at the CS location. Transients may be nonbreeders which visit the island briefly or may be breeders moving into and out of the CS area on route to other habitat on the island. Although we cannot fully explain problems of population estimation associated with the CS sampling site in 1992, estimation of survival probabilities may have been biased by the inclusion of transient birds. This possibility highlights the need to carefully select fixed-site sampling locations when conducting capture-recapture studies of storm-petrel populations. Efforts to estimate population size based upon sites where substantial movement occurs or where transients and nonbreeding birds greatly exceed numbers of local breeders may meet with difficulties, especially if the recapture probability of nonbreeders is considerably less than that for breeders as would be generally expected. Fixed-site sampling locations located in the center of preferred breeding habitat would appear most likely to produce rigorous population estimates.

POPULATION CHANGE

Efforts to estimate the breeding population in the midst of prime Ashy Storm-petrel breeding habitat (LHH) were successful in both 1972 and 1992 with regard to providing estimates with relatively small standard errors and substantial goodness-of-fit. In particular, this information on both the total and breeding population size of Ashy Storm-petrels on LHH can be used to assess population change with confidence. Changes in population size on LHH suggests a decrease of 28–44%, with the decline apparently greater for breeding birds. The population trends on LHH were supported by population estimates for all sites in 1992 in comparison with summarized information from 1971 and 1972. The analysis of all sites in 1992 and combined 1971–1972 data, although somewhat less rigorous than the information obtained for LHH alone, also indicates a substantial decline, 34–42% over the 20 year period, with the decrease also apparently greater for breeding birds. Confidence intervals indicated a range of decline of 5–66% for total and breeding populations over the 20 year period for the LHH sampling site.

The overall change in population size and apparent discrepancy in population change for the total versus breeding populations may be partially related to variability in food availability and other oceanographic conditions between the early 1970s and 1992. During 1992 the central California coastal marine ecosystem was affected by a severe El Niño event (Hayward et al. 1994). During El Niño, coastal food webs are perturbed and the availability of seabird prey is often greatly reduced (Ainley et al. 1995). In response, fewer storm-petrels may have attended the colony and a lower proportion of birds may have attempted to reproduce in 1992. This type of multifaceted response to poor food availability has been observed for other Farallon seabirds (e.g., Brandt's Cormorant, *Phalacrocorax penicillatus*; Boekelheide and Ainley 1989). Although we have no means of assessing colony attendance, incubation patch characteristics probably explain some of the differences in breeding population size between 1971–1972 and 1992, but these differences are insufficient to account for the overall magnitude of population decline. Moreover, whereas breeding population size change may be somewhat over-estimated by differences in environmental conditions, the same cannot be argued for total population trends which include all birds regardless of reproductive status. Therefore, we remain confident that the SEFI Ashy Storm-petrel population has declined considerably. Results on incubation patch scores also illustrate the value of evaluating the probable breeding status of birds lured to capture sites and the necessity of this information when evaluating population change.

POPULATION CHANGE AT OTHER COLONIES

No information is available on population change at other Ashy Storm-petrel colonies in southern or central California. On Prince Island, southern California, Carter et al. (1992) estimated ~1,150 breeding Ashy Storm-petrels, 100% higher than the 600 birds estimated in 1976–1977 (Hunt et al. 1979). Carter et al. (1992) concluded that "our higher estimate probably reflected greater survey effort ..." Similarly, at another relatively large colony in southern California, Santa Barbara/Sutil Island, Carter et al. (1992) estimated ~1,460 breeding birds, 400% higher than the 350 birds estimated in 1976–1977 (Hunt et al. 1979). Again, they attributed the higher estimate entirely to greater survey effort.

FACTORS AFFECTING THE SEFI POPULATION

In many long-lived vertebrates, including procellariid seabirds, population dynamics may be determined primarily by adult and sub-adult survival, rather than changes in fecundity (Croxall and Rothery 1991). This also may be the case for Ashy Storm-petrels on SEFI (Sydeman et al. 1998). The decline in population size between the early 1970s and 1990s may be due, in part, to an increase in the predation rate on Ashy Storm-petrel adults and sub-adults by Western Gulls. The SEFI Western Gull colony has expanded greatly over the past 40 years (Fig. 1b, c, d), as they recovered from human persecution in the late 1800s and early 1900s (Ainley and Lewis 1974). Additionally, an obvious expansion of gulls into prime Ashy Storm-petrel nesting habitat (on LHH and at the CS and DO sites) occurred after the early years of this study. Ashy Storm-petrel breeding habitat on the slopes of LHH and the southwestern marine terrace was mostly devoid of nesting gulls apparently until 1976 (Fig. 7.2 in Ainley et al. 1974). Although we have limited quantitative information on the predation rate on storm-petrel adults, it is clear that gulls take scores, possibly hundreds, of Ashy Storm-petrels each year (Sydeman et al. 1998).

Other predators which may influence the viability of the SEFI Ashy Storm-petrel population include Burrowing Owls (*Athene cunicularia*), which also prey upon storm-petrel adults (PRBO, unpubl. data), and house mice, which prey upon eggs and chicks (Ainley et al. 1990). Burrowing Owls winter on SEFI and occur less frequently during the breeding season (PRBO, unpubl. data). Indications are that few Ashy Storm-petrels are taken by owls during the summer, but we have little information concerning take during the winter and early spring when both owls and storm-petrels are present. The magnitude of owl predation, however, is likely small compared to the effect of gull predation. House mice prey upon storm-petrel eggs and chicks, although evidence is limited. However, unless this effect is chronic, changes in reproductive success are less likely to have an effect on population dynamics than changes in adult or sub-adult survival. Habitat changes also may have affected storm-petrels over the long-term, including habitat loss (and some gain) from building and pathway construction. Construction of rock walls next to pathways and elsewhere, while providing some additional nest sites, undoubtedly resulted in a loss of habitat from talus slopes when rocks were removed from their original location. Subsequent demolition of many rock walls probably resulted in a greater net loss of habitat, even though some walls were rebuilt in the early 1970s in an attempt to restore storm-petrel habitat (Ainley et al. 1990).

The Ashy Storm-petrel was listed by the U.S. Fish and Wildlife Service (USFWS) as a Category 2 candidate for endangered/threatened species in November 1994 (USFWS 1994), although since that time USFWS has abandoned use of this designation. They are currently listed as a Species of Management/Special Concern by USFWS and the California Department of Fish and Game (Remsen 1978), respectively. Given their small population size, localized distribution, numerous threats, and results herein indicating substantial decline of the SEFI population, the species may deserve additional protective status or management action. Our work, focused on SEFI, covered a significant portion of all Ashy Storm-petrel nesting habitat. Suitable habitat on West End Island appears limited, and we would not anticipate large numbers of birds there. Moreover, we could not determine if the rate of population change was constant, accelerating, or decelerating. Population studies should be repeated and expanded and an investigation of factors influencing the SEFI Ashy Storm-petrel population conducted to further assess and understand the population change described herein.

ACKNOWLEDGMENTS

Data analysis and manuscript preparation was funded by National Oceanic and Atmospheric Administration–Gulf of the Farallones National Marine Sanctuary (GFNMS), under contract CX-8140-93-016. PRBO, USFWS–San Francisco Bay National Wildlife Refuge, and Friends of the Farallones provided financial assistance for fieldwork. Early comments on the manuscript by M. Hester, J. Roletto, J. Thayer, and E. Ueber were helpful in improving the presentation. J. Thayer also prepared Figure 1. Critical reviews by J. Nichols and J. Spendenlow were particularly helpful in finalizing this work; the method for constructing CI of population change was suggested by J. Nichols. Studies on the Farallon National Wildlife Refuge are facilitated by the U.S. Fish and Wildlife Service under a unique long-term Cooperative Agreement with PRBO. We are indebted to J. Buffa, R. Colemen, M. Kolar, R. Lowe, J. Takekawa, and others for their dedication to this arrangement and efforts to keep PRBO personnel stationed on SEFI for the past 30 years. Capture and marking of storm-petrels was assisted by numerous volunteer field biologists; to all we offer our sincere gratitude. This is PRBO contribution no. 714.

LITERATURE CITED

AINLEY, D. G. 1976. The occurrence of seabirds in the coastal region of California. West. Birds 7:33-68.

AINLEY, D. G. 1995. Ashy Storm-Petrel (*Oceanodroma homochroa*). *In* A. Poole, and F. Gill [eds.], The birds of North America, No. 185. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.

AINLEY, D. G., R. P. HENDERSON, AND C. S. STRONG. 1990. Leach's and Ashy Storm-Petrel, p. 128–162. *In* D. G. Ainley, and R. J. Boekelheide [eds.], Seabirds of the Farallon Islands. Stanford Univ. Press, Palo Alto, CA.

AINLEY, D. G., AND T. J. LEWIS. 1974. The history of

Farallon Island marine bird populations, 1854–1972. Condor 76:432–446.

AINLEY, D. G., S. MORREL, AND T. J. LEWIS. 1974. Patterns in the life histories of storm-petrels on the Farallon Islands. Living Bird 13:295–312.

AINLEY, D. G., W. J. SYDEMAN, AND J. NORTON. 1995. Upper trophic level predators indicate inter-annual negative and positive anomalies in the California Current food web. Mar. Ecol. Progr. Ser. 118:69–79.

BOEKELHEIDE, R. J., AND D. G. AINLEY. 1989. Age, resource availability, and breeding effort in Brandt's Cormorant. Auk 106:389–401.

BOWMAN, R. I. 1961. Late spring observations on birds of South Farallon Island, California. Condor 63:410–416.

CARTER, H. R., G. J. MCCHESNEY, D. L. JACQUES, C. S. STRONG, M. W. PARKER, J. E. TAKEKAWA, D. J. JORY, AND D. L. WHITWORTH. 1992. Breeding populations of seabirds in California, 1989–1991. Unpubl. Final Rep., U.S. Fish Wildl. Serv., Northern Prairie Wildl. Res. Center, Dixon, CA.

COULTER, M. C., AND R. W. RISEBROUGH. 1973. Shell thinning in eggs of the Ashy Storm Petrel (*Oceanodroma homochroa*) on the Farallon Islands. Condor 75:254–255.

CROXALL, J. P., AND P. ROTHERY. 1991. Population regulation in seabirds: implications for their demography and conservation, p. 272–296. *In* C. M. Perrins, J-D. Lebreton, and G. J. M. Hirons [eds.], Bird population studies. Oxford Univ. Press, Oxford.

FURNESS, R. W. 1984. Leach's petrel on St. Kilda. British Ecol. Soc. Bull. 15:84–87.

FURNESS, R. W., AND S. R. BAILEE. 1981. Factors affecting capture rates and biometrics of storm petrels on St. Kilda. Ring. Migr. 3:137–147.

HAYWARD, T. L., A. W. MANTYLA, R. J. LYNN, P. E. SMITH, AND T. K. CHERESKIN. 1994. The state of the California Current in 1993–1994. Calif. Coop. Oceanic Fish. Invest. Rep. 35:19–35.

HUNT, G. L., JR., R. L. PITMAN, M. NAUGHTON, K. WINNETT, A. NEWMAN, P. R. KELLY, AND K. T. BRIGGS. 1979. Distribution, status, reproductive ecology, and foraging habits of breeding seabirds. Summary of marine mammal and seabird surveys of the southern California Bight area, 1975–1978. U.S. Dept. Commerce, NTIS, Springfield, VA. Publ. No. P8-81-248-205.

LOVE, J. A. 1978. Leach's and storm petrels on North Rona: 1971–1974. Ring. Migr. 2:15–19.

MOOD, A., F. A. GRAYBILL, AND D. C. BOES. 1973. Introduction to the theory of statistics. 3rd ed. McGraw Hill, New York.

POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107:1–97.

REMSEN, J. V., JR. 1978. Bird species of special concern in California. Calif. Dept. Fish Game Wildl. Branch Admin. Rep. No. 78-1, Sacramento, CA.

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. MacMillan Press, New York.

SIEVERT, P. R., AND L. SILEO. 1993. The effects of ingested plastic on the growth and survival of albatross chicks, p. 212–217. *In* K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey [eds.], The status, ecology, and conservation of marine birds of the north Pacific. Can. Wildl. Serv. Spec. Publ., Ottawa, Canada.

SOWLS, A. L., A. R. DEGANGE, J. W. NELSON, AND G. S. LESTER. 1980. Catalog of California seabird colonies. U.S. Dept. Interior, Fish and Wildl. Serv., Biological Serv. Progr., Washington, DC, FWS/OBS 37/80.

SYDEMAN, W. J., N. NUR, AND P. MARTIN. 1998. Population viability analyses for endemic seabirds of the California marine ecosystem: the Ashy Storm-petrel and Xantus' Murrelet. Unpubl. Final Rep., Point Reyes Bird Observatory, Stinson Beach, CA.

U.S. FISH AND WILDLIFE SERVICE. 1994. Endangered and threatened wildlife and plants: animal candidate review for listing as endangered or threatened. Federal Register 59:58981–59028.

WARHAM, J. 1990. The petrels: their ecology and breeding systems. Academic Press, London.