HOMING BEHAVIOR OF JUVENILE NORTHERN ELEPHANT SEALS

GUY W. OLIVER 1
PATRICIA A. MORRIS
PHILIP H. THORSON
BURNLEY J. LE BOEUF
Department of Biology,
University of California, Santa Cruz,
Santa Cruz, California 95064, U.S.A.

ABSTRACT

The aim of this study was to determine if juvenile northern elephant seals, Mirounga angustirostris, translocated from their rookery would return to it quickly and reliably. During the spring and fall of 1990 and 1991 we captured 75 seals at Ano Nuevo State Reserve, CA, U.S.A, and translocated them to release sites up to 100 km away. Eighty-eight percent of the seals returned to the capture site within 4.7 ± 4.3 d. Homing rate increased with age, but even the youngest seals (8–10 mo) homed at a 73% rate. Homing rate did not vary significantly with sex, season, or year. Data from diving instruments suggested that the seals often followed direct routes home, arrived on the rookery significantly more often at night than during the day, and when released together, returned separately. Mean homing speed of 18 seals with complete diving records was 39 km/d (range 3–70 km/d). Instruments on seals had no detectable effect on homing rate or homing speed. The translocation paradigm provides a powerful tool for conducting intensive short-term studies on free-ranging seals.

Key words: homing, translocation, elephant seal, Mirounga angustirostris.

Homing behavior is widespread in animals (Papi 1992). Those that migrate long distances and exhibit strong site fidelity, such as several species of sea turtles, birds, and mammals, excel at homing (Kenyon and Rice 1958, Carr 1967, Rogers 1988). Observations of pinnipeds that fit these criteria support this generalization.

Most observations of homing in pinnipeds resulted from attempts to move problem animals out of an area only to find that they returned. Unwanted California sea lions, Zalophus californianus, returned 20–240 km from release

1 Address all correspondence to: Guy W. Oliver, 233 Northrop Place, Santa Cruz, California 95060, U.S.A. E-mail: oliver@biology.ucsc.edu.
sites at sea to the facility in San Diego where they had previously resided and been fed (Ridgway and Robison 1985). The majority of sea lions transported from Ballard Locks in Seattle, where they were feeding on salmon, to sites 500 and 2,025 km south, returned to the capture site (Pfeifer 1989, 1991). A relocated male Australian fur seal, *Arctocephalus pusillus doriferus*, returned 450 km in 14 d to the commercial salmon farm where it was captured (Hindell and Pemberton 1997). Harbor seals, *Phoca vitulina*, returned to sites where they were raised (Goodridge and Dietz 1975; L. Dunn, personal communication) or captured while feeding (P. Olesiuk, personal communication), after being relocated distances ranging from 21 to 421 km.

Preliminary results of this homing study of northern elephant seals, *Mirounga angustirostris*, showed that 45 of 45 juveniles translocated from the Año Nuevo rookery in the spring when molting, and in the fall when resting, to release sites on a beach or at sea up to 70 km away returned to the rookery in 1–7 d (Le Boeuf 1994). This translocation paradigm has been subsequently to facilitate short-term studies of diving and physiological studies in free-ranging seals (e.g., Fletcher et al. 1996; Andrews et al. 1997; Burgess et al. 1996, 1997).

This paper reports the full study previewed in Le Boeuf (1994). Our aim was to determine the homing behavior of juvenile northern elephant seals to the rookery site where they were resting or preparing to molt. Our specific goals were to determine: (1) homing rate from a variety of release sites up to 100 km from the rookery, (2) the speed of homing, (3) effects of season and sex on homing performance, and (4) the effect of attached diving instruments on homing behavior.

Juvenile elephant seals, ranging in age from 9–35 mo old, haul out on the Año Nuevo rookery twice a year (Le Boeuf 1994). In the spring, from March through June, individuals remain onshore 30–45 d during which they molt the skin and pelage (Le Boeuf et al. 1994). Individuals reappear onshore for 22–45 d in the fall, the period from August through early December (L. Cody, personal communication).

**Methods**

This study was conducted at Año Nuevo State Reserve, California, during the spring and fall of 1990 and 1991; 75 seals were removed from the rookery and released at various sites up to 100 km away.

The seals fell into four age groups (Table 1). Seals translocated in the fall were 9–11 mo old (J10), 21–23 mo old (J22), and 33–35 mo old (J34); seals translocated in the spring were 15–17 mo old (J16). J10 seals had completed one pelagic foraging trip, while J16, J22 and J34 seals had completed two, three, and five trips, respectively. Seal mass increased with age, with males being heavier than females at all ages. Sex ratios were almost equal for all age classes except J22, which was composed of 19 males and 7 females.

We selected seals based on apparent good health and recency of their arrival on the rookery as indicated by fatness and good coat condition. In the spring,
Table 1. Age class, sex, sample size, weight, and types of instruments placed on juvenile northern elephant seals involved in homing studies at Año Nuevo State Reserve, California. Seals in age class J10 were 9–11 mo old, in J16 were 15–17 mo old, in J22 were 21–23 mo old, and in J34 were 33–35 mo old. Abbreviations: TDR = time-depth recorder, SVTDR = swim-velocity/time-depth recorder, HRTDR = heart-rate/time-depth recorder.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Sex</th>
<th>Sample size</th>
<th>Weight (\bar{x}) (range) (kg)</th>
<th>Instruments</th>
</tr>
</thead>
<tbody>
<tr>
<td>J10</td>
<td>Male</td>
<td>11</td>
<td>143 (121–158)</td>
<td>Radio TDR &amp; Radio</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>11</td>
<td>135 (120–157)</td>
<td>Radio &amp; Radio</td>
</tr>
<tr>
<td>J16</td>
<td>Male</td>
<td>12</td>
<td>167 (120–208)</td>
<td>SV &amp; HRTDR</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>13</td>
<td>148 (137–160)</td>
<td>SV &amp; HRTDR</td>
</tr>
<tr>
<td>J22</td>
<td>Male</td>
<td>19</td>
<td>217 (180–262)</td>
<td>SV &amp; TDR</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>7</td>
<td>185 (158–210)</td>
<td>SV &amp; TDR</td>
</tr>
<tr>
<td>J34</td>
<td>Male</td>
<td>1</td>
<td>260</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>1</td>
<td>245</td>
<td>None</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>75</td>
<td>175 (120–262)</td>
<td>8 &amp; 26 &amp; 20 &amp; 12</td>
</tr>
</tbody>
</table>

all seals had not yet molted. Ten of the seals were born and tagged at Año Nuevo; birth sites of the other 65 seals were unknown. The ages of the previously untagged seals were assessed by experienced observers using total size, flipper size, and head size as the primary indicators.

We anesthetized the seals with intramuscular injections of Telazol (A. H. Robins, Richmond, VA) at a mean dosage of 0.85 ± 0.14 mg/kg of body mass (range 0.62–1.14 mg/kg). Immobilization was maintained with IV injections of 0.05 mg/kg/min of ketamine (Briggs et al. 1975, Gales 1985, Burton and Gales 1987) when necessary to attach instruments.

We tagged each seal in the interdigital webbing of the hind flippers with serially numbered green jumbo rototags (Dalton, Henley, England) and marked the pelage with black hair dye (Clairol Inc., Stamford, CT) to facilitate resightings.

To facilitate recapture of returning seals, we attached VHF radio transmitters (Advanced Telemetry Systems, Minneapolis, MN) to 71 of them. These transmitters were 2.5 cm in diameter, 6 cm long, and weighed 30 g in air. They were attached to the pelage with epoxy as described by Le Boeuf et al. (1988). In addition, 41 seals carried diving instruments. Twenty carried time-depth recorders (TDRs), 12 carried both heart rate monitors and TDRs (HRTDRs), and nine carried swim-velocity/time-depth recorders (SVTDRs). The TDRs (Mark 3, Wildlife Computers, Woodinville, WA) were 2.7 cm in diameter, 15 cm long, and weighed 100 g in air; they sampled depth at 1-, 5-, or 10-sec intervals. The HRTDR packages were 5 cm high, 9 cm wide, 6.5 cm long, and weighed 555 g in air. The SVTDRs were 5.3 cm in diameter,
20 cm long, and weighed 570 g in air (Ponganis et al. 1990). These instruments were attached in the same manner as were the radios. The radios for seals carrying TDRs, HRTDRs or SVTDRs were attached directly to the diving instrument package by a stainless steel hose clamp. Only TDR data related to homing are presented in this paper.

Sedated seals were carried in cages to a truck and transported to Long Marine Laboratory, 33 km south of Año Nuevo. At the laboratory the seals were weighed and held overnight. The following day the seals were loaded on a truck for transport to the release site. Forty-five seals were released at six coastal locations. An additional 30 seals were transported from Long Marine Laboratory to either Santa Cruz or Moss Landing Harbor, where they were loaded onto a ship for transport to offshore release sites (Fig. 1, Table 2). The at-sea release sites were clustered in five areas, designated S1 through S5. All release sites were within 100 km of Año Nuevo. No attempt was made to determine the maximum distance that the seals would home.

We made no attempt to shield the seals from environmental cues during
Table 2. Summary statistics of the homing behavior of 75 northern elephant seals translocated from Año Nuevo State Reserve, by release site. See Figure 1 for locations. Number of days en route and homing speed based on when seals were first detected by visual or radio survey.

<table>
<thead>
<tr>
<th>Release site</th>
<th>Distance from Año Nuevo (km)</th>
<th>No. of seals released</th>
<th>No. of seals homing (%)</th>
<th>No. days en route</th>
<th>Homing speed (km/d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Half Moon Bay</td>
<td>48</td>
<td>2</td>
<td>2 (100)</td>
<td>2.1</td>
<td>24</td>
</tr>
<tr>
<td>Pomponio Beach</td>
<td>24</td>
<td>3</td>
<td>3 (100)</td>
<td>8.0 (2.2–19.0)</td>
<td>7 (1–11)</td>
</tr>
<tr>
<td>Santa Cruz</td>
<td>33</td>
<td>10</td>
<td>10 (100)</td>
<td>2.9 (0.4–11.2)</td>
<td>33 (3–88)</td>
</tr>
<tr>
<td>Moss Landing</td>
<td>61</td>
<td>4</td>
<td>2 (50)</td>
<td>3.5 (2.1–4.9)</td>
<td>21 (12–29)</td>
</tr>
<tr>
<td>Monterey</td>
<td>65</td>
<td>20</td>
<td>20 (100)</td>
<td>5.3 (1.9–14.8)</td>
<td>19 (4–34)</td>
</tr>
<tr>
<td>Pt. Lobos</td>
<td>75</td>
<td>6</td>
<td>5 (83)</td>
<td>4.4 (1.9–7.0)</td>
<td>23 (13–67)</td>
</tr>
<tr>
<td>At Sea (S1)</td>
<td>28–34</td>
<td>11</td>
<td>9 (82)</td>
<td>5.6 (1.0–20.1)</td>
<td>15 (2–33)</td>
</tr>
<tr>
<td>At Sea (S2)</td>
<td>50–57</td>
<td>8</td>
<td>4 (50)</td>
<td>5.2 (2.9–10.0)</td>
<td>13 (6–18)</td>
</tr>
<tr>
<td>At Sea (S3)</td>
<td>65</td>
<td>2</td>
<td>2 (100)</td>
<td>4.5 (1.9–7.1)</td>
<td>22 (9–34)</td>
</tr>
<tr>
<td>At Sea (S4)</td>
<td>83</td>
<td>2</td>
<td>2 (100)</td>
<td>4.8 (3.7–5.8)</td>
<td>18 (14–22)</td>
</tr>
<tr>
<td>At Sea (S5)</td>
<td>97–99</td>
<td>7</td>
<td>7 (100)</td>
<td>3.9 (1.9–11.2)</td>
<td>36 (9–50)</td>
</tr>
<tr>
<td>Totals</td>
<td>24–100</td>
<td>75</td>
<td>66 (88)</td>
<td>4.7 (0.4–20.1)</td>
<td>22 (1–88)</td>
</tr>
</tbody>
</table>

transport. When the release site was reached, the cage doors were opened and the seals entered the water at their own pace. We released them either singly or sequentially in small groups of two (16), three (4) and four (1), with a mean of 17 ± 15 min (range 0–53 min) between releases. One trio was released simultaneously at sea. Seals were released a mean of 24 ± 16 h (range 3–137 h) after initial capture. We observed the seals when they were released from shore or at sea, noting changes in activity, breathing and diving patterns, and direction of disappearance. We made underwater observations when sea conditions permitted (Beaufort 2 or less) by positioning a free diver near the seals’ expected point of entry into the water.

We located returning seals by conducting daily radio and visual surveys at Año Nuevo. If a seal did not return within ten days, we expanded our searches 100 km north to the Farallon Islands and 205 km south to Pt. Piedras Blancas. When returning seals were located, we removed the instruments while the seals slept or while they were physically or chemically immobilized. Epoxy mounts remained on the seals and were shed at the next molt.

We used three alternate criteria to determine time of return to the capture site: time of the first visual sighting, time of the first radio signal received, or time of landfall as indicated by diving records. Only TDR records provided exact arrival times. Homing speed was calculated by dividing the distance of the most direct route from the release site to Año Nuevo by the time at sea.

We processed the TDR records with Zero-offset-correction version 1.08 and Dive Analysis version 4.25 software (Wildlife Computers, Woodenville, WA). We conducted statistical analysis of the homing and diving data using StatView 4 (version 4.5.1, Abacus Concepts, Berkeley, CA). We defined hom-
ing as a return to the capture site by a translocated seal within the season in which it was released. We analyzed frequency distributions of data with the $\chi^2$ test, continuous dependent variables with ANOVA, and multiple pairwise comparisons with t-tests (Sokal and Rolf 1981) using a sequential Bonferroni correction factor to minimize Type 1 errors (Rice 1989). Homing rate was modeled by treating the dependent variable, return, as a binary response in an ANOVA model (after Neter et al. 1989) and using the statistical program SuperANOVA (Abacus Concepts, Berkeley, CA). Differences were judged statistically significant when $P < 0.05$.

RESULTS

Eighty-eight percent of the 75 elephant seals returned to Año Nuevo within 21 d. Homing did not differ between males and females, between seasons or between years ($P > 0.05$, $\chi^2$). The addition of diving instruments had no detectable effect on homing behavior ($P > 0.05$, $\chi^2$). All ten seals tagged at weaning at Año Nuevo homed successfully.

Age class and release site had significant effects on homing success (ANOVA: Age class: $F = 6.09$, df = 3, $P < 0.05$; release site: $F = 4.32$, df = 10, $P < 0.05$). Homing rate increased with age until the seals reached the J22 age class: J10-73%; J16-88%; J22-100%; J34-100%. All non-homing J10s ($n = 6$) were males, and all non-homing J16s ($n = 3$) were females. Animals released at Moss Landing and at the at-sea site S2 (Fig. 1) had significantly lower return rates than those released at other sites. The significance of the interaction term of release site and age class ($F = 3.81$, df = 15, $P < 0.05$) indicates that younger seals were more affected by differences in release site than older seals. Although the location of the release site was statistically significant, the distance from the site to Año Nuevo was not (homing seals: 58 $\pm$ 22 km; non-homing seals: 55 $\pm$ 14 km, $P > 0.05$, ANOVA).

Ninety-six percent of the 75 translocated seals were resighted. All nine of the non-homing seals (6 male J10s and 3 female J16s) were released from sites south of Año Nuevo: the J10s at S1, S2, and Pt. Lobos, and the J16s at S1 and Moss Landing. We found six of these seals; five were resighted at rookeries and haul-out areas south of their release sites, and one J10, released at Pt. Lobos, returned to Año Nuevo during the next haul-out cycle 104 d after release. When we resighted these non-homing seals, they, like the homing seals, were in the company of other elephant seals. Two J10s were found at the Pt. Piedras Blancas rookery (176 km from their S2 release site and 224 km from Año Nuevo), a third at the Gorda rookery (111 km from its S1 release site and 164 km from Año Nuevo) and another at an unnamed haul-out on the Big Sur coast (51 km from its S2 release site and 119 km from Año Nuevo). Instrumentation packages were removed from these four seals, and another from a fifth seal (J16) was found at the Gorda rookery, four months after the seal was released. This package was apparently shed when the seal molted there. This seal and the two J10s which hauled out at Pt. Piedras Blancas have been resighted at these sites in subsequent years but have not
Table 3. Mean and range of number of days' travel time and rate of travel to Año Nuevo State Reserve, California, by 18 juvenile northern elephant seals, based on when first sighted and when hauled out according to time-depth recorder (TDR) data. Times and rates tested using paired comparison $t$-test, significant results ($P < .05$) marked with *.

<table>
<thead>
<tr>
<th>Release location</th>
<th>Number of seals</th>
<th>Travel time to return (days)</th>
<th>Travel speed during return (km/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>via 1st sighting</td>
<td>via TDR</td>
<td>via 1st sighting</td>
</tr>
<tr>
<td>Santa Cruz</td>
<td>2</td>
<td>1.69 (1.1-2.3)</td>
<td>0.66 (0.4-0.9)</td>
</tr>
<tr>
<td>Monterey</td>
<td>5</td>
<td>2.00 (1.9-2.2)</td>
<td>1.51 (1.3-1.7)*</td>
</tr>
<tr>
<td>Pt. Lobos</td>
<td>3</td>
<td>3.65 (1.9-7.0)</td>
<td>2.94 (1.5-5.7)</td>
</tr>
<tr>
<td>S1</td>
<td>4</td>
<td>3.74 (1.0-11.0)</td>
<td>3.29 (0.5-10.6)</td>
</tr>
<tr>
<td>S4</td>
<td>2</td>
<td>4.75 (3.7-5.8)</td>
<td>3.87 (3.5-4.2)</td>
</tr>
<tr>
<td>S5</td>
<td>2</td>
<td>3.57 (2.1-5.1)</td>
<td>2.16 (1.7-4.7)*</td>
</tr>
<tr>
<td>All locations</td>
<td>18</td>
<td>3.11 (1.0-11.0)</td>
<td>2.49 (0.4-10.6)*</td>
</tr>
</tbody>
</table>

been resighted at Año Nuevo. The birth site of all non-homing seals was unknown. Three seals, each carrying a radio and one a TDR, are unaccounted for: two J16 females released at Moss Landing and one J10 male released at S2.

Mean time at sea and homing speed of the 66 homing seals, based on time of first sighting or radio reception, was $4.7 \pm 4.3$ d (range = 0.37-20.1 d) and $22 \pm 17$ km/d (Table 2). Homing speed increased significantly with age (J10: $\bar{x} = 13$ km/d (range 1-50 km/d); J16: $\bar{x} = 22$ km/d (range 2-88 km/d); J22: $\bar{x} = 25$ km/d (range 3-70 km/d); J34: $\bar{x} = 41$ km/d (range 34-48 km/d); $F = 2.79$, df = 3, 63, $P < 0.05$), although the fastest seal was a J16 homing from Santa Cruz at 88 km/d. Differences in homing speed were not significant between release sites or significantly affected by the distance translocated.

Eighteen TDR records covered the entire period at sea from release to return to Año Nuevo. Over deep water (>140 m), the seals exhibited a diving pattern similar in dive depth and dive duration to that of migrating juveniles of the same age (Le Boeuf et al. 1996, Oliver 1997). Eight seals released at Monterey and Point Lobos, requiring them to dive over the continental shelf and over the deep waters of Monterey Canyon, had a mean dive depth of 157 m (range 58-279 m) with a mean maximum depth of 656 m (range 307-987 m). The mean dive depth of two seals returning over the continental shelf from the release point in Santa Cruz was 30 m, with a maximum dive depth of 84 m. Eight seals released at sea had a mean dive depth of 177 m (range 91-310 m) with a mean maximum depth of 572 m (range 364-817 m). The TDR records indicated that the seals arrived a mean of 0.61 d (range 0-1.57 d) prior to being detected by radio or visual surveys (Table 3). For these 18 seals, mean time at sea was 2.49 d (range 0.44-10.56 d) based on TDR-derived landfall, compared to a mean of 3.11 d (range 1.10-11.00), based on time of first observation. This difference is statistically significant (paired $t$-test, $t =$
head motions. When released from a beach, after entering the water many seals settled to the bottom in shallow water and remained relatively still for several minutes. Underwater, the seals continued to appear alert, with flared vibrissae, bulging eyes, frequent horizontal scanning movements of the head, as well as opening and closing of the jaws. After several minutes the seals slowly accelerated and, swimming close to the bottom, moved offshore and disappeared. When the seals were released at sea the same attentive behavior was observed on deck as was seen on the beach. However, once they entered the water they dove rapidly, corkscrewing as they disappeared into the depths.

**DISCUSSION**

Elephant seals excel at homing. The homing rate of the youngest juveniles in this study was similar to that of adult California sea lions (Ridgway and Robison 1985; Pfeifer 1989, 1991) and harbor seals (Goodridge and Dietz 1975; L. Dunn, personal communication; P. Olesiuk, personal communication) and higher than the rates of sea otters, *Enhydra lutris* (Garshelis and Garshelis 1984, Ralls *et al.* 1992, Estes *et al.* 1993), bears (Payne 1975; Stirling *et al.* 1977; Thier and Sizemore 1981; Miller and Ballard 1982; Rogers 1986, 1987), and bats (Davis 1966) over similar distances. Moreover, homing performance improved with age, suggesting that adults would show the highest return rates. The similar homing performance of males and females in both spring and fall demonstrates both ability and motivation independent of sex or specific on-land activities such as molting or rest. The homing behavior we observed was not motivated by a return to a food source. Clearly, the seals had a strong motivation to be at Año Nuevo in the spring and fall or to be with conspecifics. The few seals that did not return to the rookery, but were located elsewhere, were found with other elephant seals. It is well known that elephant seals are gregarious ashore, but they are generally believed to be solitary at sea. Our finding that the seals released simultaneously or in rapid sequence, travelled separately while homing, supports this belief.

That most seals departed on the appropriate initial compass heading at release suggests that the seals sensed the general direction back to the rookery and took a rather direct route, with minimal wandering. The homing speed of more than half of the instrument-carrying seals was similar to that of migrating seals of similar age, above 50 km/d (Le Boeuf *et al.* 1996). Seals released from Santa Cruz returned to the rookery in shallow water on the continental shelf, the most direct route to Año Nuevo. This was confirmed by a video camera mounted on a juvenile showing it returning to Año Nuevo from Santa Cruz by a shallow, inshore route (R. Davis, B. Le Boeuf, and D. Crocker, personal communication). In contrast, seals released near Monterey exhibited a deep-diving pattern which required them to cross the Monterey Canyon while returning to Año Nuevo.

The propensity for nocturnal returns ashore may be an anti-predator strategy aimed at minimizing exposure to great white sharks, *Carcharodon carcharias,*
which are believed to be primarily visual diurnal predators (Klimley 1994, Le Boeuf and Crocker 1994).

The significance of this study, aside from its intrinsic importance in demonstrating homing in elephant seals, is in showing that the translocation paradigm can be used to facilitate short-term studies of freely diving seals, and especially studies of diving behavior and physiology requiring completion in a day or two. This is an asset in studies of a pelagic mammal that normally spends 2–8 mo at sea (Le Boeuf 1994, Stewart and DeLong 1995). Moreover, the diving behavior of translocated seals is similar to that of migrating seals (Oliver 1997). The method has already been used successfully to record acoustic stimuli impinging on the swimming seal (Fletcher et al. 1996; Burgess et al. 1996, 1998), heart rate and EKG (Andrews et al. 1997), locomotor energetics from video images (T. Williams, R. Davis and B. Le Boeuf, unpublished data), rapid depth sampling of diving behavior (Oliver 1997), and to conduct metabolic studies with doubly labeled water (D. Costa and B. Le Boeuf, unpublished data). Studies of other pinnipeds may prove similarly amenable to this method.

ACKNOWLEDGMENTS

We thank Russ Andrews, Lisa Cody, Dan Crocker, Jeanine Williams, Eric Dorfman, Paul Webb, Susanna Blackwell, Kenny Cornella, Chris Courtin, Juan Pablo and Anna Gallo, Susie Kohin, John Newman, John Sanders, Alexis Barbour, Maria Kretzmann, Gordon Rietz, Kate Stafford, Julie Hitchcock, Jim Coyer, Michael Sweet, Dan Costa, Laurie Rea and Stefano Velotti for moving 34 tons of seals over 4,000 km; Captains Gordon Smith and the other Afro Nuevo Reserve rangers, Ron Jameson, Brian Hatfield, Alan Baldridge, Sarah Allen, and Bill Sydeman for their cooperation; Ron Belknap for aerial surveys; Carl Haverl and Jacqueline Papp for creating Figure 1; and Ken Norris, Dan Crocker, Terrie Williams, Brent Stewart, and Roger Gentry for comments on the manuscript. Hair dye was provided by Clairol, Inc. This work was conducted under NMFS permit #836. Funding for this project was obtained from the Friends of Long Marine Lab, the Robert Lee Funsten Trust, the G. Macgowan Trust, and the National Science Foundation.

LITERATURE CITED


BURTON, H. R., AND N. J. GALES. 1987. Prolonged and multiple immobilizations of


Received: 28 February 1996
Accepted: 1 April 1997