

Flipping sand in elephant seals

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Abstract

Flipping sand to the dorsum with backward strokes of the foreflippers is one of the most conspicuous behaviours of elephant seals on land. Sand flipping (SF) has been described as a thermoregulatory behaviour, a response to skin irritation and a displacement activity during social conflict. We studied SF in breeding females and suckling pups of the southern elephant seal, *Mirounga leonina*, during the 1991 and 1994 reproductive seasons, at Península Valdés (PV), Argentina. At the temperate latitude of PV (42°S), elephant seals are exposed to higher temperatures and solar radiation than in other colonies. Females spend 9% of the non-resting time flipping sand. Sand flipping occurred in 73% of 145 focal animal samples (FAS) taken of different females during a wide range of weather conditions. Sand flipping did not occur in 12% of 57 FAS recorded during the most stringent thermal conditions. Lactating pups displayed SF at a higher frequency than their mothers and the behaviour was also poorly correlated with the thermal context. Sand flipping occurred during rainy days, at night and during conflict situations (e.g., female harassment by males). We found no single cause for SF. It apparently serves more than one function and may better respond to internal variables than to the external environment.

Introduction

Sand flipping (SF), the tossing of sand upon the back with alternating backward movements of the foreflippers, is a common behaviour of elephant seals, *Mirounga sp.*, while on land (Laws, 1956; White & Odell, 1971; Odell, 1974). Sand flipping has been interpreted as a heat dissipation mechanism (White & Odell, 1971), a relief of skin irritation during molting or drying of the skin due to wind and sun exposure (Laws, 1956), an insulatory mechanism during cold windy days (Rasa, 1971), and a displacement activity of aroused animals in a conflict situation (Laws, 1956; Rasa, 1971; Heath & Schusterman, 1975).

Pinnipeds are often exposed to overheating (Whittow, 1987). Behaviour enhances the efficiency of anatomical and physiological adaptations to cope with high air temperature and solar radiation (Whittow, 1974; Campagna & Le Boeuf, 1988). A heat dissipation function of SF has been proposed for the northern elephant seal, *M. angustirostris* (White & Odell, 1971; Whittow, 1987). By scooping up sand or pebbles upon its back, a seal digs a hole in the substrate exposing a wet surface. In every new bout, the sand or pebbles that fall on the back are moist, allowing for the cooling effects of evaporation.

We studied SF in adult females and pups of the southern elephant seal, *M. leonina*, at Península Valdés, Argentina. Most major breeding colonies of the species are located in subantarctic latitudes (Laws, 1994). Península Valdés (PV) is the only important rookery located in a temperate latitude (42°S; Campagna & Lewis, 1992; Laws, 1994; Lewis *et al.*, 1998). During the Austral spring (September–October), when southern elephant seals breed at PV (Campagna *et al.* 1993), reproductive animals are exposed to air temperatures that normally range around midday between 17–23°C, and may reach up to 30°C. In subantarctic colonies, such as Kerguelen and Macquarie islands, air temperature for the same time of the year ranges between 2–5°C. How does a temperate climate affect the behaviour of a subantarctic seal and what are the breeding consequences? Sand flipping could be an indicator of how well adapted the seals are to the thermal environment while breeding. The frequency of occurrence of SF may help to understand whether seals breeding at PV are exposed to heat stress.

This ethological study provides the first quantitative description of SF for the southern elephant seal. Previous work, for the species, mentioned the occurrence of the behaviour in an opportunistic or anecdotal manner (Laws, 1956). Sand flipping was described in relation to weather conditions in the northern elephant seal, although the study focused on adult males and non-breeding animals (White & Odell, 1971; Rasa, 1971; Heath & Schusterman,

1975). Our results point to the most relevant component of the breeding population, adult females and their pups, and adds information related to a more crucial part of the annual cycle and provides an opportunity for general interspecific comparisons. Sand flipping is an appropriate measure of thermoregulatory behaviour during the breeding season because reproductive females avoid male harassment by refraining to move (Laws, 1956; Baldi *et al.*, 1996). Thus, female cooling alternatives are more limited than those of males.

Methods

Behavioural observations were conducted at Punta Delgada, PV (42°30'S; 64°W) during two breeding seasons (September and October 1991 and 1994). The study site had a variety of substrates and topographies: sandy beaches bordered by cliffs or dunes, where most of the harems were found, beaches of fine pebbles (1–3 cm in diameter) and beaches of coarse pebbles (about 4–10 cm) bordered by cliffs (Campagna & Lewis, 1992). Harem density was one to five harems/km and the individual distance between females within the harem remained more than one body length throughout the breeding season (Baldi *et al.*, 1996). Harem densities were similar during both seasons studied (Lewis *et al.*, 1998).

Sand flipping was defined as 'an act in which the front flippers scoop up and flip sand upon the back [of a seal]' (White & Odell, 1971). A SF bout was defined as a sequence of foreflipper strokes. The duration of a bout was measured as the period from the start of the first stroke to the end of the last one. A different bout started when more than one minute elapsed between two consecutive strokes.

The occurrence of SF was quantified during 30-min-long focal animal samples (FASs; Altmann, 1974) of marked females (1991) and marked mother-pup pairs (1994). Sampled pups were about 1-week-old and had black lanugo. During each FAS, we recorded: (a) the number of SF bouts, (b) number of strokes per bout, and (c) movements to the surf zone. We obtained at least one FAS for each of 145 individuals (93 adult females in 1991 and 52 mother-pup pairs in 1994). We obtained two FAS, one in the morning (08:30–09:30 h) and one at midday (12:00–15:00 h), for 34 of the 145 seals.

During the 1994 season, we recorded the proportion of the surface area of the back of each seal that was covered with sand. These data were obtained for females and pups that were in the ventral position using scan samples (Altmann, 1974). We focused the observations on one harem of 136 females located on a sandy substrate in early

October, the peak of the breeding season. Sampled animals were assigned to one of two categories, based on the proportion of the dorsum covered with sand: $\leq 50\%$ and $> 50\%$. The proportion of the back covered with sand was used as an indicator of the occurrence of SF prior to the time of the sample. We conducted 2–4 scan samples per day during the warmest part of the day (11:00–15:00 h). During 1991 scans were conducted every 2 h, from 08:00 to 18:00 h.

Weather conditions were recorded at the beginning of a FAS, and immediately before each scan sample. We recorded tide condition (based on a tide table and *in situ* observations), substrate temperature (with a digital thermometer, Delta SK 1250 MC, SATO KEIRYOKI.MFG. Co. Ltd) and ambient temperature (thermistor probe exposed to the wind and sun). Ambient temperature was affected by the wind and usually was 2–5°C below air temperature, depending on wind speed and direction. We also obtained the 'black bulb' temperature (BBT), the temperature recorded with a thermistor probe located inside a black spherical container, the size of a ping-pong ball, lying on the substrate (White & Odell, 1971; Campagna & Le Boeuf, 1988). Black bulb temperature is a reliable measure of solar radiation and substrate surface temperature, and responds quickly to changes in sky overcast and air temperature (White & Odell, 1971). Black bulb temperature varied as a linear function of solar radiation ($y_{\text{BBT-C}} = 26.8 \times \text{cal/cm}^2/\text{min} + 12.8$), was significantly correlated with solar radiation (Pearson's $r = 0.98$, $r^2 = 0.94$, $P < 0.01$) and with substrate temperature (sand $r = 0.90$, $r^2 = 0.82$; pebble $r = 0.92$, $r^2 = 0.86$; $P < 0.05$). There were no significant differences between years in mean solar radiation recorded during the heat of the day (11:00–15:00 h; 1991 = 25.9°C, 1994 = 26.7°C; $t = -0.6$, $df = 61$, $P > 0.05$).

Substrate temperature was measured with a probe lying flat and in contact with the surface of the substrate and at 10 cm of depth. Substrate temperatures were recorded for all substrates at a position of the beach similar to where most individuals were located during FASs or scan samples.

We analyzed the occurrence of SF with a two-level, ordinal index of thermal condition that combined BBT and degree of wetness of an individual and of the substrate (low level of thermal condition: BBT 8–22°C, high tide, female or substrate wet; high level: BBT > 22°C, low tide, female or substrate dry). We choose a BBT of 22°C to contrast the two conditions following White & Odell's (1971) description that northern elephant seals have little SF behaviour when BBT was below 22°C.

The association between BBT and SF bouts was determined using a Spearman correlation (Siegel & Castellan, 1995). The correlation coefficient (r), was

Table 1. Ambient temperature and BBT ($^{\circ}\text{C}$, mean and SD) recorded once per day, as a function of date during the 1994 breeding season. Sample sizes (number of days with data) are in parentheses. Data for November include only the first week of the month

| Month | Ambient temperature | BBT |
|------------------------------|---------------------|---------------------|
| September | 16.7 \pm 4.0 (26) | 24.5 \pm 5.8 (23) |
| October | 18.1 \pm 4.5 (30) | 25.5 \pm 7.2 (31) |
| November | 19.4 \pm 2.7 (4) | 33.5 \pm 3.3 (10) |
| Mean for the breeding season | 17.6 \pm 4.2 (60) | 25.7 \pm 6.7 (64) |

calculated based on 145 FAS conducted on different individuals.

Results

Temperatures during the breeding season

Ambient temperature and solar radiation during the warmest part of the day increased as the breeding season progressed (Table 1). Mean BBT increased by 9°C from early in the season (September) to the end of breeding (November; Table 1). During the warmest days, ambient temperature reached 29°C , BBT rose to 40°C , and the temperature of a sandy substrate reached 37°C at the surface. Black bulb temperature went over 25°C in 30% of 70 days of the 1994 breeding season. Substrate temperature varied according to type of substrate (sand, large pebbles or small pebbles) and depth in the substrate. The mean surface temperature of the sand at BBT above 22°C was significantly lower than that of the pebble (28.6°C vs 32.3°C ; Mann-Whitney $U=440.5$, $P<0.01$). Large pebbles were cooler at the surface than small ones (27.9°C vs 32.3°C ; Mann-Whitney $U=384.5$, $P<0.05$). Substrate temperature decreased with depth. The temperature of the sand and pebbles at the surface was 10 – 15°C higher than at 10 cm under the surface (Table 2; $t=23.6$; 22.4 ; 21.1 , $P<0.05$ to sand, small pebbles and large pebbles, respectively).

Surface temperature was also affected by the distance from the surf. Within 10 m from the high-tide line, and at 10 cm below the surface, both sand and pebbles remained constantly wet and cool (11 – 15°C).

Sand flipping

Females spent 79% of the time ashore resting (from 34,195 scan samples obtained from 109 marked females). Sand flipping involved 8.7% of the active time of females with a pup (from 7345 scan recordings of animals that were not resting).

Table 2. Substrate temperature ($^{\circ}\text{C}$, mean and range) as a function of type of substrate and depth in the substrate. When BBT $>22^{\circ}$ temperatures were taken almost simultaneously in all types of substrates

| Depth in the substrate | Type of substrate | | |
|------------------------|-------------------|----------------------|----------------------|
| | Sand (n=46) | Small pebbles (n=48) | Large pebbles (n=48) |
| Surface | 27.8 (19–34) | 30.9 (18–46) | 26.8 (16–34) |
| 10 cm deep | 16.4 (10–22) | 16.6 (10–22) | 16.8 (10–23) |

Sand flipping occurred in bouts separated by resting periods. Each bout involved a variable number of strokes during which seals used one or both fore-flippers, sometimes alternating right and left, to scoop up and flip wet sand or pebbles upon their back. Most bouts lasted less than a minute (max=7 min). A maximum of 151 strokes were recorded during a 30-min FAS. As a consequence of SF, seals had all or part of the back covered with sand and pebbles. A median of 36% (range: 0–64%) of the reproductive females in a harem of 136 animals at peak season had sand on the back.

Pups were first recorded flipping sand within a few minutes after birth. A median of 22% (range: 0–100) of the pups in ventral position in a group of 88 pups within a harem had the back covered with sand. Pups engaged in SF bouts that lasted from less than 1 min to 3 min, and involved up to 197 strokes in 30 min.

Sand flipping as a response to external factors

Sand flipping occurred in 73% of 145 FAS obtained during different thermal conditions. Sand flipping was more likely to occur during a FAS taken when the index of thermal condition was high. This index was high in 57 of the 145 FASs, and SF was observed in 88% of these 57 samples. Sand flipping also occurred when the index of thermal condition was low, but in a significantly smaller proportion than during more stringent conditions (64% of 88 FAS; $\chi^2=10.20$, $df=1$ $P<0.01$). SF did not occur in 39 FAS, most of which (82%) took place during conditions of low thermal index.

The median number of SF bouts per FAS was significantly higher during a high index of thermal condition than during cooler situations. From a selection of 106 FASs during which SF occurred at least once, the median number of bouts per FAS was 5 (range 1–24) for a high thermal index vs 1 (range 1–16) for a low one (Kruskal-Wallis $\chi^2=3.78$ $df=1$ $P=0.025$).

Sand flipping was more common at midday (median=5 bouts in 30 min, range: 0–29) than during the morning (median=2, range: 0–10).

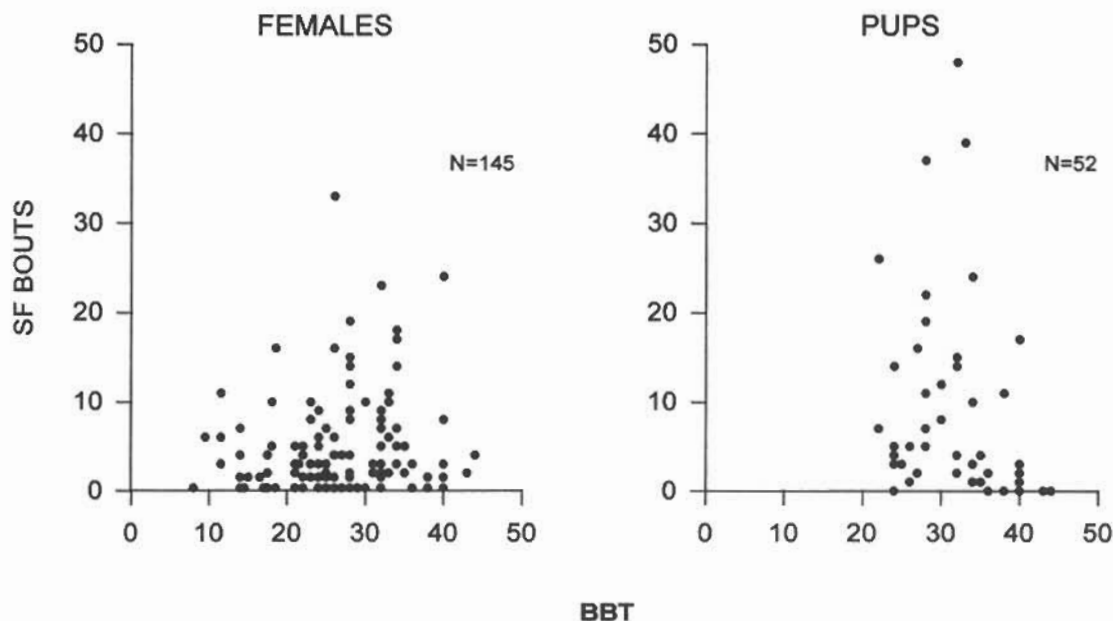


Figure 1. Occurrence of SF bouts in females and pups as a function of BBT. The number of bouts varied widely regardless of solar radiation. Pups were recorded with BBT > 20°C because the observations were conducted only in 1994 from 11:00 to 15:00 h when solar radiation was at its peak.

Thirty-seven females were sampled twice during a day, after 5–6 h of exposure to solar radiation from the first to the second observation. From them, 25 showed an increase in the frequency of SF bouts during a FAS, 9 decreased it and 3 showed no effect (Sign test, $P=0.005$, $n=34$; Siegel & Castellan, 1995).

When BBT increased over 22°C, a median of 15% of the females in a harem (range: 3–41%) had more than 50% of the surface of the back covered with sand as a consequence of SF ($n=32$ scans). The proportion of females in ventral recumbence did not vary as a function of BBT (Spearman $r=+0.06$; $n=63$; $P>0.05$).

The number of SF bouts per FAS in adult females was not correlated with BBT (Spearman $r=+0.15$, $n=145$, $P>0.05$; Fig. 1). Some females engaged in sequences of SF bouts even in the lowest ranges of BBT (Fig. 1).

The frequency of SF was not affected by the substrate of the beach. Fifty-one of 145 FAS, were taken of females on a sandy substrate while 94 involved individuals on a pebble beach. The proportion of FAS during which we recorded SF was similar for all substrates, even when we selected only those FAS taken during a high index of thermal conditions (78% of 49 females on sandy beaches vs 75% of 61 on pebble beaches ($\chi^2=0.07$, $P>0.05$).

Besides SF, some females responded to hot thermal conditions by moving to the surf. We recorded this behaviour in 28 of 145 FAS. Most of the females (78% of 28 individuals) had been involved in SF before moving to the water. All cases of females moving to the water occurred when the index of thermal condition was high. From the 28 females, those that were on a pebble substrate (54%) moved to the water when the BBT was 26°C or higher, while those located on sandy beaches (46%) moved at BBT of 36°C or higher.

Sand flipping in pups was recorded in 94% of 52 FASs. The frequency of occurrence of SF bouts in pups was similar during low and high thermal conditions (94% of 17 FASs vs 93% of 35 FASs; $\chi^2=0.37$, $P>0.05$). The median number of SF bouts during a FAS was not affected by changes in the index of thermal condition. When the index was high, the median was 5 bouts per FAS (range: 1–48) vs 4.5 (range: 1–26) when the index was low (Kruskal-Wallis $\chi^2=0.52$, $df=1$, $P>0.05$).

Compared to their mothers, pups responded to similar thermal environments following a higher frequency pattern of bouts and strokes. The correlation of SF bouts between mothers and pups was positive but not significant (Spearman $r=+0.24$, $n=52$, $P>0.05$). There was no apparent association between BBT and number of SF bouts (Fig. 1).

Discussion

Sand flipping during the breeding season at PV did not reflect the effect of any simple external thermal variable. Seals flipped sand or pebbles onto their back in a wide range of ambient temperatures and solar radiation. SF was more common during a high index of thermal condition than during cooler situations. However, the behaviour also occurred at low temperatures and levels of solar radiation, at night and on rainy days.

The type of substrate where seals breed may affect thermoregulatory behaviour. A wet substrate, for example, intensifies the gradient for conduction and heat loss (White & Odell, 1971). We found that a pebble beach reached higher temperatures at the same level of solar radiation than a sandy beach. Females located on pebble beaches tended to move to the surf at lower ambient temperatures than those on sandy substrates. The type of substrate, however, was not strongly associated with SF.

Pups responded to the thermal environment with a pattern of bouts and strokes higher in frequency than their mothers (up to four times that of an adult female exposed to the same thermal condition). As pups are almost completely black during the three-week lactation period, they absorbed more heat than their mothers. However, the frequency of SF bouts in pups was only weakly associated to solar radiation and remained almost unchanged despite variations in the thermal condition.

Elephant seals molt once a year (Laws, 1956; Le Boeuf & Laws, 1994) and the southern species does it during the Austral summer (December–January for adult females, Lewis *et al.*, 1990). As thermal conditions during the molt are more extreme than for the breeding season, a stronger association between temperature and behaviour may be expected for the former than for the latter. However, results regarding the occurrence of SF for the breeding season were similar to those recorded for the molt. A study conducted during the molt, when BBT temperatures increase up to 45°C and ambient temperature reaches 35°C, showed that females invested 10% of the non-resting time SF (based on 1956 scan samples; Rivarola, unpublished data) vs 8.7% for breeding females. Females moved to the surf in 21% of FAS taken during the molt (131 FAS lasting 30 min each; Lewis, unpublished data) vs 24% of FAS of breeding females (61 FAS of the same duration on pebble substrate).

The peak of the breeding season occurs at PV one week earlier in the Spring than in other studied colonies (Campagna *et al.*, 1993). One possible explanation advanced for this observation is that seals would be less exposed to thermal stress by avoiding the warmer weather of late October and November (Campagna *et al.*, 1993). The evidence

based on SF suggests that the present timing of reproduction is not affecting the behaviour of a subantarctic seal, such as the southern elephant seal, breeding and molting in a temperate environment.

A behavioural response to the thermal environment was also described for the same species at other sites and for other species. Laws (1956) reported the occurrence of SF in the southern elephant seals of South Georgia Island and mentioned that the frequency of SF is greatest on hot, sunny days. The intensity of SF, migrations to the surf zone and the frequency and pattern of social interactions during the day for the northern elephant seal were all considered to be related to thermal conditions (White & Odell, 1971; Rasa, 1971). During warm days, Hawaiian monk seals (*Monachus schauinslandi*) are extremely inactive. They move down the beach, dig holes to expose the cool deeper layers of the substrate, and cool down their warm, dry body surface with the moist sand (Whittow, 1978; Whittow, 1987). Sand flipping, exposing the hind flippers to the wind and moving to the surf have been observed in southern sea lions (*Otaria flavescens*) and California sea lions (*Zalophus californianus*) (Vaz Ferreira y Palerm, 1961; Odell, 1974; Campagna & Le Boeuf, 1988).

Sand flipping serves more than one function and also occurred as a byproduct of a conflict situation, independent of the thermal environment. Laws (1956) observed that SF motions often occurred on beaches where there are no loose stones or sand to be scooped up. He concluded that sand throwing may either be a practical response to physical irritation or a displacement activity resulting from emotional conflict. Individuals of the northern elephant seal exposed to social disturbance and harassment sand flip even when their skin may be wet and the day be cold and windy (Rasa, 1971). Females of both species flip sand upon their back after giving birth, when males mount them (Laws, 1956; Rasa, 1971), or even when approached by a researcher (Heath & Schusterman, 1975). SF occurs more frequently in disturbed seals than in resting individuals (Heath & Schusterman, 1975).

Female southern elephant seals at PV also engage in SF when they are harassed by males (e.g., herded, mounted, force-copulated), separated from their pups, affected by the agonistic behavior of other females or mounted by young males (Lewis, Campagna & Wainstein, unpublished data). SF may give some comfort to an animal that is ready to escape but cannot move away. However, as some conflict situations are also associated with vigorous physical activity, SF may also be responding to heat loading from metabolic sources.

A more conclusive relationship between SF and thermoregulation requires a record of skin and core

body temperatures in association to environmental and social variables. Quantitative descriptions of the behaviour for individuals at subantarctic breeding rookeries would allow a comparison with a temperate colony such as PV. In the meantime, SF remains as a multi-purpose behavioural response that bridges between heat stress and just stress.

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References

- Altmann, J. (1974) Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267.
- Baldi, R., Campagna, C., Pedraza, S. & Le Boeuf, B. J. (1996) Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. *Anim. Behav.* **51**, 717–724.
- Campagna, C. & Le Boeuf, B. J. (1988) Thermoregulatory behaviour of southern sea lions and its effect on mating strategies. *Behaviour* **107**, 72–90.
- Campagna, C. & Lewis, M. (1992) Growth and distribution of a southern elephant seal colony. *Marine Mamm. Sci.* **8**, 387–396.
- Campagna, C., Lewis, M. & Baldi, R. (1993) Breeding biology of southern elephant seals in Patagonia. *Marine Mamm. Sci.* **9**, 34–47.
- Deutsch, C. J. (1993) Temporal variation in reproductive activity of male elephant seals: effects of breeding opportunities and thermoregulatory constraints. In: *Tenth Biennial Conference on the Biology of Marine Mammals*, 11–15 November, Galveston, Texas. pp. 42.
- Heath, M. E. & Schusterman, R. (1975) 'Displacement' Sand flipping in the Northern elephant seal (*Mirounga angustirostris*). *Behavioral Biology* **14**, 379–385.
- Laws, R. M. (1956) The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. Falkland Islands Dependencies Survey. *Scientific Reports* **13**, 1–88.
- Laws, R. M. (1994) History and present status of southern elephant seal populations. In: B. J. Le Boeuf & R. M. Laws (eds) *Elephant Seals, Population Ecology, Behavior, and Physiology*. pp. 49–65. University of California Press: Berkeley.
- Lewis M., Campagna, C., Quintana, F. & Falabella, V. (1998). Estado actual y distribución de la población del elefante marino del sur en la Península Valdés, Argentina. *Mastozoología Neotropical*. (5)1: 29–90.
- Le Boeuf, B. J. & Laws, R. M. (1994) Elephant Seals: An Introduction to the genus. In: B. J. Le Boeuf & R. M. Laws (eds) *Elephant Seals, Population Ecology, Behavior, and Physiology*. pp. 1–26. University of California Press: Berkeley.
- Odell, D. K. (1974) Behavioral thermoregulation in the California sea lion. *Behavioral Biology* **10**, 231–237.
- Rasa, O. A. E. (1971) Social interaction and object manipulation in weaned pups of the Northern elephant seal, *Mirounga angustirostris*. *Tierpsychol.* **29**, 82–102.
- Ray, C. & Smith, S. R. (1968) Thermoregulation of the pup and adult weddell, *Leptonychotes weddelli* (Lesson). *Antarctica* **53**, 33–46.
- Siegel, S. & Castellan, N. J. (1995) Estadística no paramétrica aplicada a las ciencias de la conducta, 4th ed. S. A. Trillas, (ed). Printed in Mexico. pp. 437.
- Vaz-Ferreira, R. & Palerm, E. (1962) Efectos de los cambios meteorológicos sobre agrupaciones terrestres de Pinnípedos. *Rev. Fac. de Humanidades y Ciencias* **19**, 281–293.
- White, F. N. & Odell, D. K. (1971) Thermoregulatory behavior of the Northern elephant seal, *Mirounga angustirostris*. *J. Mammal.* **52**, 758–774.
- Whittow, G. C. (1974) Sun, sand and sea lions. *Natural History* **83**(7), 56–63.
- Whittow, C. G. (1978) Thermoregulatory behavior of the hawaiian monk seal (*Monachus schauinslandi*). *Pacific Science* **32**(1), 47–60.
- Whittow, G. C. (1987) Thermoregulatory adaptations in marine mammals: interacting effects of exercise and body mass. A review. *Mar. Mamm. Sci.* **3**, 220–241.