

THERMOREGULATORY BEHAVIOUR OF SOUTHERN SEA LIONS AND ITS EFFECT ON MATING STRATEGIES

by

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(With 3 Figures)

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Introduction

Sea lions and fur seals, the Otariidae, are adapted to avoid heat loss while foraging in cold water. The body surface is insulated with a thick layer of fat and, in the fur seals, by dense pelage. Heat loss may also be reduced by shunting of blood from the periphery and by counter-current heat exchange (TARASOFF & FISHER, 1970). These morphological features that serve heat conservation at sea pose problems for the animals during reproduction on land. During hot weather, the animals must augment heat loss to reduce thermal stress (BARTHOLOMEW & WILKE, 1956; GENTRY, 1973). The problem is most acute in species that breed in areas with high air temperatures and intense solar radiation (EIBL-EIBESFELDT, 1955; TRILLMICH, 1984; HEATH, 1985).

The otariids dissipate heat to the surrounding air and substrate through the skin and respiratory system (BARTHOLOMEW & WILKE, 1956; IRVING *et al.*, 1962; TARASOFF & FISHER, 1970; WHITTOW *et al.*, 1972; OHATA & MILLER, 1977). The large, highly vascularized, hairless flippers

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are particularly important cooling organs (BARTHOLOMEW & WILKE, 1956; IRVING *et al.*, 1962; TARASOFF & FISHER, 1970). However, morphological and physiological adaptations alone, do not prevent overheating when ambient temperatures and solar radiation are unusually high (WHITTOW *et al.*, 1972; WHITTOW, 1987). Under these conditions, behaviour plays a central role in the regulation of body temperature.

To maintain heat balance on land, otariids display a wide repertoire of behavioural adjustments that complement and enhance the efficiency of heat loss by anatomical and physiological means. They adopt postures that maximize exposure of the body surface for evaporative cooling. They raise and expose the hindflippers to the wind, wave them, urinate on them, and shield them from the sun by immersion in water, wet sand or moist pebbles. Individuals increase the distance between themselves to reduce the heat of body contact, spread out the foreflippers to provide maximum exposure to the wind, pant, move to cooler substrates or seek out shade, burrow into the substrate to expose wetter, cooler sand or pebbles, immerse themselves in tidepools, and in the extreme, move into the sea (BARTHOLOMEW & WILKE, 1956; VAZ-FERREIRA & PALERM, 1961; IRVING *et al.*, 1962; VAZ-FERREIRA & SIERRA DE SORIANO, 1962; PETERSON & BARTHOLOMEW, 1967; WHITTOW *et al.*, 1971, 1972; GENTRY, 1973; ODELL, 1972, 1974; DE LONG, 1982).

Behavioural adjustments that serve thermoregulation affect the activity and distribution of individuals, and in doing so, set limits on the social behaviour and mating strategies. As a result, behavioural thermoregulation influences the form of the mating system observed (VAZ-FERREIRA & PALERM, 1961; RAND, 1967; GENTRY, 1973; TRILLMICH & MAJLUF, 1981; DE LONG, 1982; TRILLMICH, 1984; HEATH, 1985). This paper reports on the effect of the thermal environment on the social behaviour and mating system of the southern sea lion, *Otaria byronia*. We show that: 1) breeding animals are exposed to high temperatures and solar radiation during the austral summer, 2) males and females have a wide range of thermoregulatory responses to hot weather, 3) thermoregulatory behaviours influence male breeding success, and 4) the topography of the breeding area, coupled with thermoregulatory constraints on males and females, affects male mating strategies and the form of polygyny.

Methods

Daily observations of thermoregulatory behaviour were conducted from 0800 to 2100, at two southern sea lion rookeries in Península Valdés, Argentina. The Punta Norte

rookery was studied during two breeding seasons, 15 December to 10 February, 1984-86, from a cliff seven metres above the colony and 30-40 m distant from it. The entire colony was in view from the blind. At peak season (third week of January), about 140 males and 350 females grouped along a 200 metre-long stretch of the shoreline at the high tide mark on the wide beach, forming the central breeding area (CBA) (CAMPAGNA, 1985; CAMPAGNA & LE BOEUF, 1988). The pebble substrate was uniform and lacked tidepools and boulders or vegetation to provide shade.

During January 1987, we conducted observations at another rookery, Puerto Pirámide, located 70 km from Punta Norte. Here, sea lions breed on flat rocky shelves bordered inland by 30-40 m high sandstone cliffs that form a steep, nearly perpendicular wall, six metres above the low-tide marks. The rocky platform contains tidepools, and large depressions of several hundred square metres of surface, both filled with sea water. Boulders, two to four times the size of an adult *Otaria* male, are scattered on the shelves and were used for shade. These topographic features were used as landmarks to define territorial boundaries by male sea lions and by the observers. The rookery was composed of 150 males and 500 females dispersed in about six groups, precluding the observation of the entire area from the same place. We observed a group of 18 adult males and 85-110 females from a cliff, 15-20 m above the animals. We marked and recorded presence, position in the rookery and key activities (*e.g.*, copulations) of 15 of the 18 males, following procedures reported in CAMPAGNA & LE BOEUF (1988). The timing of breeding events at Puerto Pirámide was similar to that at Punta Norte (CAMPAGNA, 1985).

To estimate the proportion of breeding animals engaged in thermoregulatory behaviour, censuses of the Punta Norte rookery and the study area at Puerto Pirámide were conducted at least two times per day, differentiating males, females, and pups (CAMPAGNA & LE BOEUF, 1988). The Puerto Pirámide rookery was censused twice during the study period. Males at Punta Norte were categorized as residents (located in the CBA on wet pebbles, close to the water), or peripherals (located inland of the CBA on dry pebbles, distant from the water). At Puerto Pirámide, males were categorized as territorial, defending a site on the rocky shelf, or itinerant, moving about the rookery overland, and in and out of the sea. The influence of thermoregulation on male mating success was estimated using the following criteria of mating success: mean number of females in the territory, length of tenure on territory, and number of copulations achieved. The number of females associated with a male was counted 4-6 times per day. Tenure was defined as the number of days a male was observed in the CBA, defending a territory or females (CAMPAGNA & LE BOEUF, 1988).

At both study sites, hourly scan samples (ALTMANN, 1974) were used to record the number of males and females: (a) holding at least one of the hind flippers in an upright position, exposed to the wind, (b) with hind flippers partially or totally wet or submerged in water pools, (c) with part of the body submerged in a tidepool, (d) resting or swimming in the ocean, and (e) not performing any of the previously listed thermoregulatory behaviours, with dry fur and flippers, and exposed to the sun.

Temperatures and wind conditions were sampled hourly, and solar radiation was recorded continuously with a pyranograph (Weathermeasure Corp., Sacramento, CA). Air temperature was measured with a thermistor located in a shaded and ventilated area. Substrate temperature was measured with a probe lying flat on the dry substrate, exposed to the sun and wind. Black bulb temperature (BBT) was recorded with a thermistor located inside a black spherical container, the size of a ping-pong ball, lying on the substrate exposed to the wind and sun. BBT estimates solar radiation and substrate surface temperature, and both BBT and substrate temperatures indicate the level of insolation. BBT varied as a linear function of solar radiation ($y_{\text{BBT}} \text{ } ^\circ\text{C} = 26.8 \times \text{cal/cm}^2\text{min} + 12.8$; Pearson's $r = 0.98$, $r^2 = 0.94$, $P < 0.01$). Thermistors were connected to a telethermometer (Yellow Springs Instrument, Ohio). Humidity was measured with a wet and dry bulb thermometer. Wind speed was estimated with a manual anemometer.

At Puerto Pirámide, male territories were ranked according to the presence, size, and characteristics of tidepools (*e.g.*, depth, frequency of water renewal). The ranks, a measure of quality of the territory, were correlated with the mating success of the territorial males. Ranked territories were divided into two categories: type 1 territories allowed access to and from the sea during all tides, and had large tidepools regularly replenished with fresh sea water. Type 2 territories did not contain tidepools or had small pools that dried out, and had easy access to and from the sea only at high tide. Territorial ranking was done early in the season before the arrival of females.

Binoculars and a spotting scope were used to census, identify marked individuals, and record behavioural data.

Results

I. Weather conditions during the breeding season.

The summer climate at Península Valdés was hot and dry, with clear skies and virtually no rainfall. During midday hours, solar radiation reached up to 1.42 cal/cm²/min. Air temperature during daylight hours fluctuated from 18° to 25°C, with extremes ranging between 40°C during the afternoon (1300 hrs) to 16°C in the early evening (2000 hrs). Variations of 20°C within the same day were common.

Both rookeries had similar mean air temperatures during daylight hours, but they differed in the distribution of temperature during the day (Table 1). On average, the morning and midday hours at Punta Norte were warm while the afternoons and evenings were cool; at Puerto Pirámide the mornings were cool, and the afternoons and evenings were warm or hot (Table 1). The variable distribution in air temperature between the rookeries was due to differences in wind speed and direction. At Punta Norte, it was windy most days with frequent changes in wind speed and direction. Winds from the South and West were warm (>25°C) and dry (range = 20-40% humidity), while winds from the S.E. to the N.E. were cool (<22°C) and humid (range = 70-90% humidity).

TABLE 1. Mean \pm sd values of air temperature (°C) for the southern sea lion rookeries at Punta Norte and Puerto Pirámide

Time of day	Punta Norte	Puerto Pirámide
0801-1200	26.3 \pm 4.0	20.1 \pm 2.1* ^a
1201-1600	23.9 \pm 3.9	25.6 \pm 2.5* ^b
1601-2000	19.4 \pm 2.0	25.0 \pm 2.9* ^c
0800-2100	23.9 \pm 3.5	23.3 \pm 3.9* ^d

a) $t = 9.6$, d.f. = 143; b) $t = 4.3$, d.f. = 227; c) $t = 15.1$, d.f. = 228; $p < 0.01$; d) $t = 1.46$, d.f. = 399, $p > 0.05$.

Cool winds predominated after midday. Air temperature between 1100 and 1500 hrs on clear and calm days with winds from the South or West were significantly higher ($\bar{x} = 30^{\circ}\text{C}$) than on days with winds from the East ($\bar{x} = 21^{\circ}\text{C}$, $t = 15.9$, $d.f. = 112$, $p < 0.01$). Several times per season, fluctuations of $10\text{--}15^{\circ}\text{C}$ occurred within intervals of 15–30 min due to a shift in wind direction from West or S.W. to East. The hottest temperatures—the most demanding conditions for thermoregulation that males and females encountered at Punta Norte—occurred between 1100 and 1400 hrs, at low tide on clear days with no wind, or with winds from the South or West. Conversely, at Puerto Pirámide, most days were calm or characterized by warm, dry winds particularly at noon and during early afternoon hours. The hottest weather to which breeding animals were exposed occurred between 1300 and 1600 hrs on clear days with no wind or with winds from the North.

II. Effects of the thermal environment on behaviour and distribution.

Differences in thermal conditions were correlated with behavioural adjustments by males and females. Before dawn or after sunset, sea lions typically rested on their ventrums, close to each other. As the sun came up, males and females began changing posture every few minutes, turning around, resting on their backs, sides, or bellies, and, while lying down, exposing one or both hind flippers to the circulating air. From about noon until late in the afternoon, some animals held their hind flippers upright or, from a prone position, they dug with both foreflippers into the substrate to expose moistened pebbles. Sea lions flipped pebbles onto their back, and buried the rear and foreflippers in the wet substrate, keeping the flippers wet and protected from the sun. When animals had access to tidepools, they immersed their flippers or themselves in the water; those without access to tidepools moved into the sea. As shaded places were scarce, only a few animals rested at the shade of boulders or bushes.

Behaviour of males.

The number of males involved in thermoregulatory behaviour was highly correlated with changes in insolation levels. As solar radiation increased within the same day, so did the number of males exposing their hind-flippers to the breeze (Fig. 1). The mean percentage of males with at least one hind flipper up was positively correlated with solar radiation (Ken-

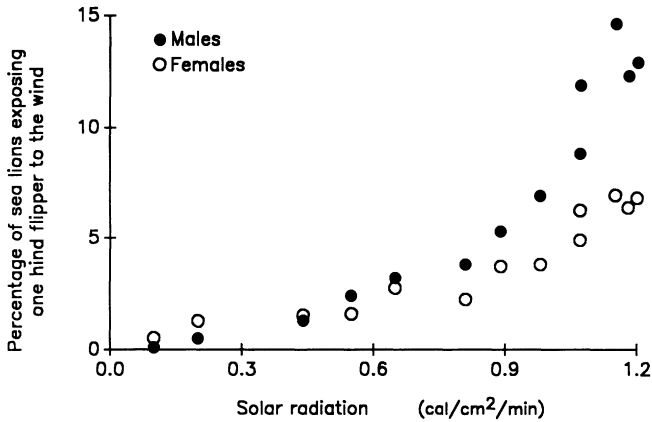


Fig. 1. Percentage of males and females at Punta Norte exposing one hind flipper to the wind as a function of solar radiation. Data points at >0.9 cal/cm²/min are statistically different. All the other means do not differ significantly. Each data point represents a mean of 73-78 observations of solar radiation, and 12-23 observations of sea lions exposing one hind flipper to the wind recorded in January 1985. Each mean summarizes data for a one-hour interval, from 0800 to 2000 hrs.

dall's tau = 0.94, $p < 0.01$; $N = 13$ hourly means plotted in Fig. 1). With increases in insolation or BBT there occurred: (a) a decrease in the mean number of males directly exposed to the sun without performing any kind of thermoregulatory behaviour (Table 2a, Anova $F = 67.9$; d.f. = 2, 108; $p < 0.01$), and (b) an increase in the number of males with their hind flippers or bodies in the water (Table 2b, Anova $F = 32.8$; d.f. = 2, 99; $p < 0.01$).

Males at Punta Norte moved toward the sea during hot weather. After 1-3 hrs of air temperatures $\geq 30^{\circ}\text{C}$ and BBT $\geq 45^{\circ}\text{C}$, itinerant males moved to the sea. Early every morning, 8-20 males were found on the inland periphery of the CBA; by noon, most of them had moved to the water's edge or into the sea. Late in the evening, when temperatures decreased, these peripheral males returned to land. Itinerant males did not move to the water when it was cool and overcast (substrate temperature $\leq 30^{\circ}\text{C}$), at night, or on rainy days. Males associated with females in the CBA were more resistant to high temperatures and seldom abandoned females to go to sea, except during unusually hot weather. During three days of unusually intense heat at midday in mid-January, 1986 (low tide, no wind, air temperature $> 30^{\circ}\text{C}$, and BBT $> 50^{\circ}\text{C}$ for 6-8 hrs), approximately 60% of the resident males and breeding females moved 10-40 m seawards to where the substrate was wet.

TABLE 2. Mean (\pm one sd) number of dry males exposed to heat and wet males and females associated with different thermal conditions at Puerto Pirámide

	Black bulb temperature ($^{\circ}$ C)		
	<30	30-35	>35
a. Males exposed and dry (N)	8.0 \pm 3.0 (27)	4.9 \pm 2.7 (24)	3.0 \pm 1.7 (51)
b. Males in pools or at sea (N)	3.6 \pm 2.9 (32)	8.5 \pm 3.1 (25)	10.5 \pm 2.2 (54)
c. Females in pools (N)	1.1 \pm 1.0 (14)	7.7 \pm 4.4 (7)	14.5 \pm 4.8 (19)

Values were calculated from N scan samples based on a similar number of individuals observed under each black bulb temperature condition.

At Puerto Pirámide, six of 16 males with territories without tidepools or shade moved to sea during hot midday and afternoon hours and stayed in the water for about three hours before returning to their territory. When the weather was cool, these males did not abandon their sites. Males defending territories containing tidepools filled with water partially submerged themselves in the pools, but stayed on their sites despite the hot weather. Two of these males often dashed into the ocean for a few seconds, got wet, and returned immediately to their territories.

Solar radiation, not air temperature, was the principal climatic variable affecting thermoregulatory behaviour, as is illustrated by the following observations. During calm days, if solar radiation remained high, a decrease from high to moderate air temperature did not significantly change the mean number of males in the CBA exposing their hind flippers to the air (Fig. 2, a *vs* b, $t = 1.06$, d.f. = 98, $p > 0.05$). Conversely, when insolation levels decreased, a lower number of males had one hind flipper exposed to the breeze, even if air temperature did not vary (fig. 2, b *vs* c, $t = 5.6$, d.f. = 63; $p < 0.01$). The least demanding thermal conditions occurred when both, air temperature and insolation, were low (Fig. 2, condition d).

The influence of high insolation levels on behaviour was partially neutralized by winds. Sudden variations in wind direction caused abrupt thermal changes, and were correlated with abrupt differences in thermoregulatory behaviours. For example, on January 11, 1985, a drop in air temperature of 13° C occurred in about 15 minutes due to a change in wind direction from the S.W. to S.E. Shortly afterwards the number of males holding their hind flippers up decreased markedly (Fig. 3). The

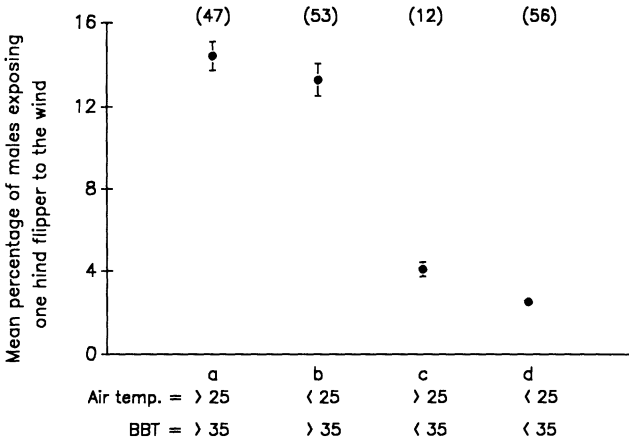


Fig. 2. Effect of insolation and air temperature on the percentage of males with at least one hind flipper exposed to the wind. Data based on 100 males at Punta Norte for each thermal category. Weather conditions represent: a) moderate to intense temperatures and isolation (air temperature: 25-37°C, BBT and substrate temperature (ST): 35-50°C, warm winds or calm, low tide); b) similar insolation as in (a) but lower air temperature (20-25°C); c) similar air temperature as in (a) but low to moderate insolation (BBT and ST < 35°C), and d) low air temperature (< 25°C) and low insolation (BBT-ST < 35°C). Numbers above columns are sample sizes. Deviations from the means are standard errors.

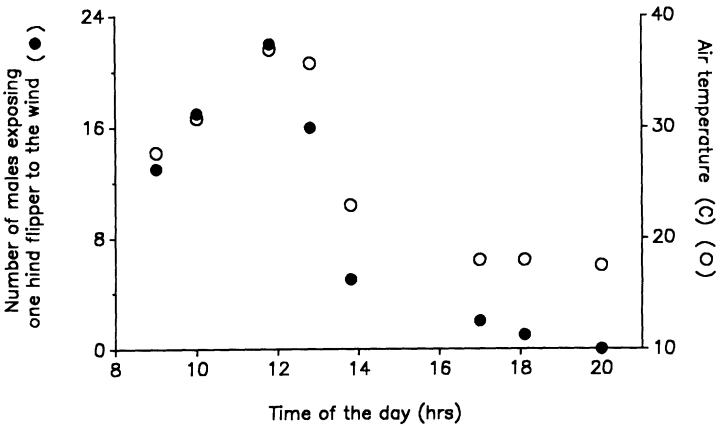


Fig. 3. Number of males exposing at least one hind flipper to the wind (open circles) associated with an abrupt decrease in air temperature (closed circles) caused by a change in wind direction at between 1200-1230 hrs (the number of males remained similar during the day).

tide was high, and solar radiation was similar before and after the change in wind direction (1.20 cal/cm²/min). Similar abrupt changes in thermal conditions were observed about seven times per season. All of them occurred between midday and early afternoon hours, and were associated with dramatic shifts in thermoregulatory behaviours.

Substrate cooling caused by moisture at high tides also altered the effect of insolation on behaviour. The mean number of males with flippers exposed to the air decreased significantly from 14 to five when the substrate and the animals were wet ($t = 7.3$, d.f. = 59, $p < 0.01$), despite the maintenance of similar temperatures and insolation conditions.

Behaviour of females and pups.

Female thermoregulatory behaviour was similar to that of males. The mean percentage of females with at least one hind flipper exposed to the air was positively correlated with solar radiation (Fig. 1; Kendall's tau = 0.86, $N = 13$ hourly means, $p < 0.01$). Likewise, as BBT increased, more females submerged their hind flippers in tidepools (Table 2c, Anova $F = 49.4$; d.f. = 2,37; $p < 0.01$).

Females were apparently less affected by heat, above a certain solar radiation level, than males. At similar high levels of solar radiation (≥ 0.9 cal/cm²/min) more males exposed one hind flipper to the wind than females (Fig. 1; at solar radiation levels of and above 0.9 cal/cm²/min, percentages differed significantly between sexes. t values were calculated after arcsine transformation of percentages. t values for statistically different means varied between 3.04 and 4.19, d.f. = 28-30, $p < 0.01$).

Most pups were wet during the hottest part of the day, because they were immersed in tidepools or located at the edge of them. Some pups rested in the shade of small boulders. During low tide, at Punta Norte, pups moved seaward and entered shallow pools in the exposed rocky intertidal. At noon and during early afternoon hours, approximately 80% of the pups in both study areas were wet.

Distribution.

Thermoregulatory requirements restricted the places suitable for reproduction. Heat stress prevented males from defending certain positions or expanding their territories inland. The best places in the breeding area for cooling purposes were those with access to water, *i.e.*, near the surf line or containing tidepools. The density of breeding animals was greatest at these places.

At Punta Norte, the location of the CBA was, in large part, determined by thermoregulatory requirements. Animals bred in a narrow zone, just above the high-tide water mark and close to the spray zone, where digging into the substrate gave access to wet pebbles. At 1200 hrs on a clear day, the temperature of the wet pebbles 0.5 m below the surface averaged 15°C lower than the dry pebbles at the surface. Twice a day, the high tide came up to the CBA, wetting most animals and cooling the substrate.

Only a few males held females on the inland periphery of the CBA, where the substrate was hotter, and cool, damp pebbles were further from the surface. These groups usually dissolved in 1-2 days, presumably, because of thermal stress. Typically, during a clear and calm day, the sun rapidly heated the dry pebbles and substrate temperature rose above 50°C after a few hours of intense solar radiation (1-1.4 cal/cm²/min). Inland males became overheated, abandoned their positions to move to sea, and lost their females (CAMPAGNA, LE BOEUF & CAPPOZZO, 1988). Field notes recorded January 18, 1984 illustrate this point:

- 0900 Males V and X are each associated with one female with a pup inland of the CBA. The sky is clear and it is calm.
- 1200 Air temperature is rising and has reached 32°C. The temperature of the pebbles where X and V are located is 48°C.
- 1500 Male X abandons his female and rushes to the water passing straight through the CBA. Air temperature and insolation conditions are similar to those recorded at noon. Substrate temperature reaches 50°C.
- 1505 Male V attempts to copulate. Between 1505 and 1518, he mounts a few times but does not attain intromission.
- 1525 Male V abandons his female and rushes to the water. Within a few minutes, the females leave the periphery and enter the CBA followed by their pups.

We saw males with females on the inland periphery of the CBA moving to the water at high temperatures, like X and V, about ten times per season.

At Puerto Pirámide, animals stayed close to large tidepools to places at the edge of the shelf sprayed by the breaking waves. The substrate away from these places often reached temperatures of 40-50°C. Areas near the cliffs away from the water were not regularly occupied by breeding individuals except during storms or unusually high tides, when the substrate was wet and cool. Only itinerant males were seen hauling-out for a few hours away from the water, but they always abandoned these places during midday hours.

III. Thermoregulation and male copulatory success.

Males in the CBA or in the territories that had access to water: (1) associated with more females, (2) had longer tenures in the breeding area, and (3) copulated more than males breeding in the periphery of the CBA or defending territories without access to water.

Number of females in a territory.

At Punta Norte, virtually all breeding males on the periphery of the CBA were associated with only one female, *versus* a mean of 2.8 females for resident CBA males at peak season (CAMPAGNA & LE BOEUF, 1988).

At Puerto Pirámide, the rank of the territory with respect to its quality for thermoregulation was positively correlated with the mean daily number of females located in it (Kendall's tau = 0.80, $n = 16$, $p < 0.001$). This was not due to variation in territory size because territories were estimated to have similar surface area (20-30 m²). At peak season, males that had access to large water pools were associated with more females than those males who were in territories without pools or with small pools; mean number of females per territory of 10.7 ± 4.1 ($n = 7$) and 0.9 ± 1.3 ($n = 10$), respectively ($t = 6.9$, d.f. = 14, $p < 0.001$). Four males in inferior territories held only one or two females and only for a few hours. When these males abandoned their territories during the hottest hours of the day, their females moved to territories having water. One male, having only a shallow tidepool on his territory, attempted to control his female by swimming close to the border of the rocky shelf and rushing back to her if she started to move away.

Females at Puerto Pirámide abandoned territories with dry pools and, when they had the opportunity, moved to areas with large tidepools filled with water. This caused rearrangement in the distribution of females in the breeding area. For example, early in January, three males defended adjacent territories and shared a large tidepool that contained water. About twenty females used the pool during the hottest part of the day. As the water of the tidepool was not renewed at high tide, the pool was nearly dry by mid-January. As the tidepool dried up, the area was abandoned by all but six females. Most of them moved to a neighbouring territory with a large water-renewable pool. The male in the latter territory was associated with 33 females during the last week of January, when several pools were almost dry. Most of the females that moved to his territory copulated with him; a few of them had already copulated in the previous location and did not copulate again.

At Puerto Pirámide, the mean daily number of females in a territory was positively correlated with the number of copulations achieved by the territorial male (Kendall's tau = 0.86, N = 16, $p < 0.01$). At Punta Norte, the mean daily number of females with whom a CBA male was associated did not predict his mating success. Most males in the CBA were associated with a similar number of females (only 2-3 females at a time). However, some males copulated at least 18 times by the end of the season because of turnover in females within territories (CAMPAGNA & LE BOEUF, 1988).

Tenure.

Males defending advantageous positions for thermoregulation, such as a site in the CBA or a territory with a tidepool, had the longest tenures. At Punta Norte, mean tenure of 33 resident males in the CBA was 24 ± 5 days (CAMPAGNA & LE BOEUF, 1988), while 18 marginal males on the hotter inland side of the CBA had a mean tenure of 0.9 ± 0.8 days.

From January 7-31, the mean tenure of males on territories without water at Puerto Pirámide was slightly shorter than that of males on territories with water. Six males on territories with water had a mean tenure of 23.2 ± 1.7 while four males on territories without water had a mean tenure of 20.1 ± 1.5 ($t = 2.6$, d.f. = 7, $p < 0.05$). At midday hours of every hot day, males defending territories without tidepools vacated their territories for 2-4 hrs per day to enter the water. This occurred 65% of the days in January. The territories of the males that went to sea was left unoccupied until they returned. In contrast, males in territories with water never vacated their territories to enter the sea and, therefore, they had more opportunities to copulate.

Males in territories with tidepools remained longer in the breeding area. Six out of seven males with dry territories ended their tenure by January 29th, while four out of six males with type 1 territories were still actively defending their positions and copulating four days later.

Copulations.

Males located in the CBA at Punta Norte, or with access to tidepools at Puerto Pirámide, copulated more than males on the inland periphery of the CBA or in dry territories, respectively. At Punta Norte, virtually all copulations occurred in the CBA (CAMPAGNA & LE BOEUF, 1988). All marked males in the CBA ($n = 32$) copulated at least once. Conversely, only 39% of 18 males associated with females on the inland periphery of

the CBA copulated; the rest abandoned the female to rush to the water. At Puerto Pirámide, seven males defending territories with water (type 1) copulated a mean of 11.6 ± 4.2 times, *versus* 1.4 ± 1.4 times for ten males defending territories without water (type 2). The most successful male in the study site achieved 20 copulations in 24 days (about 240 daylight hours of observed tenure), while males located near the cliffs, away from tidepools and from the sea, or in areas covered by the sea during high tides, did not copulate. The more suitable the territory was for thermoregulation (the higher its rank) the larger the number of copulations that took place in it (Kendall's tau = 0.80, N = 16, $p < 0.001$). Eighty five percent of the copulations observed at Puerto Pirámide occurred in type 1 territories and only 15% occurred in type 2 territories.

At peak season, the two rookeries had similar distributions of copulations per male (coefficients of variation = 0.80 [Punta Norte] and 0.86 [Puerto Pirámide]). Between January 8-28, 23 males in the CBA achieved a mean of 4.5 ± 3.6 copulations. At Puerto Pirámide, 11 males defending territories during the same period accomplished a mean of 7.1 ± 6.1 copulations.

IV. Effect of topography on the type of polygyny.

Males at both rookeries combined female defence and site defence behaviours to monopolize mates. The topography of the rookery, with respect to thermoregulation, dictated which of these behaviours was used to monopolize mates and in what proportion they were displayed.

At Punta Norte, males did not attract females by having better territories than their neighbours; sites along the high tide mark did not offer differential advantages for thermoregulation. Once a male became a resident in the CBA, he defended females rather than a fixed place for mating and often abandoned his position if the females deserted the site (CAMPAGNA & LE BOEUF, 1988).

Conversely, at Puerto Pirámide, site defence behaviour prevailed over female defence by males. This was evident from the following observations:

1. Males defended sites, especially if they contained water, even when they were not associated with females. Six of 16 males in the study area defended territories at peak season even when these sites did not contain females most of the time. Males that momentarily abandoned a territory to go to sea returned to it and defended the site against other males, even if females had moved to other sites.

2. A territorial male disputing a site with a contender did not interrupt the fight to rush after females that started to move away from him. Four times in three weeks a territorial male fought with another male for 6-30 min. During the fight most females abandoned the site. A few hours later, some of the females had returned to the site.

3. During storms, females near the edge of the shelf moved inland with their pups, away from the breaking surf. Despite female desertion, about half of the territorial males stayed in position and continued to defend the site against intruders. Males that extended their territorial boundaries inland patrolled even that part of the territory that had been deserted by the females.

Discussion

In the southern sea lion, thermoregulatory requirements interact with rookery topography to shape mating strategies, variation in mating success, and the form of the mating system. At Punta Norte, the pebble substrate is homogeneous with respect to thermoregulatory advantages. Thus, sites advantageous for thermoregulation are not a limited resource that can be used to attract females. Consequently, males achieve mates through sequestering females rather than by the defence of rigid territories (CAMPAGNA & LE BOEUF, 1988). Conversely, at Puerto Pirámide, variation in the quality of the substrate with respect to reducing thermal stress favours the development of a territorial system where the best territories contain water or are close to water. Here, sequestering of females or direct defence of females by males is not required since females preferentially gather in wet territories. Thus, the topography and substrate of the breeding area, coupled with thermoregulatory requirements, are a driving force that generates adaptive changes in male mating behaviour.

The effect of thermoregulation on breeding behaviour has been documented for several otariids. Male Australian fur seals, *Arctocephalus forsteri*, that defend territories unsuitable for thermoregulation achieve half the copulatory success of males with direct access to the water (GENTRY, 1973). Female California sea lions, *Zalophus californianus*, and Steller sea lions, *Eumetopias jubatus*, move to and from the cool spray zone near the water to a dry, warm area inland, in response to fluctuation in temperature and solar radiation. These changes in distribution cause oestrous females to cross male territories and bring females into contact with many males, potentially allowing females to exercise mate choice

(GENTRY, 1970; HEATH, 1981, 1985, pers. comm.). The form of territorial defense in California sea lions varies with the thermal properties of the rookeries; in some Southern California rookeries, such as San Miguel Island where the weather is temperate and cool, male territories are predominantly terrestrial; in the Sea of Cortez, Mexico, where the weather is hot and dry, male territories are exclusively aquatic (ODELL, 1975; HEATH, 1981; LE BOEUF, unpublished data). In several species of fur seals (VAZ-FERREIRA & PALERM, 1961; RAND, 1967; TRILLMICH & MAJLUF, 1981), access to water is essential to maintaining a territory during the hottest part of the day. In the Galapagos fur seal, *Arctocephalus galapagoensis*, virtually all territories have access to the water. The limited space suitable for thermoregulation may cause the unusually low density breeding aggregations of this otariid (TRILLMICH, 1984).

The thermoregulatory behaviour of the southern sea lion is mainly affected by solar radiation and wind direction and speed, and by the topography and substrate of the breeding area. Solar radiation is a key variable affecting the thermal environment. During a clear day, intense insolation has a twofold effect: (a) it causes heat gain by radiation, and (b) it increases the temperature of the rocks and pebbles, neutralizing and eventually inverting the temperature gradient between the body of the animal and the substrate. Once substrate temperature rises above body temperature, animals start to gain heat by conduction in addition to radiation. If, besides being a clear day with high insolation, there is no wind or winds are warm, air temperature may rise close to body temperature, thus decreasing or even eliminating the alternative of losing heat by convection to the air. Once the animal gains heat from the sun, and the gradients to the substrate and the air are neutralized by the effect of insolation and winds, the available options to lose heat are evaporation and conduction to the water. These phenomena, driven by solar radiation, were well correlated with the behaviour of males and females. By keeping their flippers wet and exposed to the wind, sea lions facilitate heat loss by evaporation and convection to the air, and decrease heat gain by conduction from the substrate. By burrowing their flippers into the substrate to expose wet and cool pebbles, sea lions lose heat by evaporation and conduction. Immersing themselves in tidepools or going to the sea allows heat loss by conduction to the water, and by evaporation and convection to the air once the wet animal leaves the water.

The thermoregulatory behaviour of southern sea lions at Península Valdés is similar to that reported for the same species at Lobos Island, Uruguay (VAZ-FERREIRA & PALERM, 1961; VAZ-FERREIRA & SIERRA DE

SORIANO, 1962). Southern sea lions do not depart from other otariids in most of their thermoregulatory patterns. The same behavioural adjustments are observed in *Otaria* as those seen in other sea lions and fur seals, but the frequency of each pattern varies with the species and the habitat (BARTHOLOMEW & WILKE, 1956; VAZ-FERREIRA & PALERM, 1961; RAND, 1967; GENTRY, 1971, 1973; WHITTOW, 1974; MARLOW, 1975; DE LONG, 1982; HEATH, 1985; J. FRANCIS, pers. comm.). However, southern sea lions do not pant or swim holding their flippers straight up, and rarely wave their flippers as some otariids do.

Phocids are also susceptible to thermal stress and have behavioural adaptations to lose heat similar to those of the otariids. The tropical Hawaiian monk seal, *Monachus schauinslandi*, regulates its body temperature by moving to wet sand and by remaining inactive most of the day, exposing the ventral pale-coloured hair coat to the atmosphere (OHATA *et al.*, 1972; WHITTOW, 1978). Similarly, as insolation increases, northern elephant seals, *Mirounga angustirostris*, sequentially rest "belly up", flip moist sand to the dorsum, and move to the water's edge to get wet (WHITE & ODELL, 1971). Thermoregulatory demands in cold weather are also important in shaping the social system, behaviour, and distribution of pinnipeds (FAY & RAY, 1968).

We conclude that the breeding behaviour of southern sea lions hinges on the combined effects of three inter-locking factors: (a) the thermal environment, (b) the topography and substrate of the rookery, and (c) the thermoregulatory requirements of males and females. These variables affect the social behaviour and distribution of animals on the breeding grounds, the male mating strategies, and, ultimately, the variance in male reproductive success.

Summary

Southern sea lions, *Otaria byronia*, breed during the Austral summer on flat rocky shelves containing tidepools and boulders, or on wide, uniform pebble beaches lacking tidepools and shade. The first substrate provides breeding animals with relief from heat stress, the second does not. A three-year study of two rookeries at Península Valdés, Argentina, from 1985 to 1987 revealed major differences in mating behaviour and mating success of males, associated with temperature, solar radiation and rookery topography.

At Puerto Pirámide, males defended territories containing tidepools throughout the breeding season. Thermoregulatory requirements caused females to concentrate in tidepool areas, and males completed aggressively for these resources. Seven males that defended territories with large, water-renewable tidepools copulated a mean of 11.6 ± 4.2 times during three weeks, *versus* a mean of 1.4 ± 1.4 times for ten males that defended territories without tidepools. The latter lost their females and went to sea when air temperature rose over 30°C.

At Punta Norte, the homogeneous pebble substrate forced animals to breed in a narrowly confined area along the high tide mark, where the substrate remained wet. Only those males holding females in this narrow zone copulated. All of 32 marked males that associated with females near the high tide mark copulated. Males breeding outside of this narrow strip of beach deserted and lost females after 1-3 hrs of air temperatures $\geq 30^{\circ}\text{C}$, and solar radiations $\geq 1.2 \text{ cal/cm}^2/\text{min}$.

Rookery topography and associated thermoregulatory constraints are critical variables shaping breeding behaviour in southern sea lions. The thermal and physical environment is a determinant of the social behaviour of otariids and has been important in shaping their social system.

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Resumen

Los lobos marinos del sur, *Otaria byronia*, se reproducen durante el verano austral en dos situaciones: sobre plataformas rocosas que contienen piletones y rocas, y en amplias playas de canto rodado, sin piletones y sin sombra. El primer tipo de substrato permite que los animales obtengan alivio de la alta temperatura ambiente, no así el segundo. Un estudio de tres años, efectuado entre 1985 y 1987 en dos loberías de la Península Valdés, Argentina, reveló marcadas diferencias en la conducta de reproducción y en el éxito reproductivo de los machos asociadas a la temperatura ambiente, la radiación solar y la topografía de la lobería.

En Puerto Pirámide, los machos defendían territorios conteniendo piletones con agua de mar durante toda la temporada de reproducción. Requerimientos relacionados con la termoregulación ocasionaban que las hembras se agrupasen en áreas con piletones conteniendo agua; los machos competían agresivamente por dichas áreas. Siete machos que defendían territorios con piletones amplios, conteniendo agua que se renovaba regularmente, copularon una media de 11.6 ± 4.2 veces durante un período de tres semanas, mientras que diez machos que defendían territorios sin piletones copularon una media de 1.4 ± 1.4 veces. Cuando la temperatura ambiente superaba los 30°C , estos últimos machos se iban al mar y perdían a sus hembras.

En Punta Norte, debido al substrato homogéneo de canto rodado, los animales debían reproducirse en un área estrecha de playa cercana a la línea de pleamar, donde la piedra

permanecía húmeda. Sólo aquellos machos que defendían hembras en este sector estrecho de playa copularon. De los 32 machos marcados asociados con hembras en zonas cercanas a la línea de pleamar, todos copularon. Los machos asociados con hembras fuera del sector húmedo de playa, abandonaron y perdieron a sus hembras luego de soportar, durante 1-3 hrs, temperaturas $\geq 30^{\circ}\text{C}$ y radiaciones solares $\geq 1.2 \text{ cal/cm}^2/\text{min}$.

La topografía del área de reproducción asociada con limitaciones de la termoregulación son variables críticas que afectan el comportamiento reproductivo del lobo marino del sur. El ambiente térmico y físico determina y moldea la conducta y el sistema social de los otáridos.
