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REPRODUCTION, SURVIVAL AND TAG LOSS IN CALIFORNIA SEA OTTERS

DONALD B. SINIFF
Ecology and Behavioral Biology,
University of Minnesota, Minneapolis, Minnesota 55455

KATHERINE RALLS
National Zoological Park,
Smithsonian Institution, Washington, DC 20008

ABSTRACT

We observed 40 California sea otters, *Enhydra lutris,* that were instrumented with implanted radio transmitters and flipper-tagged, and obtained additional data on the reproduction of tagged female otters from the California Department of Fish and Game.

The proportion of instrumented females accompanied by a pup peaked in the spring, with a secondary peak in the fall. Two methods of estimating the annual reproductive rate gave comparable values of 0.90 and 0.94. The average inter-birth interval was 389 d. Two methods of estimating pup survival to weaning gave values of 0.46 and 0.58. Pups either remained with a female less than 80 or more than 120 d. Early mortality of dependent pups appears to be more frequent in California than in Prince William Sound, Alaska.

Two methods of estimation indicated that adult females had the highest survival rates and adult males the lowest. Juvenile females had lower survival rates than adult females but juvenile males had higher survival rates than adult males. The survival rate of juvenile females was lower than that of juvenile males.

The estimated annual loss rate for flipper-tags, based on the instrumented individuals, was 0.26. More individuals lost two tags than would be expected by chance. It is unlikely that accurate estimates of sea otter survival rates can be derived from observations of tagged individuals.

Key words: California, *Enhydra lutris,* inter-birth interval, reproduction, sea otter, survival rate, tag loss.

The California sea otter population is listed as threatened on the U.S. Endangered Species List and its status and management are of concern to several state and federal agencies (Ladd 1986*a, b*; Wendell *et al.* 1986). A population model is a basic tool for understanding and managing any wildlife population. The development of a population model requires reliable estimates of reproductive and survival rates; no estimates of these rates are available for the California sea otter population.

Early knowledge of the general biology of the sea otter reproductive cycle was gained mostly by examination of reproductive tracts from animals collected in the U.S.S.R. or Alaska (Barabash-Nikiforov *et al.* 1947, Sinha *et al.* 1966, Kenyon 1969, Schneider 1973). These studies showed that the litter size is typically one, with maternal care extending at least four months after parturition, and that a peak of births occurs in the spring, although birth can occur at any time of year. These early studies generally placed the inter-birth interval at about two years. However, subsequent observations of tagged sea otters in both California and Alaska have indicated that the inter-birth interval is closer to one year (Jameson and Johnson 1979, Loughlin *et al.* 1981, Estes and Jameson 1983, Wendell *et al.* 1984, Garshelis *et al.* 1984).

Considerable data on tagged individuals are available for the California sea otter population (Estes and Jameson 1983, Wendell *et al.* 1984), and tag-resight data can potentially be used to estimate annual survival rates, using mark-recapture techniques (Seber 1973). However, the difficulty in resighting tagged otters and the lack of information on tag loss rate greatly complicate the calculation of such an estimate. The only available estimates of tag loss rates are based on the resighting of tagged individuals (Ames *et al.* 1983) and are thus estimates of the rate at which tagged individuals disappear from the pool of regularly resighted animals, rather than a direct estimate of the rate at which individual tags are lost.

In this paper, we present estimates of reproductive, survival, and tag loss rates; the proportion of females accompanied by pups throughout the year; the inter-birth interval; and the period the pup remained with the female for the California sea otter population. Most of our estimates are based solely on observations of the otters that were flipper-tagged and instrumented with implanted radio transmitters. However, additional data based on sightings of tagged otters provided by the California Department of Fish and Game (CDFG) (R. Hardy, personal communication) contributed to estimates of the inter-birth interval, the period the pup remained with the female, and pup survival to weaning.

METHODS

Adult sea otters were captured with the Wilson trap developed by the CDFG (Ames *et al.* 1986); most of the juveniles were captured with dip-nets. When possible, a vestigial premolar was extracted for age estimation (Garshelis 1984). Sea otters were assigned to age/sex classes on the basis of their weight, estimated age based on tooth cementum layers (when available), and, in the case of females, reproductive history during the monitoring period, which lasted up to 700 d for some individuals.

Intraperitoneal radio transmitters were implanted in 40 sea otters between 7 March 1984 and 30 December 1985: nine adult males, 16 adult females, 10 juvenile females, and five juvenile males. The transmitters, developed by the University of Minnesota's Cedar Creek Bioelectronics Laboratory, measured about 7.6 × 5 × 2.5 cm and weighed about 120 g (Ralls *et al.* 1989).

For the implant operation, the otters were immobilized with fentanyl given intramuscularly in combination with azaperone (Williams et al. 1981). Surgery was carried out on board the capture boat, using the methods described in Williams and Siniff (1983). Narcan was used to reverse the effects of the fentanyl and the animals were released near the capture site after a total handling time of about 45 min. Instrumented animals were tagged with one Temple tag in each hind flipper, following the procedure developed by the CDFG (Ames *et al.* 1983).

Individual otters were located by radiotelemetry on an almost daily basis. We attempted to observe them with the aid of binoculars and a telescope (Questar, up to 80 power) and record the presence or absence of each flipper tag, and in the case of adult females, the presence or absence of a pup. This was often difficult due to weather conditions, such as fog or rough seas, or unfavorable lighting conditions. Some individuals were in locations that made them more difficult to observe than others, depending upon factors such as distance offshore and proximity to coastal access areas. Thus the length of time between successive visual observations varied greatly across individuals and ranged from 1 d to over 300 d. Naturally, we obtained much more complete data on those individuals seen frequently. Unless otherwise noted, the data we present were obtained from these instrumented otters.

We obtained additional data on reproduction and pup survival from the CDFG (R. Hardy, personal communication). Wendell *et al.* (1984) estimated the period of pup dependency and the inter-birth interval from observations of 139 flipper-tagged females. For many of these females, there were long periods between successive observations. We selected the records for a small subset of these females with the most complete reproductive data and combined them with our best data to estimate the inter-birth interval, the period the pup remained with the female, and pup survival to weaning.

To determine the proportion of instrumented females accompanied by pups each month of the year, we considered that a female had been accompanied by a pup for a given month if we knew that she had been accompanied by a pup for more than a 15-d period that month. Months where the status of a particular female was unknown were not considered in the analysis.

The variation in the number of days between sightings of the individual female otters created a problem in estimating the inter-birth interval (the time from the birth of one pup to the birth of the next). We usually did not know the exact birth dates of the two pups, although we knew that each birth occurred within some, usually short, time period. The type of data obtained from observations of either instrumented or tagged females and the problem of estimation are illustrated in Figure 1. We followed the procedure of Eberhardt and Siniff (1988) in the calculations of interbirth interval. This method is demonstrated in Figure 1.

We estimated the annual reproductive rate in two ways: (1) we divided the total number of days all the adult instrumented females were monitored by the known number of pups born to them during this period to give the average number of days per female needed to produce one pup, which we then divided

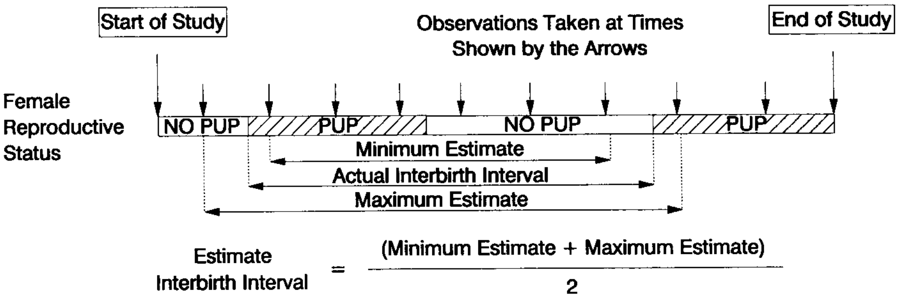

Figure 1. Method of estimating the length of the inter-birth interval from observations on instrumented or tagged females. The actual periods that the female was alone are indicated by the white rectangles and the periods that she was accompanied by a pup by the hatched rectangles. Days on which observations were made are indicated by arrows. Only minimum and maximum estimates of the actual inter-birth interval can be made from such data; the best estimate of the actual interval is taken as the average of the minimum and maximum estimates. Modified from Eberhardt and Siniff (1988).

into 365 to obtain an estimate of the annual pupping rate; (2) we divided our estimated average inter-birth interval into 365 d to obtain another estimate of the annual pupping rate.

One survival rate estimate for pups was based on the ratio of the number of pups that could have survived the period of dependency to the number of pups born over the monitoring period. The period of time a pup spent with the female was estimated as the average of the minimum possible time the pup spent with the female (the number of days from the first to the last sighting of the female together with the pup) and the maximum possible time (the interval between the last sighting of the female without a pup and the first resighting after the last day she was seen with a pup). We assumed that pups that remained with the female less than 150 days died and subtracted this number from the number of pups born. This assumption was based on the estimated period of pup dependency of six months (Payne and Jameson 1984, Wendell *et al.* 1984). A second estimate was based on all pups, in our study and the CDFG records, where the period of time the pup spent with the mother was known to be either less than or greater than 150 d.

Survival rates for independent otters were based on the fact that instrumented animals are known to be alive or dead on a daily basis, either from sightings or characteristics of the radio signal. The procedure that has been developed for radio-telemetry data (Heisey and Fuller 1985) has shown that this daily survival rate can be expanded to annual survival rate, under the assumption of a constant survival rate across the yearly cycle. To use this method, it is necessary to assume that the status of each individual (dead or alive) is known for each day. This became impossible when individuals disappeared and we were unable to determine their fate, violating the assumption of known status. These animals were classified as missing (Table 4), because when they disappeared they might have died or their transmitters might have expired. The way in which these missing animals are classified can affect the survival rate estimate. The way we handled this problem was to assume that our transmitters were very reliable for some number of days and that animals that disappeared prior to this time died. Such an assumption seemed reasonable for our data because our transmitters were extremely reliable (Ralls *et al.* 1989). Based on the average life span, 485 d, of the five transmitters in which expiration was verified, we used 450 d for the decision point as to the probable fate of missing animals. Thus, we assumed that otters missing in less than 450 d from the capture date had died and those missing after 450 d or more were alive on the date they became missing, probably due to transmitter expiration.

We also calculated survival rates based on the fates of individuals over the duration of the study. The number of individuals in each sex and age class was used as the basis for these calculations. For this estimate, we followed the binomial model, $S = 1 - d/n$ (S = survival, d = number of animals that died, n = sample size for the particular sex/age category). For this model an estimate of variance is easily calculated by the standard $s^2 = pq/n$ ($q = d/n$ or the proportion dying, $p = 1 - q$ or the proportion surviving). It only remains to specify the time interval over which the animals either lived or died, which is normally taken to be one year. However, in this case we followed the same 450-d criterion as in our previous estimate, thus the binomial model for an estimate of the annual survival rate becomes:

$$S = (1 - d/n)^{365/450}$$

We estimated the annual survival rate both ways for the four sex and age classes of adult females, adult males, juvenile females and juvenile males.

Our data on the presence or absence of tags were similar to our data on reproduction. However, tags were more difficult to see than pups, so many of the intervals between the last date a tag was seen and the first date it was seen to be missing were longer than the corresponding intervals for pups. We analyzed these data using the same method we used to analyze the data on the survival of individual animals. However, we assumed that a tag had survived until the date it was seen to be missing and thus calculated only the maximum possible tag survival rate.

RESULTS

Reproduction—The proportion of adult females accompanied by pups peaked in the spring, with a secondary peak in the fall. These seasonal relationships, based on a total of 225 adult female otter-months, are shown in Figure 2.

Our reproductive data set includes information on the 13 adult females that were monitored at least 355 d (Table 1). However, our best data for the determination of the inter-birth interval and the period a pup remained with its mother (Table 2) came from five females from this study and three tagged females observed by the CDFG. The minimum and maximum intervals in Table 2 were calculated as shown in Figure 1. The average inter-birth interval was 389 d, with a range of 313 to 586 d.

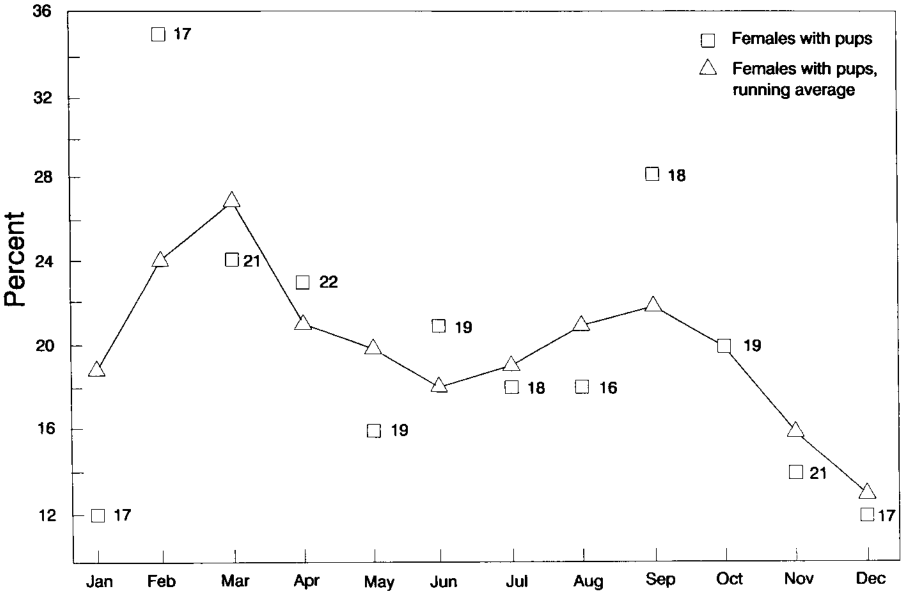

Figure 2. The percent of the adult female sea otters that were accompanied by pups each month of the year. Numbers to the right of the squares show the sample sizes, in numbers of otter-months, for each month. The running average is composed of three monthly values.

Table 1. Reproductive data, age, and length of monitoring period for adult female sea otters.

Otter number	Age (yr)	Days monitored	Pups born	Pups died	Pups unknown fate	Pups lived
6	—	355	0	0	0	0
9	5+	544	2	1	1	0
11	—	621	1	0	1	0
14	6+	744	2	0	1	1
15	5[a]	725	1	0	1	0
16	—	608	2	0	2	0
19[b]	—	587	3	0	2	1
22	8	585	0	0	0	0
25	7	555	1	0	0	1
27	10	540	1	1	0	0
31	11	637	2	2	0	0
33	10	630	2	2	0	0
36	9	609	2	2	0	0
Totals		7,740	19	8	8	3

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[a] Only a minimum age could be estimated because of damage to the tooth sections for this individual.

[b] Was accompanied by a large pup when captured.

Table 2. Estimates of the inter-birth interval and the time the pup spent with the female for California sea otters together with the assumed fate of the pup. Based on data from both instrumented otters (indicated by the UMN prefix) and tagged otters (indicated by the CDFG prefix). Data for individual females are arranged within pup-fate categories by increasing length of the estimated inter-birth interval.

Otter number	Minimum[a] inter-birth interval (days)	Maximum[a] inter-birth interval (days)	Best[a] estimate of inter-birth interval (days)	Estimate[b] of time pup with female (days)	Assumed fate of pup
UMN 36	286	340	313	45	died
UMN 31	337	373	355	24	died
CDFG 34	355	367	361	42	died
UMN 9	377	441	409	48	died
UMN 33	409	424	417	37	died
CDFG 188	329	365	347	150	lived
CDFG 188	329	373	351	176	lived
CDFG 188	337	395	366	193	lived
CDFG 67	364	405	384	194	lived
UMN 14	559	612	586	165	lived
		Mean	389		

[a] Calculated as shown in Figure 1.

[b] Data from Table 3.

Our first estimate of the annual reproductive rate was based on the information summarized in Table 1. Nineteen pups were produced during 7,740 otter-monitoring days; thus, an average of 407 d was required to produce one pup. This gives an estimated annual reproductive rate of 0.90. Our second estimate is based on the data in Table 2. The average inter-birth interval of 389 d corresponds to an annual reproductive rate of 0.94.

Survival—Eight of the 19 pups born to the females with implanted transmitters almost certainly died before weaning (Table 1, Table 2), giving an estimated pup survival rate to weaning of 0.58. This may be a maximum estimate, as it assumes that eight pups whose fate was unknown lived. We obtained a second estimate of pup survival by combining our best data with comparable data on pups born to tagged females observed by CDFG biologists. We had 10 pups where the period of time spent with the female was known to be either less than or greater than 150 days and we obtained data on an additional 14 pups from the CDFG records (Table 3). If a pup spent less than 150 d with the female, we assumed it died. For the combined data set, 11 pups lived and 13 died, giving an estimated pup survival rate to weaning of 0.46.

A histogram of the best estimates of the time each pup was with the female (*i.e.*, minimum time plus maximum time/2) is shown in Figure 3. These data have a bimodal distribution with pups falling into two categories: less than 80 d or more than 120 d with the mother (Fig. 3). The pups of the instrumented females had a significantly ($P < 0.05$) higher mortality rate than the pups of the tagged females.

Table 3. Data used for estimating the period of time a pup remained with a female and its assumed fate. Based on data from both instrumented otters (indicated by UMN prefix) and tagged otters (indicated by the CDFG prefix).

	Number of days pup remained with female:			
Otter number	Minimum estimate	Maximum estimate	Best[a] estimate	Assumed fate of pup
UMN 36	1	23	12	died
UMN 33	8	32	20	died
UMN 31	16	32	24	died
CDFG 34	12	52	32	died
UMN 33	31	43	37	died
UMN 27	24	61	43	died
CDFG 34	20	64	42	died
UMN 36	26	65	45	died
UMN 9	36	60	48	died
CDFG 34	6	96	51	died
UMN 32	41	89	65	died
CDFG 67	50	110	80	died
CDFG 89	130	139	135	died
CDFG 188	139	161	150	lived
CDFG 34	154	162	158	lived
UMN 14	149	180	165	lived
CDFG 188	156	196	176	lived
UMN 25	176	186	181	lived
CDFG 188	170	216	193	lived
CDFG 67 (Table 2)	187	201	194	lived
CDFG 41	163	245	204	lived
CDFG 194	211	267	239	lived
CDFG 34	176	309	243	lived
CDFG 34	245	332	289	lived

[a] The average of the minimum estimate of the time the pup spent with the female (interval between the first and last sightings of the female with the pup) and the maximum estimate (interval between the last sighting of the female alone prior to the first sighting of her with the pup and the first sighting of the female alone after the last sighting of her together with the pup).

The data on which we based our survival rates estimates for independent animals are presented in Table 4. Both methods for estimating survival rates indicated that survival rates were highest for adult females and lowest for adult males (Table 5). Both estimates for juvenile females were lower than those for adult females, while both estimates for juvenile males were higher than those for adult males. The survival rate of juvenile females was lower than that of juvenile males for both methods of estimation.

Tag loss—Considering all 80 flipper tags in our sample (Table 6), the estimated annual tag survival rate was 0.74 (Table 7A), corresponding to an annual tag loss rate of 0.26. Survival rates for right and left tags were not significantly different. Assuming that tag loss followed a binomial distribution, and using the number of tags lost over the period of monitoring to derive the expected probabilities of losing one, two, or no tags, we found that significantly

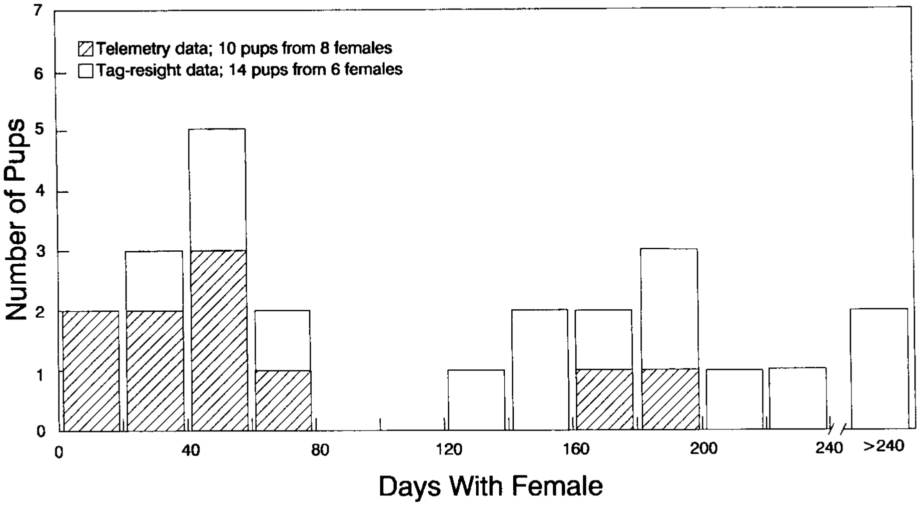

Figure 3. Distribution of the best estimates of the length of the period a pup spent with the female. Data from Table 3.

more otters lost two tags then expected (Table 7B). This result is perhaps not surprising, as some individual otters have been seen to bite and manipulate their flipper tags, ultimately removing them, while other individuals appear to ignore the presence of tags. If the otters that lost two tags are excluded, the estimated annual tag loss rate decreases to 0.09 (1 − 0.91) (Table 7C).

DISCUSSION

Our data on the proportion of females accompanied by pups throughout the yearly cycle, which show a peak in the spring and a smaller peak in the fall, are similar to data on the ratio of pups to independent otters recorded by the CDFG in their monthly counts of index areas (Brody 1988). The independent otters counted in these index areas are probably largely adult females along with a few territorial males and juvenile females.

Our estimated average inter-birth interval of 389 d is in agreement with the emerging consensus that many female sea otters pup on an approximately annual basis. One interesting aspect of our data is the rather large degree of variation in this interval, with a range of 313 to 586 d. Female otters that lose or abandon a pup (Garshelis and Garshelis 1987) have been reported to mate shortly thereafter (Brosseau *et al.* 1975, Garshelis *et al.* 1984), while it is generally agreed that female otters rarely mate while still accompanied by a pup (Kenyon 1969, Calkins and Lent 1975, Garshelis *et al.* 1984). Thus, one might expect that those females that lost a pup prior to weaning would give birth again after a shorter interval than those that successfully raised a pup (Rotterman and Simon-Jackson 1988). However, our data show no relationship between the length of time a pup remained with the female and the time from its birth to

Table 4. Data on instrumented otters used for estimating survival rates.

Otter number	Age/sex	Capture date	Last date heard	Status	Days trans-mitting
1	AM	07-Mar-84	28-May-85	missing	447
2	AM	16-Mar-84	15-Sep-84	missing	183
3	AM	21-Mar-84	28-Aug-85	TX expired	525
4	AM	21-Mar-84	26-Aug-85	TX expired	523
6	AF	03-Jul-84	23-Jun-85	TX expired	355
7	AM	15-Feb-85	10-Nov-86	missing	633
9	AF	01-Mar-85	27-Aug-86	missing	544
10	AM	01-Mar-85	12-Nov-86	missing	621
11	AF	15-Mar-85	26-Nov-86	missing	621
13	JM	16-Mar-85	05-Jan-87	missing	660
14	AF	16-Mar-85	30-Mar-87	missing	744
15	AF	20-Mar-85	11-Dec-86	TX expired	631
16	AF	03-Apr-85	02-Dec-86	missing	608
17	AM	03-Apr-85	28-Mar-86	missing	359
19	AF	03-Apr-85	11-Nov-86	missing	587
21	AF	10-Apr-85	13-Apr-85	missing	3
22	AF	10-Apr-85	16-Nov-86	missing	585
23	AM	10-Apr-85	27-Apr-85	dead	17
25	AF	13-Apr-85	20-Oct-86	missing	555
26	AF	08-May-85	05-Jun-85	dead	28
27	AF	04-Oct-85	31-Oct-86	TX expired	392
28	AF	04-Oct-85	04-Nov-86	TX failed	31
29	JF	11-Oct-85	14-Mar-87	missing	519
30	JM	11-Oct-85	29-Jul-87	missing	656
31	AF	11-Oct-85	24-Jul-87	missing	651
33	AF	18-Oct-85	26-Sep-87	missing	708
34	AM	19-Oct-85	23-Sep-86	missing	339
35	JM	08-Oct-85	21-Mar-87	missing	498
36	AF	08-Nov-85	07-Oct-87	missing	698
37	JF	22-Nov-85	17-Oct-86	missing	329
38	JM	22-Nov-85	02-Jan-86	missing	41
39	JF	22-Nov-85	25-Mar-87	missing	488
40	JF	17-Dec-85	03-Dec-87	transmitting	716
41	JM	17-Dec-85	13-Apr-87	dead	482
42	JF	17-Dec-85	09-Oct-87	missing	661
43	JM	18-Dec-85	10-Nov-87	missing	692
44	JF	18-Dec-85	29-Jun-86	dead	193
45	JF	18-Dec-85	22-Mar-87	missing	459
46	JF	18-Dec-85	25-Dec-87	transmitting	737
47	JF	30-Dec-85	28-Dec-87	transmitting	728

the birth of the next pup (inter-birth interval). Obviously, more study is needed on the relationship between the inter-birth interval and the length of the period of pup dependency and the manner in which each of these time intervals varies with the age and condition of the female.

Minimum reproductive rates for sea otters in Alaska have been suggested by the reproductive condition of females in samples killed in late winter and spring

Table 5. Annual survival rate estimates for the instrumented otters. Two estimates were made for four age/sex classes of adult females, adult males, juvenile females, and juvenile males. The first was obtained by converting the daily survival rate of the instrumented otters to an annual rate (Heisey and Fuller 1985). The second used the standard binomial model (see text for explanation) and the status of individual sea otters as a basis.

	Basis of estimate		
Age/sex class	Transmitter days survival rate	Individuals survival rate	SD
Adult females	0.91	0.89	0.088
Adult males	0.61	0.52	0.167
Juvenile females	0.80	0.75	0.145
Juvenile males	0.88	0.85	0.179

(Kenyon 1969, Schneider 1973). Kenyon found that 71% of the adult females collected in this period were pregnant and 17% had recently given birth. Schneider found that 59% of females collected in May were pregnant and 14% had recently given birth. Combining these values gives approximate annual reproductive rates of 0.88 and 0.73 for these two studies, respectively. These are minimum estimates, since non-implanted embryos might have been missed and females were not collected over the entire annual cycle. No previous estimates are available for the California population. Our estimates of 0.90 and 0.94 are, as expected, slightly higher than the minimum estimates available for the Alaska population, since they are based on data collected over the complete annual cycle. Because of the sea otter's ability to produce pups throughout the year, it seems likely that estimates of annual reproductive rates in sea otters will be quite dependent upon conditions during the particular time period over which the data are collected.

The reasons for the apparent higher mortality of pups born to the females with implanted transmitters compared to those born to the tagged females are unknown. The fact that twenty percent of the pups born to instrumented females but none of those born to the tagged females died within 20 d after birth suggests that the data on tagged females may have underestimated pup mortality. Unless tagged animals are observed at frequent intervals, pups that die soon after birth may be missed entirely. If the difference in pup mortality rates is real, a variety of factors, such as temporal and geographical variation in mortality rates and a greater proportion of young females in the sample of instrumented females, could conceivably be responsible. Pup mortality no doubt varies from year to year and from location to location and the data on the tagged and instrumented females were collected in different years in different areas. Otter pups sometimes become separated from their mothers during storms and even wash ashore. Thus, severe weather could have been a contributing factor as most of the CDFG tag-resight data came from females in the Monterey Bay area, while the telemetry data came from females along the more exposed central coast to the south. However, the difference does not seem to be due to a large

Table 6. Tag loss information on instrumented sea otters in California as of 10 July 1987.

Otter number	Date tagged	Right tag		Left tag		Days from tagging to date last seen or missing	
		Last seen	Missing	Last seen	Missing	Right tag	Left tag
1	07-Mar-84	28-May-85		28-May-85		447	447
2	16-Mar-84	15-Sep-84		15-Sep-84		183	183
3	21-Mar-84	28-Aug-85		28-Aug-85		525	525
4	21-Mar-84	26-Nov-86		26-Nov-86		980	980
6	03-Jul-84	21-Feb-85	06-Mar-85	21-Jun-85		246	353
7	15-Feb-85	06-Aug-86		06-Aug-86		537	537
9	01-Mar-85	07-Oct-85	23-Oct-85	05-Feb-86	29-Apr-86	236	424
10	01-Mar-85	14-Nov-85	06-Apr-86	11-Sep-85	14-Nov-85	401	258
11	15-Mar-85	07-Sep-85		07-Sep-85		176	176
13	16-Mar-85	31-Aug-85		31-Aug-85		168	168
14	16-Mar-85	25-Sep-85	15-Nov-85	29-Jun-85	24-Jul-85	244	130
15	20-Mar-85	06-Mar-87		06-Mar-87		716	716
16	03-Apr-85	16-Aug-85	11-Sep-85	16-Aug-85	11-Sep-85	161	161
17	03-Apr-85	11-Nov-85		11-Nov-85		222	222
19	03-Apr-85	01-Nov-86		11-Sep-85	11-Dec-85	577	252
21	10-Apr-85	13-Apr-85		13-Apr-85		3	3
22	10-Apr-85	22-Oct-86		22-Oct-86		560	560
23	10-Apr-85	27-Apr-85		27-Apr-85		17	17
25	13-Apr-85	21-Sep-86	03-Oct-86	24-Jun-86	06-Aug-86	538	480
26	08-May-85	06-Jun-85		06-Jun-85		29	29
27	04-Oct-85	28-Mar-87		28-Mar-87		540	540
28	04-Oct-85	15-Oct-85		15-Oct-85		11	11
29	11-Oct-85	30-Oct-85	11-Feb-86	30-Oct-85	11-Feb-86	123	123
30	11-Oct-85	30-May-87		30-May-87		596	596

Table 6. Continued.

Otter number	Date tagged	Right tag		Left tag		Days from tagging to date last seen or missing	
		Last seen	Missing	Last seen	Missing	Right tag	Left tag
31	11-Oct-85	18-Apr-86	02-May-86	16-May-87		203	582
33	18-Oct-85	07-Jul-87		07-Jul-87		627	627
34	19-Oct-85	13-Aug-86		06-Jul-86	13-Aug-86	298	298
35	08-Nov-85	03-Mar-87		03-Mar-87		480	480
36	08-Nov-85	01-Jul-87		06-Jul-87		600	605
37	22-Nov-85	17-Jul-86		17-Jul-86		237	237
38	22-Nov-85	18-Dec-85		18-Dec-85		26	26
39	22-Nov-85	28-Mar-87		28-Mar-87		491	491
40	17-Dec-85	06-Jun-86	17-Jul-86	09-Jul-87		212	569
41	17-Dec-85	17-Oct-86		17-Oct-86		304	304
42	17-Dec-85	25-Jun-86	17-Jul-86	25-Jun-86	17-Jul-86	212	212
43	18-Dec-85	28-Jan-86	27-Feb-87	11-Apr-87		41	479
44	18-Dec-85	04-Jul-86		04-Jul-86		198	198
45	18-Dec-85	11-Jun-86	17-Jul-86	17-Jan-87		211	395
46	18-Dec-85	09-Nov-86	29-Mar-87	09-Nov-86	29-Mar-87	466	466
47	30-Dec-85	01-Jul-87		01-Jul-87		548	548

Table 7. Estimates of annual tag survival rates based upon the survival rate estimation procedures for instrumented animals given by Heisey and Fuller (1985). The only difference here is that the "death" of tags rather than individuals is counted in A and C, below. A comparison of tag loss to expected tag loss based on the binomial distribution is shown in B.

A. Tag survival rate estimate based on all otters

Tag location	Number of tags lost (of 80)	Estimated annual tag survival rate
Right rear flipper	13	0.70
Left rear flipper	10	0.78
Left and right	23	0.74

B. Comparison of tag loss to that expected from the binomial distribution. The estimated probability of losing one tag is 23/80 or 0.2875.

	Number of otters	
Number of lost tags	Expected	Observed
None	21	25
One	16	7
Two	3	8

C. Tag survival rate estimate excluding the otters that lost two tags.

Tag location	Number of tags lost (of 64)	Estimated annual tag survival rate
Left and right	7	0.91

proportion of young females among the instrumented animals, as most of the pups that died were born to females estimated to be 9 to 11 yr of age (Table 1).

The rather unusual bimodal form of the distribution of the number of days the pup remained with the female, with many pups disappearing (and probably dying) before the age of 80 d, suggests that early pup mortality contributes significantly to the overall population dynamics of sea otters in California. By the age of 70 to 98 d, pups have lost their natal pelage, are rarely carried by the female, and are proficient swimmers and divers (Payne and Jameson 1984). Pups that remained with the mother more than 80 d remained with her at least 120 d and probably survived to weaning.

Early mortality of dependent pups appears to be more frequent in California than in Prince William Sound, Alaska (Table 8). Because the California population is threatened, it is important to collect additional data to confirm this pattern of early pup mortality in California and, if so, to determine its cause. Possible contributing factors might include differences in weather patterns, contamination of Californian waters with pesticides or other pollutants, fixation of deleterious alleles in the California population, or greater energetic constraints on females in California than in Alaska.

Our estimated survival rates for pups from birth to weaning, 0.58 to 0.46, are close to the 0.50 estimate required, when combined with our survival rate estimates for the other age/sex classes, to produce a zero growth rate in the

Table 8. A comparison of the length of time pups were seen with the female in California and Alaska. The Alaska data are from Garshelis (1983). The California data are based on 10 pups born to the instrumented females and 16 pups born to tagged females observed by California Department of Fish and Game biologists.

Days pup seen with female	Alaska	California
0–50	0	8
51–100	3	5
101–150	1	2
151–200	4	11

population model for California sea otters developed by Brody (1988). However, recent surveys indicate that this population, after a pause beginning in the early 1970s, has resumed growth in the last few years (R. J. Jameson and J. A. Estes, U.S. Fish and Wildlife Service, unpublished data).

The annual estimates of survival rates we obtained by expanding the daily survival rate based on transmitter-days also appear reasonable. The relatively close correspondence between our two estimates is encouraging, as is their general agreement with other aspects of the data collected on our instrumented individuals, such as the time budgets (Ralls and Siniff 1990), and movement and feeding patterns of the different age/sex groups (Siniff and Ralls 1988). Our adult females, which had the highest survival rates, were in areas of the range where human activities were minimal and they traveled the least of the four age/sex groups. Adult males had the lowest survival rates. They sometimes traveled long distances and tended to be particularly vulnerable during these periods. Juvenile males also traveled extensively but tended to remain farther offshore than otters in the other age/sex classes, which may provide some degree of protection from human activities, such as shooting (Wild and Ames 1974, Morejohn *et al.* 1975) and incidental capture in gill-nets (Wendell *et al.* 1986), and thus contribute to their higher survival rate.

Juvenile females had low survival rates compared to adult females. They also had lower survival rates than juvenile males. Juvenile females in Alaska also have lower survival rates than juvenile males (Monnett and Rotterman 1988) and the juvenile females in our California study clearly worked harder than other otters to obtain food (Ralls and Siniff 1990). Taken as a whole, our data strongly suggest that the age/sex groups are differentially affected by the various sources of sea otter mortality.

Our observations of tags on instrumented individuals provide estimates of annual tag loss rates that are independent of mortality and the movements of tagged individuals out of the study area. The overall estimate of 0.26 probably represents a realistic annual loss rate for the Temple tag. The only other estimates of tag loss rates are those of Ames *et al.* (1983), who used three methods of tag application and attempted to resight the tagged individuals over time. They are thus estimates of the rate at which tagged individuals disappear from the pool of regularly resighted animals, rather than direct estimates of the rate at which individual tags are lost. The use of resighting data to estimate tag loss

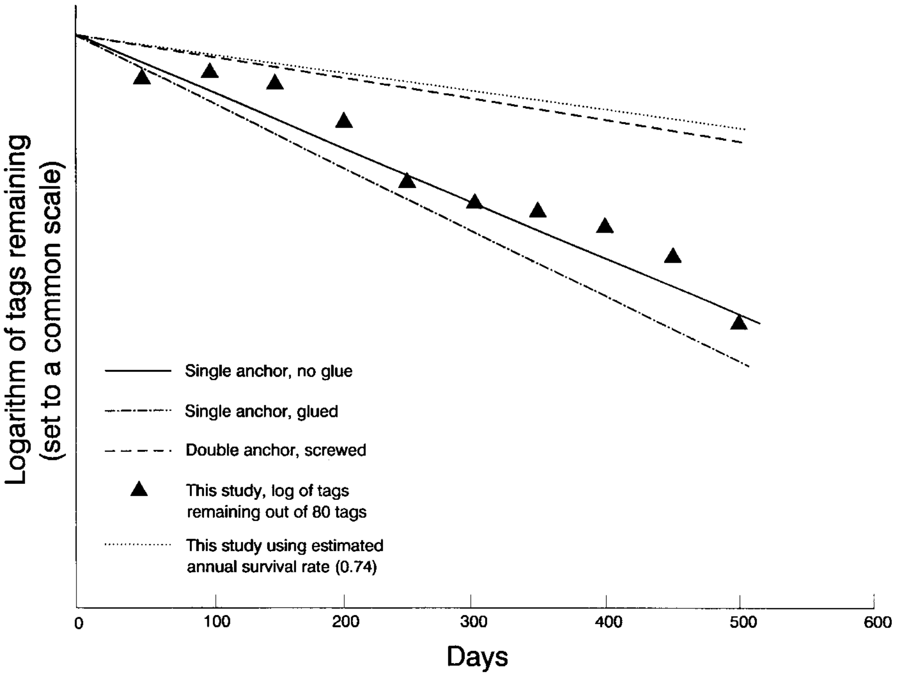

Figure 4. A comparison of the tag-loss rates found in this study with those in Ames *et al.* (1983).

has the potential to include loss due to death and movement of tagged individuals out of the study area in addition to tag loss and thus one would expect it to overestimate actual tag loss. Curiously, however, our annual tag survival rate of 0.74 (which excludes these other sources of tag loss present in the resighting data) corresponds almost exactly to the survival rate for double-anchored tags (*i.e.,* the tag is inserted through two holes in the flipper instead of the usual single hole) determined by Ames *et al.* (1983) (Fig. 4). When we used our data and plotted the number of tags remaining on the otters that were still being located on a regular basis over time (subtracting from the original 80 tags all those on missing or dead otters and on otters with expired or failed transmitters plus those that were lost by the animals with functioning transmitters), the estimated tag loss rate was of course higher and corresponded very closely to that for the other two methods of tag application (single anchor, unglued and single anchor, glued) in Ames *et al.* (1983, Fig. 2).

Ames *et al.* (1983) found that the apparent loss rate of double-anchored tags was less than that of single-anchored tags (whether glued or not). Our data suggest two possible reasons for this difference. The first possibility is that the retention of double-anchored tags was very high and that the observed loss rate was almost entirely due to mortality and/or movements of animals out of the study area. The second is that the small number of animals on which this method was used rarely, if ever, moved out of the study area and did not suffer significant mortality during the study period. These conditions could occur, for example, if the tagged individuals were mostly adult females.

Tag-resight data can potentially be used to estimate annual survival rates for various age/sex classes of animals. However, mark-recapture techniques, using the appropriate models must be used for these survival rate estimates (Seber 1973). For sea otter tag-resight data, the combined effects of unequal probability of sighting among individuals, movements of animals out of the intensive study area, and the differential mortality patterns among age/sex groups make the application of such methods extremely difficult. When tag loss is added to these complications it becomes rather unlikely that accurate estimates of annual survival rates for sea otters can be derived from such data. Furthermore, the comparison of our data with those of Ames *et al.* (1983) suggests that for sea otters, even under the best conditions, it would be difficult to separate tag loss from actual mortality and movement away from the study area. In our study, known tag loss, added to verified mortality, would have produced unrealistically low survival rate estimates.

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