

SURVIVAL RATES FOR THE HAWAIIAN MONK SEAL (*MONACHUS SCHAUINSLANDI*)

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ABSTRACT

Endangered Hawaiian monk seal (*Monachus schauinslandi*) pups at all the major breeding islands in the Northwestern Hawaiian Islands have been tagged since the early 1980s. Pups were double flipper tagged as soon as possible post-weaning. With few exceptions, an extensive tag resighting effort was conducted annually at the same islands. These resighting data were used to estimate seal survival rates from the time of tagging to age one at all locations using the ratio of seals alive in the second year to number of pups tagged. These survival rates among the islands, from weaning to age one, averaged over the years of the study, ranged from 0.80 to 0.90. For young seals over age one, capture-recapture methods were used to calculate survival pooled through several years, and these rates ranged from 0.85 to 0.98. At French Frigate Shoals and Laysan Island, the higher numbers of tagged pups allowed separate estimates of male and female survival to be calculated. These rates suggested that survival of immature females was better than males. Beginning in 1989, survival of immature seals at French Frigate Shoals declined sharply.

Key words: Hawaiian monk seal, *Monachus schauinslandi*, survival, tag resighting, Jolly-Seber.

The Hawaiian monk seal population has declined substantially in numbers since the first reliable range-wide counts were made in the late 1950s (Rice 1960; Johnson *et al.* 1982; NMFS, unpublished data). Concern over this decline led to the species being listed as endangered under the U.S. Endangered Species Act in 1976. In order to assess possible causes of the decrease, monitor the status of the population, and evaluate the efficacy of recovery actions, tagging of weaned pups was initiated on Kure Atoll in 1981 (Gilmartin *et al.* 1986), Lisianski Island in 1982 (Henderson and Johanos 1988), and then expanded to all other major breeding islands by 1984. Pup tagging and intensive resighting

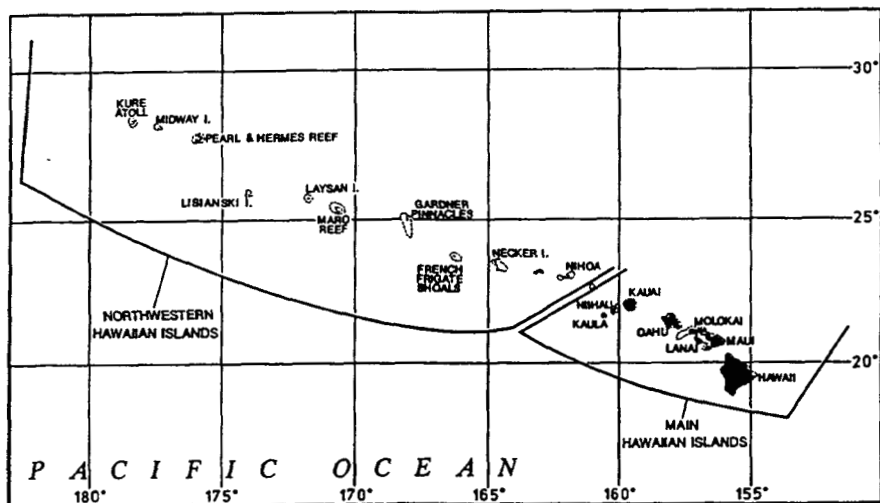


Figure 1. Hawaiian Archipelago.

efforts have involved long visits to most of the sites in subsequent years, resulting in resighting of a high fraction of the surviving tagged individuals. Assessment of survival from birth to weaning for the Hawaiian monk seal has been based on counts of dead pups of preweaning age recovered annually from the breeding islands. These data show preweaning survival among the breeding sites to be approximately 93% (NMFS, unpublished data).

The present paper reports survival rates among the five major monk seal breeding locations at Kure Atoll, Pearl and Hermes Reef, Lisianski and Laysan Islands, and French Frigate Shoals (Fig. 1) determined from the resighting data of pups tagged post-weaning.

METHODS

Pup tagging—Beginning in 1981, weaned Hawaiian monk seal pups were tagged with colored and engraved plastic Temple Tags® between the fourth and fifth digit of each rear flipper as described by Gilmartin *et al.* (1986). A study to evaluate the effects of tagging weaned pups was conducted on Lisianski Island in 1982 utilizing a control group of weaned pups that were only marked with identifying numbers applied to the pelage with a commercial hair bleach when the seals were sleeping (Henderson and Johanos 1988). Results of this pilot study did not indicate significant differences between the tagged and control groups and enabled the pup tagging effort to be conducted at all breeding locations in subsequent years. Pups are double-tagged and lost tags are replaced soon after one tag is observed missing. Identities of seals based on photographs of scars and natural markings are also annually updated and cataloged. The latter effort provides a means of individual identification should both flipper tags be lost at the same time and assures that tag loss is of minor importance.

No tagging or resighting effort occurred at Lisianski Island in 1989, and abbreviated visits were necessary at Lisianski Island in 1988 and Pearl and Hermes Reef in 1990, reducing the number of pups tagged and the resighting effort for those years.

Estimation of survival rates—Although high annual resighting rates of tagged individuals were common, a few individuals were not seen in some intervening years, and others were identified at sites other than those at which they were tagged initially. Therefore, the most general capture-recapture model, the Jolly-Seber method (Seber 1982), was used for parts of the study. However, in most instances the very high resighting rates and fidelity to birth sites facilitated the use of much simpler estimation models, described by Haldane (1955) and Chapman and Robson (1960).

Even though nearly all of the weaned pups were tagged in most years, the low number of pups born annually at sites other than French Frigate Shoals resulted in small numbers being available for tagging, thus males and females were combined for many of the analyses. The small numbers also made it advantageous to use the simplest survival model available.

The simple model used here assumes a constant annual survival rate, and can be written as:

$$n_x = ps^x N \quad (1)$$

where N is the initial number tagged, s is annual survival rate, p is proportion of those present actually resighted in a given year, and n_x is the number resighted in year x . Haldane (1955) used a similar geometric model but considered the numbers of tagged individuals dying in each year. Chapman and Robson (1960) gave an extensive analysis of the geometric distribution for use in estimating survival rates from a "catch curve"; *i.e.*, numbers of individuals of successive ages in a sample. Seber (1982: Sec. 5.4) gives a general model for tag recoveries from dead animals.

If one takes the natural logarithm of Equation 1, a linear equation results:

$$\log_e n_x = \log_e(pN) + x \log_e s, \quad (2)$$

and this can be fitted by ordinary regression methods. This approach is not as satisfactory as methods based on Equation 1 because using Equation 2 on results of a tagging study is not likely to conform to the normal theory model for linear regression (Chapman and Robson 1960). However, some of the data of this study has missing years and years of low resighting rates, so the regression model is useful for provisional analyses of such data because these years can be excluded in the regression model.

Chapman and Robson (1960) gave an equation for the maximum likelihood estimator for a sequence of observations from a geometric distribution:

$$\frac{T}{n} = \frac{s}{1-s} - \frac{(k+1)s^{k+1}}{1-s^{k+1}}; \quad (3)$$

where k denotes the number of successive observations beyond the first used, $n = n_0 + n_1 + n_2 + \dots + n_k$, where n_i is the number of individuals observed

on the i th occasion, and $T = n_1 + 2n_2 + \dots + kn_k$. This equation must be solved by iteration.

Haldane (1955) considered the situation where several such sequences were combined. Using the notation above, his equation becomes:

$$\Sigma \left\{ \frac{T_j}{n_j} - \left[\frac{s}{1-s} - \frac{(k_j + 1)s^{k_j+1}}{1-s^{k_j+1}} \right] \right\} = 0; \quad (4)$$

with the variance estimate:

$$\text{Var}(s) = \left[\Sigma \left\{ \frac{n_j}{s(1-s)^2} - \frac{(k_j + 1)^2 s^{k_j-1} n_j}{(1-s^{k_j+1})^2} \right\} \right]^{-1}. \quad (5)$$

It should be noted that the above methods all assume that both p and s are constant throughout.

First-year survival rates were estimated differently. Long visits to each site and frequent observations resulted in very high resighting rates in most instances. Occasionally, an individual was not observed in a given year, but survivors were almost always seen in the second year. Consequently, "back-corrections" could be used after an interval of two or three years, and first-year survival calculated as the ratio of numbers alive in the second year over number of weaned pups tagged. For consistency, and to be virtually certain of the back-calculations, we based first-year survival estimates on data for cohorts tagged through 1987.

Pollock *et al.* (1990) note that estimates of the kind used here to calculate first-year survival may be subject to a negative bias. This possibility was evaluated by using equation 5.2 of Pollock *et al.* (1990) along with an equation for the probability that an individual will be sighted again given by Lebreton *et al.* (1992). Jolly-Seber calculations for sites other than Kure (where survival is very high and potential bias negligible) gave an average probability of sighting (P) of 0.98 at sites other than Pearl and Hermes Reef, where it averaged 0.95. Assuming a first-year survival rate of 0.8 and subsequent annual survival rates of 0.9, the bias was less than one percentage point of survival, and thus was neglected.

A Kure Atoll recovery project (Gerrodette and Gilmartin 1990) involved collection and rehabilitation of some emaciated female pups from French Frigate Shoals and release of them at Kure, so the first-year survival at French Frigate Shoals is based on the number of tagged pups less those removed for rehabilitation (listed separately in Table 1).

The Jolly-Seber method—The general Jolly-Seber method is discussed in detail by Seber (1982: chapter 5). In this form the method utilizes repeated releases of newly tagged individuals, along with those animals caught on the i th capture occasion that had been tagged previously. Seber denotes these releases of previously and newly tagged animals as R_i , while previously tagged animals caught on the i th occasion are denoted as m_i . Inasmuch as there was no tagging after the first release of a tagged cohort in the present context, we have $R_i = m_i$. Two other quantities needed here are r_i , the number of tagged individuals caught later of those (R_i) released on the i th occasion, and z_i , the number of individuals tagged before the i th sampling occasion and caught after that occasion but not

caught on the i th occasion. With this notation, the estimate of survival from occasion i to occasion $i + 1$ (Seber 1982: equation 5.9) becomes:

$$\hat{\Phi}_i = \frac{m_{i+1} \left(\frac{z_{i+1}}{r_{i+1}} + 1 \right)}{m_i \left(\frac{z_i}{r_i} + 1 \right)}. \quad (6)$$

Because a very high fraction of tagged animals are seen each year, the z_i are frequently zero (or very small), so the survival estimates by this equation reduce largely to the ratio of tagged individuals resighted in two successive years. With relatively small samples such ratios will be highly variable so Equation 6 is only used for the largest samples here. However, the Jolly-Seber calculations were conducted on data from all sites other than Kure, to provide estimates of the probability of sighting to check on the bias in estimating first-year survival described by Pollock *et al.* (1990).

Variance of survival estimates—Because the present application of the method of Haldane (1955) is based on repeated observations of the same individuals, it seemed worthwhile to check the variance estimate of Equation 5. This was done with a monte carlo simulation with 30 tagged seals in each of 6 cohorts, survival of 0.90, annual sighting probability of 0.95, and runs of 1,000 simulations. The outcomes gave survival estimates very close to 0.90, but 95% confidence limits were appreciably too wide (“coverage” of about 99.9%) while percentile confidence limits from bootstrapping (Efron and Gong 1983) in the simulations were close to 95%. Consequently, bootstrapping confidence limits (B.C.L.) are given here for all estimates, with the exception of data from Kure Atoll, where convergence problems in the bootstrapping led to use of Equation 5.

RESULTS

A summary of the tagging and resighting data appears in Table 1, and the analyses are discussed by individual sites below:

Kure Atoll—Kure sample sizes are small, but survival rates were 100% for tagged cohorts over long time periods (Table 1), and only in two instances was a tagged individual not seen in one year, then seen later. Using the ratio of one-year-olds to those tagged as weaned pups from 1981 through 1987 gave a first-year survival of $28/32 = 0.88$. Pooling all of the Kure Atoll sighting data from the first resighting onwards gave an overall survival rate Equation 4 of 0.98 (0.03). The standard error from Equation 5 is given in parentheses after the estimate. Clearly, the main losses observed at Kure Atoll were in the first year after tagging. The Kure Atoll data in Table 1 are from Kure-born seals only. However, rehabilitated yearlings placed at Kure have also shown good survival after release.

Pearl and Hermes Reef—This site is difficult to survey adequately for tag resightings because the atoll contains many small islets scattered along the fringing reef on which monk seals haul out and can be easily disturbed by an observer.

Table 1. Resighting data for Hawaiian monk seals tagged as weaned pups on major sites. KUR = Kure Atoll, PHR = Pearl and Hermes Reef, LIS = Lisianski, LAY = Laysan, and FFS = French Frigate Shoals. The tag resighting effort was low in some years.^a Some undersized weaned pups were removed from the population for rehabilitation and eventual release or for permanent captivity.^b The table excludes survival data from these seals, however, the total number tagged, including these seals, is shown in parentheses.

Island	Year	Sex	No. tagged	Number seen in year X										
				1	2	3	4	5	6	7	8	9	10	
KUR	1981	F	5	4	4	4	4	4	4	4	3	4	4	2
KUR	1982	M	3	3	3	3	3	2	2	2	2	2	2	2
KUR	1982	F	3	3	3	3	3	3	3	3	3	3	3	3
KUR	1983	M	1	0	0	0	0	0	0	0	0	0	0	0
KUR	1983	F	0											
KUR	1983	M	4	3	3	3	3	3	3	2	3	3	3	
KUR	1984	F	2	2	2	2	2	2	2	2	2	2	2	2
KUR	1984	M	4	3	2	2	2	2	2	2	2	2	2	2
KUR	1985	F	3	3	3	3	3	3	3	3	3	3	3	3
KUR	1985	M	2	2	2	2	2	2	2	2	2	2	2	2
KUR	1986	F	0											
KUR	1986	M	1	1	1	1	1	1	1	1	1	1	1	1
KUR	1987	F	3	3	3	3	3	3	3	3	3	3	3	3
KUR	1987	M	1	1	1	1	1	1	1	1	1	1	1	1
KUR	1988	F	5	3	3	3	3	3	3	3	3	3	3	3
KUR	1988	M	2	2	2	2	2	2	2	2	2	2	2	2
KUR	1989	F	4	2	1	1	1	1	1	1	1	1	1	1
KUR	1989	M	5	5	4	4	4	4	4	4	4	4	4	4
PHR	1983	F	2	1	1	1	1	1	1	1	1	1	1	1
PHR	1983	M	8	5	6	6	5	6	6	6	6	6	6	5

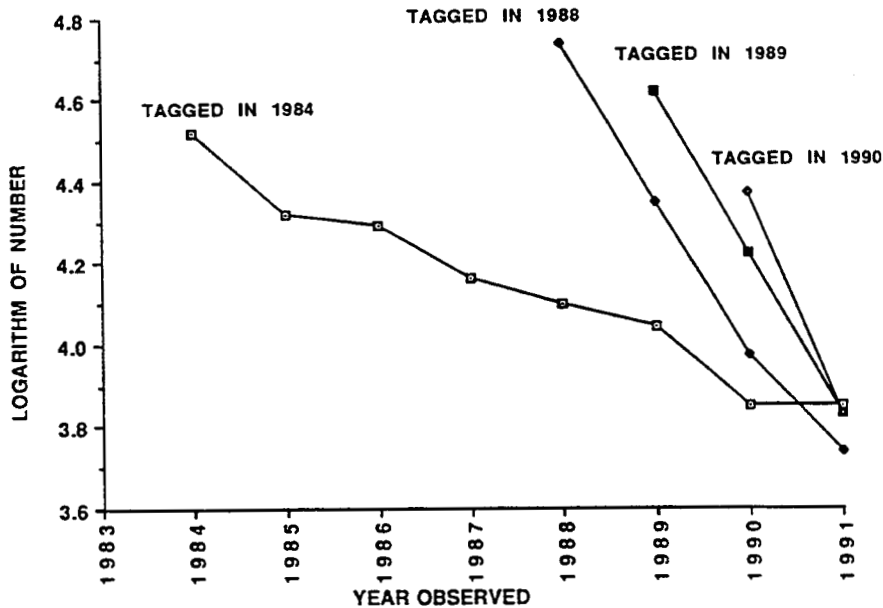


Figure 2. Logarithms of resightings of tagged seals at French Frigate Shoals. First points in each series are number tagged.

Most of the births occurred on the two northernmost islands (Westlake and Gilmartin 1990). Only a short duration field camp was possible in 1990, so that the number of resightings dropped sharply in that year. However, the number of sightings rose again in 1991, indicating that survival remained high (Table 1). When another year or two of data have been collected, adjustments of the type utilized in Equation 6 may serve to permit utilization of the 1990 data. However, for the present, we have used regression calculations (Equation 2) for cohorts tagged in 1983 through 1987 to estimate survival beyond the first year. First-year survival was estimated as the ratio of the total seals known to be alive one year after tagging to the total tagged for the years 1983 through 1987, or $62/77 = 0.80$ (this calculation involves "back-correcting" two individuals not observed in the first year after tagging but seen in later years). Survival from the regression calculations was: 1983, 0.98; 1984, 0.93; 1985, 0.99; 1986, 0.94 and 1987, 0.93. For pooled survival data through 1989, Equation 4 gave a survival rate of 0.94 (95% B.C.L.: 0.88 to 0.98).

Lisianski Island—Only a short field camp was established on Lisianski Island in 1988 and resightings in that year dropped rather sharply. Also, no field camp was present at Lisianski Island in 1989. However, of the 18 weaned pups tagged in 1988, 15 were seen in 1991, and 13 in 1992. Survival calculations by the regression method for cohorts of weaned pups tagged in 1983 through 1986 gave: 1983, 0.92; 1984, 0.90; 1985, 0.77 and 1986, 0.90. First-year survival using back-corrected data for 1982 through 1987 was $88/104 = 0.85$.

Laysan Island—Annual field camps of long duration that have included pup

Table 2. Survival estimate by the Chapman-Robson estimator for monk seals tagged at weaning on French Frigate Shoals. First-year survival not included.

Year tagged	Survival		
	Female	Male	Combined
1984	0.94	0.91	0.93
1985	0.93	0.89	0.91
1986	0.90	0.86	0.88
1987	0.91	0.90	0.91

tagging have been maintained on Laysan Island since 1983. First-year survival using back-corrected data for 1983 through 1987 gave $119/139 = 0.86$ (only one individual was not seen in the first year, but subsequently observed). Inasmuch as field camps were present on Laysan Island in all recent years, an overall estimate by Equation 4 was calculated as 0.85 (95% B.C.L.: 0.81 to 0.88) from the cohorts tagged from 1983 through 1989. Separate estimates for males and females gave 0.82 (95% B.C.L.: 0.73 to 0.86) and 0.87 (95% B.C.L.: 0.81 to 0.91), respectively. Using resightings through 1988 of the first 4 cohorts tagged (1983 through 1986) gives an estimate of 0.89 (95% B.C.L.: 0.84 to 0.94) for males and females combined.

French Frigate Shoals—This large atoll is geographically similar to Pearl and Hermes Reef in that the seals use a substantial number of islands, some of small size and difficult to access, making a difficult task of detecting seal tag numbers. However, resighting effort here is much greater due to annual field camp presence of 4–6 mo.

Back-corrected first-year survival from 1984 through 1987 was $344/383 = 0.90$, somewhat higher than on any of the other sites. However, first-year survival has appeared to drop sharply in recent years, along with the appearance of sizable numbers of pups and immature seals in poor physical condition. Survival of tagged seals over all tagged cohorts also appears to have declined since 1988 or 1989. This sharp decline in recent survival is very evident in comparison with the numbers sighted from seals tagged in 1984 (Fig. 2).

The larger samples at French Frigate Shoals (Table 1) make it feasible to consider separate survival estimates for males and females. Female survival was somewhat higher than that of males based on use of Equation 2 to calculate the estimates given in Table 2. Only resightings through 1989 were used in this calculation, due to the evidence of a drop-off in survival beginning in 1989 (Fig. 2). Pooling data through 1989 from cohorts tagged from 1984 through 1987 gave a survival estimate using Equation 4 for females of 0.93 (95% B.C.L.: 0.90 to 0.96) and 0.90 (95% B.C.L.: 0.86 to 0.93) for males. The estimates given thus far used all or part of the successive resightings to estimate survival for a cohort of seals tagged in a given year. This pooling was necessary due to the small samples available. With the larger samples from French Frigate Shoals, it was possible to examine estimates for individual years. For females tagged from 1984 through 1986, the results suggest a higher survival rate for seals born in the first years of the study (Table 3).

Table 3. Annual survival estimates for female monk seals tagged at weaning on French Frigate Shoals using the Jolly-Seber estimator.

Year tagged	Year of estimate			
	1984-1985	1985-1986	1986-1987	1987-1988
1984	0.90	1.00	0.95	0.88
1985		0.97	0.94	0.98
1986			1.00	0.94

DISCUSSION

In assessing the results given here, it is important to note that nearly all of the seals in a cohort of weaned pups were tagged in most years, so that the overall survival of a given cohort is recorded by subsequent resighting data (apart from those relatively few cases where a tagged seal was not seen in one year, but was seen subsequently). In many reports of survival calculations, data on a sample of a much larger population are reported. Standard errors may then largely reflect variability introduced by using samples to estimate survival rates. In the present example similar variability results, but the fluctuations are due almost exclusively to chance processes governing whether individual seals lived or died, because all or nearly all seals in a given year-class were tagged.

Discussions of the observed variability are thus not so much concerned with "reliability" of the data as they are with what might have happened to the population by chance; *i.e.*, to some hypothetical population of seals living under identical circumstances to the cohorts actually observed. Because the major purpose of the overall study is to assess the threats to monk seal survival and seek methods for restoration of this endangered population, we need to base decisions on the observed results, and thus have not given much emphasis to variance estimates here.

The monk seal population at Kure Atoll declined severely during the 1960-1970s due to human occupation of Green Island and associated disturbance of pupping beaches (Kenyon 1972). In 1981 a program was initiated to rebuild that population (Gerrodette and Gilmartin 1990), and it appears to have been successful (VanToorenburg *et al.* 1993). With a reduction in human disturbance, the primary birth site has returned to its original location on Green Island (Gerrodette and Gilmartin 1990, Westlake and Gilmartin 1990). The very high survival rates at Kure Atoll suggest that a monk seal population with ample resources can do very well indeed. As is most evident at Kure Atoll, but also apparent at the other sites, and is common in most species of large mammals, first-year survival is lower than that observed in subsequent years.

Survival at Pearl and Hermes Reef, while not as high as at Kure Atoll, is nonetheless adequate to allow population growth, as confirmed by the fact that an initial small population has been increasing steadily over the years of the study (NMFS, unpublished data). Overall survival rates at Laysan and Lisianski Islands seem likely to be generally similar, and appreciably lower than at the

other sites. Populations at both islands are not increasing and may be decreasing, a result that we believe is associated with the "mobbing" phenomenon, in which an excess of adult males has caused numerous injuries and outright deaths of adult females in breeding attempts (Hiruki *et al.* 1993). The high survival (0.95) for the first few years at Lisianski Island may well be a consequence of the fact that the younger seals are less affected by the "mobbing" phenomenon, which is mainly noted as individuals approach the breeding age of 5–7 years (NMFS, unpublished data). With the prospect that survival may be lower as individuals, especially females, approach the breeding age, the simple model used here becomes of uncertain utility. Unfortunately, the small sample sizes available make it unlikely that more complex models or statistical tests may be of much help in analysis of the survival data alone. Combining survival, reproductive, and trend count data will be required to clarify the situation at Laysan and Lisianski Islands.

The main pupping site at French Frigate Shoals is East Island (Westlake and Gilmartin 1990) which was the site of military occupation from 1944 to 1952. After abandonment of the site by the U.S. Coast Guard in 1952, pup production at French Frigate Shoals increased substantially (Gerrodette and Gilmartin 1990) and the monk seal population built up rapidly, leveling off in the mid-1980s (NMFS, unpublished data). This population differs in this respect from all of the other sites in that it was small in the late 1950s, when all of the other populations were large, then it increased very substantially, reaching an asymptote in the late 1980s. First-year survival of 0.90 from 1984 through 1987 was a little higher than any other site. The recent dramatic change in immature survival at French Frigate Shoals (apparent in the resighting data since 1989) and other population data suggest this continuing decline is the result of environmental factors affecting food availability, but interpretation is complicated by possible losses of seals in a longline fishery for swordfish in 1990.

Research on the monk seal populations is being continued and intensified. As better understanding of the data and the dynamics of the populations evolves, we believe that more detailed models can be developed for specific analytical purposes.

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LITERATURE CITED

- CHAPMAN, D. A., AND D. S. ROBSON. 1960. The analysis of catch curve. *Biometrics* 16:345–368.
- EFRON, B., AND G. GONG. 1983. A leisurely look at the bootstrap, jackknife, and cross-validation. *American Statistician* 37:36–48.
- GERRODETTE, T., AND W. G. GILMARTIN. 1990. Demographic consequences of changed

- pupping and hauling sites of the Hawaiian monk seal. *Conservation Biology* 4:423-430.
- GILMARTIN, W. G., R. J. MORROW AND A. M. HOUTMAN. 1986. Hawaiian monk seal observations and captive maintenance project at Kure Atoll, 1981. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFC-59. 9 pp.
- HALDANE, J. B. S. 1955. The calculation of mortality rates from ringing data. *International Ornithological Congress* 11:454-458.
- HENDERSON, J. R., AND T. C. JOHANOS. 1988. Effects of tagging on weaned Hawaiian monk seal pups. *Wildlife Society Bulletin* 16:312-317.
- HIRUKI, L. M., W. G. GILMARTIN, B. L. BECKER AND I. STIRLING. 1993. Wounding in Hawaiian monk seals (*Monachus schauinslandi*). *Canadian Journal of Zoology* 71:458-468.
- JOHNSON, A. M., R. L. DELONG, C. H. FISCUS AND K. W. KENYON. 1982. Population status of the Hawaiian monk seal (*Monachus schauinslandi*), 1978. *Journal of Mammalogy* 63:415-421.
- KENYON, K. W. 1972. Man versus the monk seal. *Journal of Mammalogy* 53:687-696.
- LEBRETON, J., K. P. BURNHAM, J. CLOBERT AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* No. 107.
- RICE, D. W. 1960. Population dynamics of the Hawaiian monk seal. *Journal of Mammalogy* 41:376-385.
- SEBER, G. A. F. 1982. The estimation of animal abundance. Second Edition. Charles Griffin and Company Limited, High Wycombe, Bucks, England.
- VANTOORENBURG, R. A., W. G. GILMARTIN AND J. R. HENDERSON. 1993. Composition of the Hawaiian monk seal population at Kure Atoll, 1990. *Pacific Science* 47: 211-214.
- WESTLAKE, R. L., AND W. G. GILMARTIN. 1990. Hawaiian monk seal pupping locations in the Northwestern Hawaiian Islands. *Pacific Science* 44:366-383.

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