

Thermal budgets and climate spaces: the impact of weather on the survival of Galapagos (*Arctocephalus galapagoensis* Heller) and northern fur seal pups (*Callorhinus ursinus* L.)

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Abstract. The ability of fur seal pups to cope with diverse climatic conditions on land was investigated by constructing a thermal budget based on published physiological studies. The model was applied to northern fur seals (*Callorhinus ursinus* L.) breeding on the Pribilof Islands, Alaska, and on San Miguel Island, California; also to the Galapagos fur seal pup (*Arctocephalus galapagoensis* Heller) on the Galapagos Islands. The combinations of environmental extremes that pups can withstand during the first week of life were identified. The study concluded that a healthy, average-sized pup on the Pribilofs could have tolerated any combination of air temperature, wind speed and level of humidity recorded since the mid 1950s, but that pups with low birth weights could have succumbed during periods of cold, wet and windy weather. On San Miguel Island, the model predicts high mortalities of large pups during hot, dry weather, which suggests strong selection pressures towards the survival of smaller animals. The model further suggests that the success of the Galapagos fur seal at the equator is related to its small body size and behavioural attributes, such as seeking shade and periodically wetting its fur.

Key-words: *Arctocephalus galapagoensis*, *Callorhinus ursinus*, climate space, energetics, Galapagos fur seal, northern fur seal, seal pups, thermal budget

Introduction

Historically, northern fur seals (*Callorhinus ursinus* L.) were believed to come ashore only to reproduce on the Pribilofs and a few other islands in the Bering and Okhotsk Seas. It was commonly thought they were restricted to the North Pacific by a thermoregulatory need for cool wet summers (Bartholomew & Wilke, 1956). However, in 1968 a

growing colony of northern fur seals was discovered breeding on San Miguel Island, California, under hot and dry conditions (Peterson, Le Boeuf & DeLong, 1968a), which indicates that fur seals can tolerate a wider range of environmental conditions than was initially believed.

Fur seals, like all pinnipeds, must cope with diverse climatic conditions during the terrestrial phase of their life cycle (Whittow, 1987). Newborn fur seals on the northern and southern breeding islands appear to experience extreme thermal stress. In the Bering and Okhotsk Seas, rain in combination with wind and low air temperatures appear to bring pups to their lower limit of tolerance (Irving *et al.*, 1962; Keyes, 1965; Ohata & Miller, 1976; Blix *et al.*, 1979a) causing high pup mortality (Roppel *et al.*, 1963; Vladimirov, 1974). In the south, on San Miguel Island, high air temperatures and low wind speeds are linked with high mortality rates (Antonelis & DeLong, 1985a,b, 1986).

In the present study, I employ Porter & Gates's (1969) 'climate space' approach to investigate the impact of weather on the thermal balance of neonatal northern fur seals breeding on the Pribilof Islands and San Miguel Island. I also consider the ability of pups of a related species, the Galapagos fur seal (*Arctocephalus galapagoensis* Heller), to cope with the equatorial climate of the Galapagos archipelago. Climate space analysis is one of the simpler, well-tested, biophysical models that offers insight into biophysical constraints on animals (Spotila *et al.*, 1989) and has been applied to many species (e.g. Porter & Gates, 1969; Spotila, Soule & Gates, 1972; Morhardt & Gates, 1974; Gates, 1975, 1980; Morhardt, 1975; Campbell, 1977; Scott, Tracy & Pettus, 1982; Christian, Tracy & Porter, 1983; Spotila, Foley & Standora, 1990).

I begin by outlining the general biology of fur seal pups and the thermal budget equation that accounts for the exchange of energy between an animal and its environment. After discussing

model assumptions and choice of parameters, I plot a 'climate space diagram' containing all combinations of air temperature and solar radiation that a pup can withstand under various levels of humidity and wind speed. A sensitivity analysis shows the reliability of model predictions and the effect of faulty parameters. Finally, I consider the effect of weather on pup mortality, and the roles of behaviour modification and body size in light of the climate space diagrams.

Biology of the pup

The northern fur seal is the second largest of nine fur seal species (King, 1983; Croxall & Gentry, 1987), with a mean birth mass of 5.67 kg for males and 5.13 kg for females (Scheffer & Wilke, 1953; Lander, 1979a; Fowler, 1987). On the Pribilofs (St. Paul and St. George Islands), pups are born on 20 rookeries (Lander, 1980) consisting of sand or dark basalt rocks. Most pupping occurs from the last week of June until the third week of July with 80% being born during the first 2 weeks of July (Peterson, 1968). Over the next 3 months, pups are fed a lipid-rich milk with a low water content for 2 days while their mother is ashore, and fast for the next 4–8 days when she is absent (Bartholomew & Hoel, 1953; Costa & Gentry, 1986). Most pup mortality occurs within the first few weeks of life (Kenyon, Scheffer & Chapman, 1954) and is highly variable between years (Chapman, 1961; Lander, 1975; 1979b; Trites, 1989).

The San Miguel colony is 10 m from the sea on a wide sandy beach at Adams Cove. The presence of adult fur seals bearing tags from Soviet and American rookeries in the north indicates that the new colonies are the result of immigration from those areas (Peterson *et al.*, 1968b). San Miguel pups are born during June and early July, with the mean date falling in the last week of June (Antonelis & DeLong, 1985a). Their mass at birth is identical to those born on the Pribilof Islands (DeLong, Jameyson & Antonelis, 1981) with the majority of pup deaths occurring within 1–4 days postpartum (DeLong, Antonelis & Jameyson, 1982).

The Galapagos fur seal is the smallest fur seal species, occurring only on the Galapagos archipelago (King, 1983; Bonner, 1984). Their mean mass at birth is in the order of 3.0–3.8 kg (Trillmich & Limberger, 1985; Limberger *et al.*, 1986; Trillmich, 1987). Pups are born along a 20-m wide zone that runs parallel to the water, consisting of lava flows, caves and large boulders. Pupping begins in mid-August and lasts until mid-Novem-

ber, peaking about the last week of September. The young are nursed until 2 years of age.

Fur seal pups are insulated by fat, skin and fur. Heat loss is under cardiovascular control (Blix *et al.*, 1979a) and is affected by the boundary layer of air next to the animal surface. The fat layer at birth is thin (2–4 mm) in the northern fur seal and does not increase much over the first 2 weeks of life (Blix *et al.*, 1979a). Subcutaneous tissues (skin and fat) provide little insulation (Irving *et al.*, 1962). Unlike other pinniped pups, such as harp seals (Davydov & Makarova, 1964; Blix, Grav & Ronald, 1979b) and Weddell seals (Elsner *et al.*, 1977), fur seals increase fur density rather than blubber thickness. Northern fur seal pups have a short dense fur with a mean length of underfur of 7.7 mm and guard hairs 16.3 mm (Scheffer, 1962). The guard hairs make the fur stand up, which increases its thickness and insulative quality, and help to maintain the layer of air trapped in the underfur when the seal is immersed in water (Romanenko & Sokolov, 1988). The insulation provided by the air is easily destroyed by wind and rain and is maintained by fluffing the flattened fur (Webb & King, 1984). Adult-type underfur and guard hairs do not appear among the northern fur seal pup hairs until mid-August, prior to the September moult. At this time the colour of the pup coat begins to change from black to silver.

Under thermal neutral conditions, excess metabolic heat is easily dissipated across the body surface. However, when stressed by heat fur seals will lower their metabolic rate, increase the flow of blood to their limbs and body surface, and begin panting (Bartholomew & Wilke, 1956; Ohata & Miller, 1977a). At the other extreme, should pups begin to cool below their lower critical temperature, they will increase their metabolic rate and reduce the flow of blood to the appendages.

Methods

Thermal budget

The balance between heat input and heat loss for any endotherm maintaining a constant body core temperature is described by the thermal budget equation:

$$R_{\text{abs}} - \epsilon\sigma(273.15 + T_b)^4 + M - \lambda E - \frac{\rho C_p(T_b - T_a)}{r_{\text{Ha}}} + \frac{r_{\text{Hb}}(M - \lambda E)}{r_e} = 0 \quad \text{Equation 1}$$

The notation follows Campbell (1977), where R_{abs} is the flux of short- and long-wave radiation absorbed by the animal from the environment per unit body surface area (W m^{-2}). The second term $\epsilon\sigma(273.15 + T_b)^4$ is the long-wave emittance of the animal (assuming $T_s = T_b$) where ϵ is the surface emissivity, σ is the Stephan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$), T_s is the animal's surface temperature and T_b is the deep body core temperature ($^{\circ}\text{C}$). The flux of metabolic heat to the body surface per unit area is M (W m^{-2}). The flux density of latent heat lost through the evaporation of water from the respiratory tract and skin of the animal is denoted by λE where λ is the latent heat of vaporization and E is the water vapour flux density. The fifth term $\rho c_p(T_b - T_a)/r_{\text{Ha}}$ is the flux density of sensible heat from the body assuming $T_s = T_b$, where ρ is the air density, c_p is the specific heat of air, T_a is the air temperature, and r_{Ha} is the thermal laminar boundary layer resistance. The volumetric heat capacity of the air is a constant ($\rho c_p = 1200 \text{ J m}^{-3} \text{ K}^{-1}$). The first five terms of equation 1 describe the heat exchange for an animal that has the same surface and deep body temperature and hence no internal resistance to heat loss. The sixth term $r_{\text{Hb}}(M - \lambda E)/r_e$ is a correction factor for the assumption of $T_s = T_b$, where r_{Hb} is the resistance of the fur seal coat and peripheral tissue layer and r_e is the parallel equivalent resistance of r_{Ha} and the radiative transfer resistance (r_r), where $r_e^{-1} = r_{\text{Ha}}^{-1} + r_r^{-1}$ and $r_r = \rho c_p / (4\epsilon\sigma[273.15 + T_b]^3)$. Note that the boundary layer resistance in s m^{-1} is estimated as $r_{\text{Ha}} = 307 \sqrt{d/u}$ (Campbell, 1977), where d is the diameter (m) of the pup, and u is the wind speed (m s^{-1}).

The thermal budget can be used to identify the combination of radiation levels and air temperatures that a fur seal pup can tolerate. The extreme conditions that a pup can withstand are determined by balancing equation 1 for an animal with a body temperature, metabolic rate and evaporative water loss that are near upper and lower sustainable physiological limits. This assumes that there are thresholds above and below which animals die when so exposed. The lethal combination of radiation level and air temperature can be computed and plotted to bound the set of environmental conditions that are tolerable by a pup. Such a plot is referred to as a 'climate space diagram' (Gates, 1980; Tracy, 1982; Spotila *et al.*, 1989).

Available radiant energy

The 'space' can be further bounded by excluding

all combinations of environmental conditions that could never occur on the Pribilof Islands. These physical limits prescribe the minimum and maximum amounts of energy available at any air temperature and are derived as follows.

The minimum radiant energy available to the fur seal pup is the night-time long-wave irradiance from the sky and the ground. Absorbed night-time irradiance is calculated as a function of σ , T_a , a_L (the long-wave absorptivity of the seal), and $\bar{\epsilon}_s$ (the average emissivity of the surroundings), such that:

$$\text{Night } R_{\text{abs}} = a_L \bar{\epsilon}_s \sigma (273.15 + T_a)^4 \quad \text{Equation 2}$$

The maximum flux of radiation that could be absorbed by a basking fur seal pup in direct sunlight at any temperature is equal to the direct, scattered and reflecting sunlight at solar noon, plus the long-wave radiation. It is written as:

$$\text{Sun } R_{\text{abs}} = a_s \frac{A_p}{A} S_p + a_s \bar{S}_d + \text{Night } R_{\text{abs}} \quad \text{Equation 3}$$

where a_s is the short-wave absorptivity, A is the surface area of the animal's body, A_p is the projected area of the animal's body on a plane perpendicular to the solar beam, S_p is the direct beam solar irradiance, and \bar{S}_d is the diffuse solar irradiance.

Parameterization

The thermal budget equation contains many parameters and constants that need to be estimated. In many cases this means making simplifying assumptions about the uniformity of the physical environment, cloud cover and substrate. It also means making sweeping generalizations about the size, body temperature, metabolic rate and physiology of a 'typical' newborn fur seal pup.

The extreme combinations of radiation levels and air temperatures that a pup can tolerate are largely determined by the range of body temperatures, metabolic rates and peripheral tissue resistance levels that a pup can sustain. In general there is a good understanding of the lower physiological limits of northern fur seal pups. Information on the upper limits is not as good; hence I must rely on data recorded for subadult northern fur seals, Galapagos fur seal pups and other pinniped species.

The following outlines how and why particular values were chosen to describe the physical and physiological characteristics of northern fur seal pups, and the environmental conditions that bound the climate space.

Mass and diameter of the pup

Measurements made in the field indicate the average newborn northern fur seal weighs about 5.4 kg (Scheffer & Wilke, 1953; Lander, 1979a; Fowler, 1990). To my knowledge, the diameter of pups has never been recorded, but can be determined analytically by relating mass to surface area in the following manner. Based on a study of harbour seals, the relationship between surface area A (cm²) and mass W (kg) is $A = 800 W^{2/3}$ (Irving *et al.*, 1935). Recent calculations suggest this equation can be applied to otariid seals without introducing major errors (Innes *et al.*, 1990). Thus the surface area of a 5.4-kg fur seal pup should be 2462 cm². Interestingly, Blix *et al.* (1979a) found the surface area of an average size newborn, which they measured, was 2447 cm², of which 40% was flippers. The diameter of the pup (d) can be estimated by assuming the body core has a cylindrical geometry where $d = 0.60 A (\pi L)^{-1}$. Given the length (L) of a pup is about 62 cm (Scheffer & Wilke, 1953; Lander, 1979a), then the average diameter should be about 7.6 cm. I compared this method of determining diameter with the measurements taken by Luecke, Natarajan & South (1975) from two female sea lions, where flippers account for about 35% of total body area. The results suggest that the cylinder approximation could underestimate diameter by as much as 12.5%. Thus, failing any field measures, I believe the diameter of an average pup lies between 7.6 and 10.0 cm and use a value of 8.7 cm in subsequent calculations.

Body core temperatures

The minimum body core temperature that a pup can sustain is based on studies of pups exposed to cold air and immersed in water. In one study, the body temperature of a pup immersed in 10°C water dropped from 37.4°C to a stable 34.8°C after 20 min (Blix *et al.*, 1979a). Pups immersed in ice water experienced a linear drop in body temperature for 30 min to 30°C, at which point they were removed. These studies suggest a minimum sustainable temperature of about 34°C which is probably accurate to within 1°C.

While no studies have been done on heat-stressed pups, several body temperatures have been taken from hyperthermic subadult males that were immobilized and near death during the harvest roundup. In one study, Ohata & Miller (1977a) recorded body temperatures of 43°C and higher. This and other studies suggest the upper sustainable limit of subadult males aged 2–5 years

lies between 40 and 43°C (Bartholomew & Wilke, 1956; Irving *et al.*, 1962; Ohata & Miller, 1977a). I suspect the upper sustainable temperature of a pup lies between 40 and 41°C and use a value of 41°C in subsequent calculations. Such values are comparable to the maximum core temperature taken from Galapagos fur seal pups of 39.8°C (Limberger *et al.*, 1986).

Metabolic rates

The thermal budget equation requires minimum and maximum metabolic rates in terms of the flux of heat to the pup's surface per unit area. In the case of fur seals, this means converting metabolic rates measured per unit of animal mass, taking into consideration the ability of pinnipeds to control blood flow to the peripheral regions of their bodies. An important criterion in determining the extreme metabolic rates is that they be maintainable for some extended period of time.

Blix *et al.* (1979a) found the oxygen consumption of a fasting pup, sleeping at air temperatures down to 6°C, was 3.5 W kg⁻¹. If we consider the ability of the pup to increase blood flow to the flippers in response to heat (which increases the effective surface area by 40%), then the metabolic rate is approximately equal to 77 W m⁻² (i.e. 3.5 W kg⁻¹ × 5.4 kg/0.2462 m²). I believe this to be the minimum sustainable rate. Work by Worthy (1987) shows that the metabolic rates of harp seals and grey seals are lower (2.5–49.1%) during sleep than when resting. Therefore it is unlikely that a fur seal pup could maintain rates lower than the 3.5 W kg⁻¹ recorded when sleeping.

Identifying the maximum sustainable metabolic rate (MR) is difficult. We know that the average daily metabolic rate of fasting pups (based on water influx values) is 7.56 W kg⁻¹ for males and 10.00 W kg⁻¹ for females (Costa & Gentry, 1986). We also know that values as high as 18 W kg⁻¹ have been recorded from pups immersed in ice water (Blix *et al.*, 1979a), although it is unlikely that this five-fold increase is sustainable. One experiment conducted on a 4-month-old female pup weighing 9.4 kg showed that the resting metabolic rate at thermoneutrality was 0.72 ml g⁻¹ h⁻¹, while the maximum MR was 3.2 times higher at 2.3 ml g⁻¹ h⁻¹ (4–12.7 W kg⁻¹) (Miller, 1978). Young harbour seals (*Phoca vitulina richardsi*) when worked stressed through carrying lead weights while treading water, increased their oxygen consumption by a factor of 3.7 (Elsner & Ashwell-Erickson, 1982). Studies of other mammals such as shrews (Campbell, 1977), chipmunks (Heller & Gates,

1971), and deer (Gates, 1980) all further support the notion that the ratio of maximum to minimum sustainable rates lies between three and four. I have therefore assumed that the highest sustainable metabolic rate of a fur seal pup is 3.2 times more than its absolute minimum based on Miller's (1979) fur seal study. Thus if we accept the minimum MR is 3.5 W kg^{-1} , then maximum MR would be 11.2 W kg^{-1} . In terms of the amount of heat supplied to the pup's surface, the metabolic rate would be 409 W m^{-2} if the pup reduced its effective surface area by decreasing blood flow to the flippers in response to cold (i.e. $11.2 \text{ W kg}^{-1} \times 5.4 \text{ kg} / [0.2462 \text{ m}^2 \times 60\%]$).

Heat transfer resistance

The resistance to heat transfer of the coat and tissue (r_{Hb}) is determined in two parts. The first, the resistance of the coat, was estimated from portions of fur sewn around a copper cylinder (Blix *et al.*, 1979a). The thermal conductance of the pelt at birth was found to be 33.3 and $3.3 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$ when wet and dry, respectively. The second part, the tissue resistance, can be derived from measurements of heat flux density recorded from heat flow discs implanted subcutaneously in the backs of three newborn animals (Blix *et al.*, 1979a). In dry air, heat flux through the skin was unrecordable (less than 100 W m^{-2}) and subcutaneous temperature remained within 1°C of rectal temperature. But, under a drizzle-like rain of 6°C , the heat flux rose to between 500 and 600 W m^{-2} and the subcutaneous temperature dropped by 20°C . This means the thermal conductance (I) of the wet pups was between 25 and $30 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$, based on the relationship $H = (T_b - T_s)I$, where H is the heat flux from inside the animal through a layer of fat or tissue, and T_b and T_s are the temperatures of the body core and subcutaneous tissue (Gates, 1980). Thermal conductance of the dry pup was about $100 \text{ W m}^{-2} \text{ }^{\circ}\text{C}^{-1}$. Converted to units of s m^{-1} , the mean tissue resistance of a pup is about 44 s m^{-1} when the blood vessels are constricted and about 12 s m^{-1} when they are dilated. The summation of the tissue resistance and coat resistance (either 364 s m^{-1} if dry or 36 s m^{-1} if wet) is equal to r_{Hb} .

Surface emissivity and evaporative heat loss

Two parameters remain. The first, surface emissivity (ϵ), has not been measured and is assumed to be 0.95 , which is within the range for most natural surfaces of 0.90 – 0.98 (Campbell, 1977). The second, total evaporative heat loss from fur seals

on land, is estimated from a study of California sea lions exposed to heat. In this sea lion study, evaporative heat loss accounted for 20% of heat production (Matsuura & Whittow, 1974). The same value has been shown for most homeotherms (Campbell, 1977), which indicates total latent heat loss by respiration is around 20% of the metabolic rate (i.e. $\lambda E = 0.20M$).

Environmental conditions

The thermal budget equation for Pribilof fur seals was solved for two levels of relative humidity (0% for dry pups and 100% for wet pups) and four wind speeds ($u = 0.1, 2.4, 7.4$ and 17.5 m s^{-1}). The first wind speed corresponds to calm conditions and the remaining three to the minimum, mean and maximum daily wind speeds recorded during July from 1956 to 1981 on one of the Pribilof Islands, St. Paul (NOAA, National Climatic Center, Asheville, NC). Little or no weather data are recorded on San Miguel or any of the surrounding islands. Minimum and maximum average monthly air temperatures were available for only 3 years (DeLong, 1982). Wind speeds and relative humidity levels were available from Los Angeles, which is 150 km east. Although this is the closest weather station to San Miguel, data recorded here should only be regarded as an index of possible conditions that the fur seals might experience on their rookeries. From 1951 to 1986, the minimum, mean and maximum recorded wind speeds were $0.1, 3.4$ and 13.8 m s^{-1} , respectively. The range of air temperatures, relative humidities and wind speeds for St. Paul and San Miguel are contained in Table 1.

Thermal budgets

The limiting lethal combinations of air temperature, wind speed and radiation were calculated for the physical and physiological characteristics of northern fur seals outlined above. The surface area of a Galapagos fur seal pup weighing 3.4 kg is 1809 cm^2 according to the above method. The relationship between the mass and length of northern fur seal fetuses ($W = 10^{-4.2} L^{2.75}$; A.W. Trites, unpublished observation) suggests the pup is about 53 cm long. Bias in the diameter (6.5 cm) estimated from the above cylinder approximation was corrected by increasing the estimate by 12% to 7.3 cm . Metabolic rates for the Galapagos fur seal were extrapolated from the northern fur seal studies. All remaining model parameters were assumed equal to those of the

Table 1. Average daily weather conditions recorded at St. Paul¹ (1956–1981) during July and at the Galapagos Islands² (1982–1984) during September. Wind speeds and relative humidity levels were unavailable for San Miguel Island and were hence taken from Los Angeles³ (1950–1986), the closest weather station. The July air temperatures recorded at San Miguel⁴ are mean monthly values (1970, 1972–1973).

Weather condition	St. Paul			San Miguel			Galapagos
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Mean
Wind speed (m s^{-1})	2.2	7.4	17.6	0.1	3.4	13.8	1.17
Dry air temperature ($^{\circ}\text{C}$)	4.4	9.9	15.6	17.0	20.5	24.0	23.8
Relative humidity	0.6	1.0	1.0	–	0.8	–	–

¹ NOAA, National Climatic Center, Asheville, North Carolina.

² Limberger *et al.* (1986).

³ US Department of Commerce (1987).

⁴ DeLong (1982).

northern fur seal pup, owing to a lack of data. Major model parameters for both species are found in Tables 2 and 3 for dry and wet pups (also see Appendix 1 for a listing of parameter definitions, values and units).

Radiant energy available

The minimum and maximum irradiances of the pup were estimated from equations 2 and 3 as follows. Long-wave absorptivity (a_L) of most plants and animals varies between 95 and 98% (Gates, 1980) and was assumed to be 95% for the fur seal. Note that the seal absorptivity a_L is equal to the surface emissivity ϵ (Kirchhoff's Law). The average emissivity of the surroundings ($\bar{\epsilon}_s$: clear sky and ground) was estimated at 0.77. Thus, with the inclusion of the Stephan–Boltzmann constant, the absorbed night-time radiation calculated from equation 2 is $4.15 \times 10^{-8}(273.15 + T_a)^4 \text{ W m}^{-2}$.

From equation 3, the maximum daytime irradiance from all sources on the Pribilofs at solar noon is $342.42 + 4.15 \times 10^{-8}(273.15 + T_a)^4 \text{ W m}^{-2}$. This was calculated for St. Paul Island (latitude 57°N) for July. The elevation angle of the sun from the horizon is 56.2 degrees at solar noon. This means that a pup oriented perpendicular to the sun will cast a shadow that is 26% of its total surface area ($A_p/A = 0.26$). The calculated short-wave flux density ($S_p = 1103 \text{ W m}^{-2}$) is a function of the sun elevation angle and an atmospheric transmittance coefficient for a clear day of 0.84 (see Campbell, 1977). The short-wave absorptivity of fur is set at 0.87 based on studies conducted on Galapagos fur seal pups (Limberger *et al.*, 1986). Finally, mean diffuse solar irradiance ($\bar{S}_d = 107 \text{ W m}^{-2}$) was estimated using the methodology outlined by Campbell (1977).

On San Miguel Island (latitude 34°N) the maximum radiation flux under full sun in July is 391.72

$+ 4.42 \times 10^{-8}(273.15 + T_a)^4 \text{ W m}^{-2}$ (from equation 3). At this time of the year, the elevation angle of the sun is 79 degrees at solar noon and northern fur seal pups cast shadows that are 30% of their surface area. Average emissivity of the surroundings is about 0.82. Further south on the Galapagos Islands (latitude 0°S), the sun's elevation is 81 degrees from the horizon during pupping in September and emissivity of the surroundings is 0.84. Approximately 30% of the surface area of Galapagos fur seal pups is exposed to direct sunlight (Limberger *et al.*, 1986). Thus the maximum radiation flux on the Galapagos Islands, during September, is $392.14 + 4.52 \times 10^{-8}(273.15 + T_a)^4 \text{ W m}^{-2}$ (from equation 3).

Results

Climate space diagrams are drawn for dry and wet pups on the Pribilof Islands (Fig. 1) and on San Miguel Island (Fig. 2). Within each polygonal space lie combinations of environmental conditions that are energetically tolerable by the pup. The space is bounded on the left and right by curves that represent the most extreme combinations of radiation and air temperature that could ever occur at each location. The left curve is defined by equation 2 and the right by equation 3. The upper and lower sets of lines represent the limiting combinations of air temperature, radiation and wind speeds, above and below which the pup cannot survive (equation 1). The ends of all lines indicating physical and lethal limits are truncated to enhance the visual perception of the climate space. Pups can tolerate the combination of environmental conditions (air temperatures, radiation levels and wind speeds) that lie within the 'space'.

The set of lines that describes the lower thermal limits of a dry pup includes extremely low air

Table 2. Parameters used to estimate the upper and lower physiological limits of northern fur seal pups and Galapagos fur seal pups. Metabolic rates are measured in W m^{-2} , resistances are in s m^{-1} and temperature is in $^{\circ}\text{C}$.

Variable	Northern fur seal		Galapagos fur seal	
	Thermal minimum	Thermal maximum	Thermal minimum	Thermal maximum
T_b	34.0	41.0	34.0	41.0
M	409.0	77.0	351.0	65.8
λE	81.8	15.4	70.2	13.2
Dry r_{Hb}	408.0	376.0	408.0	376.0
Wet r_{Hb}	80.0	48.0	80.0	48.0
r_t	192.2	179.6	192.2	179.6

temperatures that are well below the most extreme conditions found on either island (top panels of Figs. 1 and 2). Thus, only the upper thermal limit is plotted for dry pups that are maintaining body temperatures of 41°C and a low metabolic rate of 77 W m^{-2} . These are plotted for pups subject to four different wind speeds. The bottom panels of Figs. 1 and 2 show the climate space for a wet pup. Both upper and lower thermal limits are included for varying wind speeds. Note that the lower limits reflect a pup having a core temperature of 34°C and a high metabolic rate of 409 W m^{-2} .

Fig. 3 contains the climate space of a Galapagos fur seal pup weighing 3.4 kg and exposed to an average daily wind speed of 1.17 m s^{-1} as recorded by Limberger *et al.* (1986). A second climate space of a northern fur seal pup exposed to the same wind speed (1.17 m s^{-1}) on the Pribilofs is overlaid for comparison.

Discussion

For the most part, our understanding of pinniped energetics has come from the laboratory, although more recently there has been an increasing emphasis placed on studies made under natural field conditions. While these studies have provided valuable insights, few have attempted to put all the pieces together into a mathematical model that

considers the total thermal balance of pinnipeds (see Luecke *et al.*, 1975; Øritsland & Ronald, 1978; Limberger *et al.*, 1986). Porter & Gates's (1969) climate space analysis is one such approach to a holistic understanding of neonatal fur seal energetics and its environmental implications.

The conclusions drawn from the linear thermal budget model are limited by the quality of the data used, which ranges from laboratory measurements to educated guesses. In each case I have tried to justify my choice of parameters and show my confidence in each estimate.

Air temperature significantly affects heat transfer through animal fur (McClure & Porter, 1983; Webb & McClure, 1988) and may have been more extreme on the fur seal breeding beaches than I have considered. The standard height for meteorological measures is 2 m above ground. It is therefore possible that air temperatures in the south could be as much as 20°C higher at pup height during the day than the values recorded. In the north, ground surface temperature will tend to approximate sky temperatures at night and might be $10\text{--}15^{\circ}\text{C}$ colder than local air temperatures. Unfortunately, better estimates of the microclimates at pup height are lacking.

The results of a sensitivity analysis (Appendix 2) indicate that further refinement of the thermal

Table 3. Estimates of resistance (measured in s m^{-1}) used to determine the upper and lower physiological limits of fur seal pups. Columns numbered 1–4 correspond to wind speeds of 0.10 , 2.24 , 7.40 and 17.56 m s^{-1} on the Pribilof Islands and 0.10 , 3.40 and 13.80 m s^{-1} on San Miguel Island; and 1.17 m s^{-1} on the Galapagos Islands.

Location	Variable	Thermal minimum				Thermal maximum			
		1	2	3	4	1	2	3	4
Pribilofs	r_{Ha}	286.4	60.5	33.3	21.6	286.4	60.5	33.3	21.6
	r_e	115.0	46.0	28.4	19.4	110.4	45.3	28.1	19.3
San Miguel	r_{Ha}	286.4	49.1	24.4	—	286.4	49.1	24.4	—
	r_e	115.0	39.1	21.6	—	110.4	38.6	21.5	—
Galapagos	r_{Ha}	76.7	—	—	—	76.7	—	—	—
	r_e	54.8	—	—	—	53.7	—	—	—

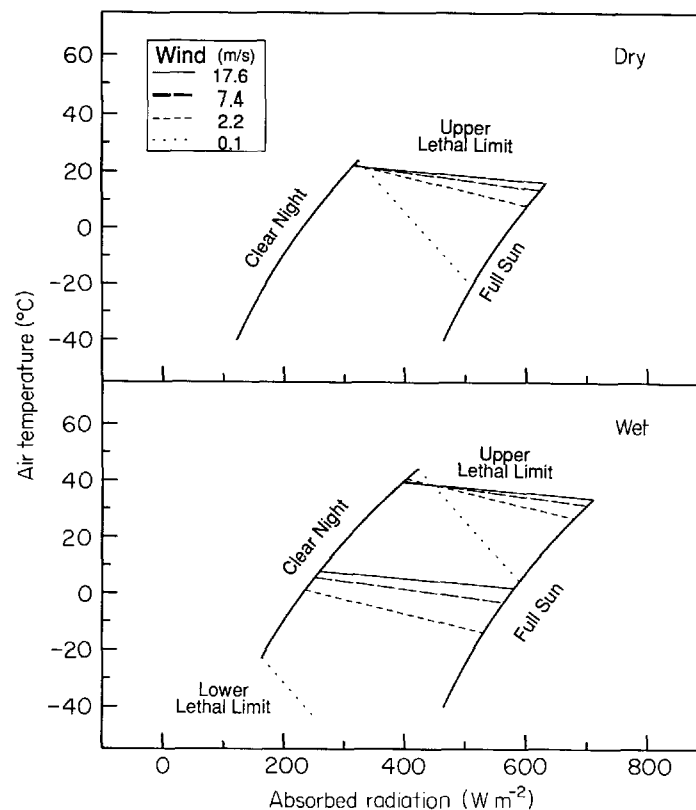


Fig. 1. Climate space diagrams for northern fur seal pups on the Pribilof Islands, Alaska. The polygons bound the combination of air temperatures, radiation levels and wind speeds that pups can tolerate when dry (top panel) and wet (bottom panel). The set of steady state lines describing the lower physiological limits of a dry pup are not shown because they are not contained within the scaling of the figure.

budget parameters is unlikely to alter the general conclusions and predictions. Linearization of long-wave radiation (equation 1) can introduce errors (Roughgarden, Porter & Heckel, 1981; Tracy, 1982); but they are probably small because the temperature of the fur air interface is unlikely to differ much from the free stream air. An additional error might arise from using a resistance model for fur-bearing mammals because fur is a porous medium that does not behave like an ordinary solid insulation (Porter, Parkhurst & McClure, 1986); however, such an error is likely minimal because the high hair density of fur seal pelts (Scheffer, 1962) would cause conduction effects to predominate.

Weather and pup mortality

The mortality of fur seal pups on the Pribilof beaches is often high and variable between years (Chapman, 1961; Lander, 1975, 1979b; Trites, 1989). However, the results of the present model

do not support the contention of Roppel *et al.* (1963) and Vladimirov (1974) that it is caused by inclement weather conditions. All the air temperatures, wind speeds and humidity levels recorded on the Pribilofs (1956–1981) fall within a range that fur seal pups can tolerate (Table 1). Given the range of daily July air temperatures (4.44–15.65°C), the high humidity levels (0.65–1.00), and the general cloudiness of the region, pups appear to reside near the centre of their climate space away from their lethal limits. Weather conditions would have to be more extreme than those recorded since 1956 to account for the high pup mortality observed on the Pribilof Islands.

The ability of pups to cope with cold wet periods on the Pribilofs depends largely upon good cardiovascular control and maintaining high metabolic rates. Young fur seal pups are able to increase their heat production by both shivering and non-shivering thermogenesis (provided by loosely coupled mitochondria in certain muscles, Grav & Blix,

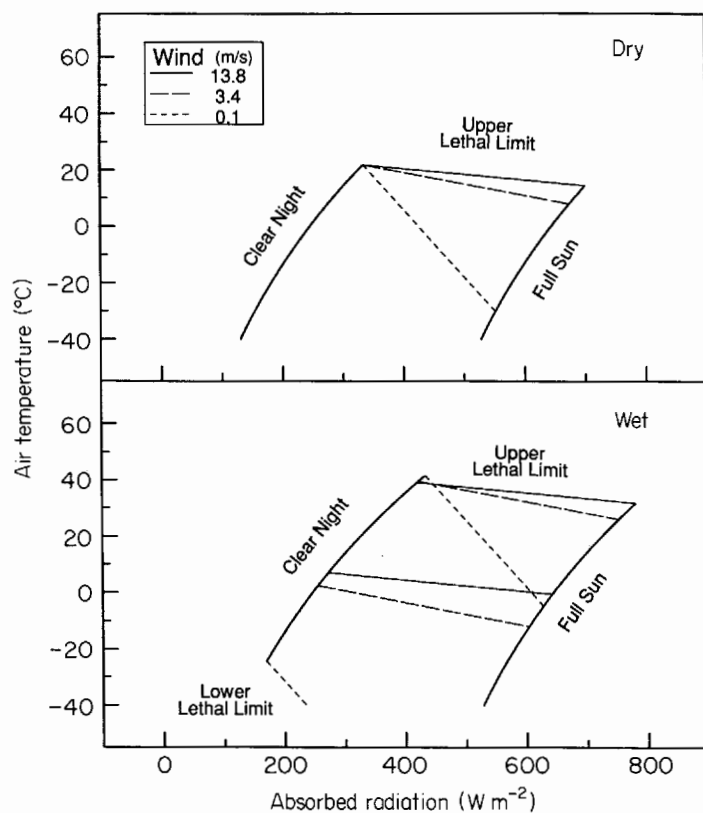


Fig. 2. Climate space diagrams for northern fur seal pups on San Miguel Island, California. Rest of legend as in Fig. 1.

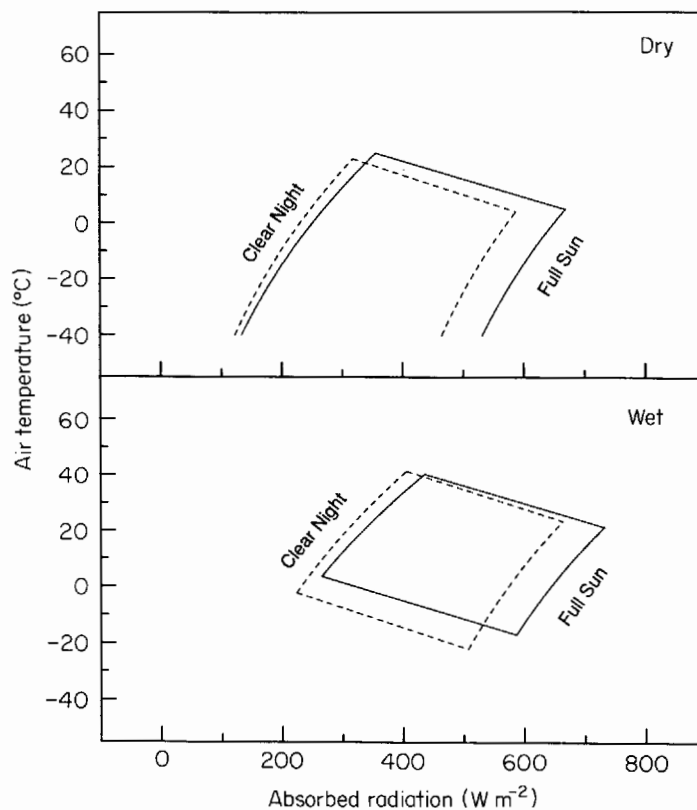


Fig. 3. Climate space diagrams of a northern fur seal pup on the Pribilof Islands (dashed lines) contrasted with that of a Galapagos fur seal pup on the Galapagos Islands (solid line). Both pups are subject to the same wind speed of 1.17 m s^{-1} . Rest of legend as in Fig. 1.

1979). Body tissues and the thin fat layer provide pups with surprisingly little insulation. As for their fur, its good insulative properties are lost almost entirely when wet. Wind and rain compress the fur and reduce thermal resistance (Webb & King, 1984). Note for example that a wet pup on a windy night would have trouble coping with air temperatures below 5°C (Fig. 1).

Neither dry nor wet fur seal pups should have problems coping with high air temperatures at the Pribilof Islands. Air temperatures of 20 and 35°C are physiologically tolerable depending upon factors that dissipate heat from the body. Typical wind speeds at St. Paul Island (2.2–17.6 m s⁻¹) do not significantly affect the upper lethal limit. However, the lethal limit changes markedly if the wind stops blowing. According to Fig. 1, a dry pup exposed to full sun in still air (wind speed 0.1 m s⁻¹), would die unless air temperatures stayed below -20°C. Wetting the pelt would move the lethal limit up to about 5°C.

It is clear that young pinnipeds, like all young mammals, have higher metabolic rates for their size than do similar-sized adults (Schmitz & Lavigne, 1984; Lavigne *et al.*, 1986). What is not clear is whether these high rates are due to the cost of forming new tissues while growing (Brody, 1945; McNab, 1980, 1986; Worthy, 1987), or are the result of sustaining body temperatures during exposure to cold (Oftedal, Iversen & Boness, 1987; Thompson *et al.*, 1987; Whittow, 1987).

The possibility that weather could slow growth and thereby reduce the ability of fur seal pups to survive the rigours of the rookery and the subsequent winter migration, was not considered in the thermal budget. This model assumes that the high metabolic rate of lactating pups is maintained by unlimited supplies of lipid-rich milk. It does not account for interactions between nursing patterns and thermoregulation, affecting pup mortality, nor does it consider the trade-off between growth and maintenance. Both these factors deserve further consideration and could enhance the predictive powers of the model. Unfortunately, few or no thermoregulatory data have been collected from fur seal pups fasted for prolonged periods of time.

On San Miguel Island, fur seal pups are susceptible to heat stress. In contrast to conditions on the Pribilof Islands, radiation levels and air temperatures in California are higher and the wind speeds lower (Table 1). Virtually no rain falls on San Miguel during the summer and sheltered air temperatures in excess of 21°C and surface sand temperatures in excess 42°C are recorded each year (DeLong, 1982). Pups can contend with 20°C

daily temperature if the wind is blowing, but to survive in still air must seek shade or wet their fur (Fig. 2). Part of the difficulty that northern fur seals have in the southern climate is due to their having no effective way of losing heat by evaporation.

Behavioural modifications

Pups should show a preference for an environment that is in the centre of the climate space, away from the lethal limits. To achieve this, they can alter their metabolic rates and modify their behaviour. This latter option is the least costly. When cold, the seal should therefore move from wind to still air, huddle with other pups, curl up to reduce surface area, move into full sun, or remove water from the pelt by shaking and shuddering. A dry, heat-stressed pup should seek shade and breezes and wet its fur by entering the water. Field observations indicate that northern fur seal pups do seek shelter behind logs and rocks and huddle in groups during cold and windy weather (Ohata & Miller, 1977b). In addition, pups frequently shiver in cold weather and shake water from their pelage when wet (Bartholomew & Wilke, 1956; Irving *et al.*, 1962). Similar behaviour has been noted for other otariid species (Whittow, Ohata & Matsuura, 1971; Gentry, 1972).

Many species of otariids breeding near the equator are born on territories that are shaded and/or near the water. They protect themselves from extreme heating by keeping intermittently wet in the surf or in tidepools during sunny daylight hours. Such behaviour has been observed in the South American fur seal (*Arctocephalus australis*), Guadalupe fur seal (*A. townsendi*), Galapagos fur seal, and Stellar sea lion (Vaz-Ferreira & Palerm, 1961; Peterson *et al.*, 1968a; Odell, 1974; Bonner, 1984; Trillmich, 1984; Fleisher, 1987; Pierson, 1987). Only one fur seal study has documented pup behaviour in detail. In it, Limberger *et al.* (1986) estimated that Galapagos fur seal pups were wet for an average of 3 h day⁻¹. They also noted that lactating females usually dragged their pups with them to tidepools during the first few days after pupping. Undoubtedly, this sort of behaviour is critical to the survival of naive newborn pups. Similar behaviour appears to be absent in the northern fur seal.

DeLong (1982) observed the behaviour of heat-stressed northern fur seal pups on San Miguel Island after their mothers left for the splash zone. The abandoned newborn pups initially stayed in their territory, then began to move in a single random direction. All those that moved across the

hot sand became prostrated, began convulsing, and died. Others moving towards the splash zone were revived by the cool water. Pups appeared to learn to move to the splash zone at about 10 days of age when the mother had left and the pup had joined other pups in exploratory movements away from their place of birth.

Role of body size

Another significant factor in the mortality of northern fur seal pups in southern climates is their large body size at birth (5.4 kg). This is shown by superimposing the climate space diagrams of the Galapagos fur seal pup and the Pribilof fur seal pup (Fig. 3). Inspecting the upper thermal limit indicates the lighter Galapagos fur seal pup (3.4 kg) can contend with air temperatures that are 7°C higher than the heavier northern fur seal pup, when both species are dry and exposed to the same wind speed. Body size is not as important when the pups are wet. Under this condition the upper thermal limit of both species is almost identical. Thus the advantage of being heavy is only realized when animals are coping with the cold.

The model makes several predictions about the expected pattern of mortality during inclement weather. The first is that heavier northern fur seal pups should succumb to the hot weather of San Miguel before smaller ones. Given that there is about a half kilogram difference in birth masses between the sexes, it follows that there is likely a greater mortality of males than females. The ability of fur seals to cope with high air temperatures will depend primarily on their ability to wet their fur. On the Pribilof Islands, where pups are brought close to their lower limits, the model predicts a higher mortality of pups with low birth masses.

There appears to be some general agreement between model predictions and the limited amount of data collected on pup mortality.

On St. Paul Island, the birth masses and life histories of 410 pups were recorded (Calambokidis & Gentry, 1985). Of the 25 pups that died from various causes, 10 were males and 15 females. Even more striking is the observation that all the dead pups were significantly lighter at birth than those in the total marked population. Perhaps small pups on the Pribilofs are more susceptible to sources of mortality because they must allocate a greater portion of their energy to maintenance than growth.

On San Miguel Island there is some evidence that young male pups are more susceptible to heat than females. A 1981 survey of 106 dead pups (45

males and 61 females), found 98% of the males had died during hot weather compared with 71% of the females (DeLong *et al.*, 1982). Most of the deaths (75%) occurred within 1–4 days postpartum.

The model suggests that the climate of San Miguel Island should impose heavy mortalities on large pups, thereby suggesting strong selection pressures for pups with light birth weights. This sort of mechanism may account for the small size of the Galapagos fur seal (3.4 kg at birth). The Galapagos fur seal is closely related to the larger South American fur seal, *A. australis* (King, 1983), which weighs 4.6 kg at birth (Vaz-Ferreira & Ponce de Leon, 1987). Some have speculated that the ancestors of the Galapagos fur seal were South American fur seals that followed the northerly directed Peruvian current (King, 1983; Bonner, 1984).

Future research

The proposed thermal budget describes the ability of the pup to cope with weather conditions during the first few days of life. A second critical stage in survival is the transition from land to sea (Ichihara, 1974), particularly in the Bering Sea. No marine mammals appear to have trouble in warm water (Whittow, 1987). However, young fur seals seem to have difficulty maintaining their body temperatures at low sea temperatures, despite the development of adult pelage. The lower critical water temperature of a 4-month-old northern fur seal pup was 16°C (L.K. Miller, personal communication). The pup had to shiver and raise its metabolic rate to maintain body temperature. Average sea surface temperatures of the Bering Sea are 7.38°C in October and drop to 5.45°C in November (Ingraham, 1983). Thus, it should not be surprising if pups lose nearly half their body mass during their first winter at sea (Scheffer, 1950, 1981). Given the severity of the pelagic transition, it would be useful to develop a thermal budget for this stage of life (Ohata, Miller & Kajimura, 1977).

Several extensions of the pup's thermal budget might be of interest for future research. In addition to predicting thermoregulatory behaviour, the equation can be used to predict food requirements. The amount of milk required to maintain maximum sustainable metabolic rates can be determined by knowing the caloric value of the milk. Climate spaces could also be used to gain insight into the worldwide geographic distribution of all pinniped species.

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References

- Antonelis, G.A., Jr & DeLong, R.L. (1985a) Population growth and behavior, San Miguel Island (Adams Cove and Castle Rock). In *Fur Seal Investigations, 1982* (ed. P. Kozloff), pp. 54–60. NOAA Technical Memorandum NMFS-F/NWC-71.
- Antonelis, G.A., Jr & DeLong, R.L. (1985b) Population and behavior studies, San Miguel Island, California (Adams Cove and Castle Rock). In *Fur Seal Investigations, 1983* (ed. P. Kozloff), pp. 32–41. NOAA Technical Memorandum NMFS-F/NWC-78.
- Antonelis, G.A., Jr & DeLong, R.L. (1986) Population and behavior studies, San Miguel Island, California (Adams Cove and Castle Rock). In *Fur Seal Investigations, 1984* (ed. P. Kozloff), pp. 49–53. NOAA Technical Memorandum NMFS-F/NWC-97.
- Bartholomew, G.A. & Hoel, P.G. (1953) Reproductive behaviour of the Alaska fur seal, *Callorhinus ursinus*. *Journal of Mammalogy*, **34**, 417–436.
- Bartholomew, G.A. & Wilke, F. (1956) Body temperature in the northern fur seal, *Callorhinus ursinus*. *Journal of Mammalogy*, **37**, 327–337.
- Blix, A.S., Miller, L.K., Keyes, M.C., Grav, H.J. & Elsner, R. (1979a) Newborn northern fur seals (*Callorhinus ursinus*) – do they suffer from cold? *American Journal of Physiology*, **236**, R322–R327.
- Blix, A.S., Grav, H.J. & Ronald, K. (1979b) Some aspects of temperature regulation in newborn harp seal pups. *American Journal of Physiology*, **236**, 188–197.
- Bonner, W.N. (1984) Seals of the Galapagos Islands. *Biological Journal of the Linnean Society*, **21**, 177–184.
- Brody, S. (1945) *Bioenergetics and Growth, with Special References to the Efficiency Complex in Domestic Animals*. Reinhold, New York.
- Calambokidis, J. & Gentry, R.L. (1985) Mortality of northern fur seal pups in relation to growth and birth weights. *Journal of Wildlife Diseases*, **21**, 327–330.
- Campbell, G.S. (1977) *An Introduction to Environmental Biophysics*. Heidelberg Science Library, Springer-Verlag, New York.
- Chapman, D.G. (1961) Population dynamics of the Alaska fur seal herd. *Transactions of the North American Wildlife and Natural Resources Conference*, **26**, 356–369.
- Christian, K.A., Tracy, C.R. & Porter, W.P. (1983) Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology*, **64**, 463–468.
- Costa, D.P. & Gentry, R.L. (1986) Free-ranging energetics of the northern fur seals. In *Fur Seals: Maternal Strategies on Land and at Sea* (eds. R.L. Gentry & G.L. Kooyman), pp. 79–101. Princeton University Press, Princeton, New Jersey.
- Croxall, J.P. & Gentry, R.L. (eds.) (1987) *Status, Biology, and Ecology of Fur Seals*. US Department of Commerce, NOAA Technical Report NMFS 51.
- Davydov, A.F. & Makarova, A.R. (1964) Changes in heat regulation and circulation in newborn seals on transition to aquatic form of life. *Fiziologicheskii Zhurnal SSSR imeni I.M. Sechenova*, **50**, T563–T566.
- DeLong, R.L. (1982) *Population biology of northern fur seals at San Miguel Island, California*. PhD thesis, University of California, Berkeley, California.
- DeLong, R.L., Jameyson, E.C. & Antonelis, G.A., Jr (1981) Population growth, San Miguel Island (Adams Cove and Castle Rock). In *Fur Seal Investigations, 1980* (ed. P. Kozloff), pp. 38–47. NOAA NAWFC Processed Report 81–82.
- DeLong, R.L., Antonelis, G.A., Jr & Jameyson, E.C. (1982) Population growth, San Miguel Island (Adams Cove and Castle Rock). In *Fur Seal Investigations, 1981* (ed. P. Kozloff), pp. 33–38. NOAA Technical Memorandum NMFS-F/NWC-37.
- Elsner, R. & Ashwell-Erickson, S. (1982) Maximum oxygen consumption of exercising harbor seals. *Physiologist*, **25**, 279 (abstr.).
- Elsner, R.W., Hammond, D., Denison, D.M. & Wyburn, R. (1977) Temperature regulation in newborn Weddell seal, *Leptonychotes weddelli*. In *Symposium: Adaptations Within Antarctic Ecosystems* (ed. G.A. Liano), pp. 531–540. Procedures of the 3rd SCAR Symposium. Antarctic Biology, Washington DC, 1974.
- Fleischer, L.A. (1987) Guadalupe fur seal, *Arctocephalus townsendi*. In *Status, Biology, and Ecology of Fur Seals* (eds. J.P. Croxall & R.L. Gentry), pp. 43–48. US Department of Commerce, NOAA Technical Report NMFS 51.
- Fowler, C.W. (1990) Northern fur seals of the Pribilof Islands. In *The Northern Fur Seal. Species of the USSR and the Contiguous Countries*. USSR Academy of Sciences. Nauka, Moscow. [Available National Marine Mammal Laboratory, National Marine Fisheries Services, NOAA, 7600 Sand Point Way N.E., Seattle, Washington, USA.]
- Gates, D.M. (1975) Introduction: biophysical ecology. In *Perspectives of Biophysical Ecology* (eds. D.M. Gates & R.B. Schmerl), pp. 1–30. Springer-Verlag, New York.
- Gates, D.M. (1980) *Biophysical Ecology*. Springer-Verlag, Berlin.
- Gentry, R.L. (1972) Thermoregulatory behavior of eared seals. *Behaviour*, **46**, 73–93.
- Grav, H.J. & Blix, A.S. (1979) A source of nonshivering thermogenesis in fur seal skeletal muscle. *Science*, **204**, 87–89.
- Heller, H.C. & Gates, D.M. (1971) Altitudinal zonation of chipmunks (*Eutamias*): energy budgets. *Ecology*, **52**, 424–433.
- Ichihara, T. (1974) Possible effect of surface wind force on the sex-specific mortality of young fur seals in the eastern Pacific. *Bulletin of the Far Seas Fisheries Research Laboratory (Shimizu)*, **11**, 1–8.
- Ingraham, W.J., Jr (1983) *Temperature Anomalies in the Eastern Bering Sea, 1953–1982 for the DYNUMES 24×24 Ecosystem Model Grid*. US Department of Commerce, NOAA, NMFS, NAWFC, processed report no. 83-31.
- Innes, S., Worthy, G.A.J., Lavigne, D.M. & Ronald, K. (1990) Surface areas of phocid seals. *Canadian Journal of Zoology*, **68**, in press.

- Irving, L., Solandt, D.M., Solandt, D.Y. & Fisher, K.C. (1935) The respiratory metabolism of the seal and its adjustment to diving. *Journal of Cellular and Comparative Physiology*, **7**, 137–151.
- Irving, L., Peyton, L.J., Bahn, C.H. & Peterson, R.S. (1962) Regulation of temperature in fur seals. *Physiological Zoology*, **35**, 275–284.
- Kenyon, K.W., Scheffer, V.B. & Chapman, D.G. (1954) *A Population Study of the Alaska Fur Seal Herd*. US Department of Commerce, Special Scientific Report on Wildlife, no. 12.
- Keyes, M.C. (1965) Pathology of the northern fur seal. *Journal of the American Veterinary Medical Association*, **147**, 1090–1095.
- King, J.E. (1983) *Seals of the World*. Oxford University Press, Oxford.
- Lander, R.H. (1975) Method of determining natural mortality in the northern fur seal (*Callorhinus ursinus*) from known pups and kill by age and sex. *Journal of the Fisheries Research Board of Canada*, **32**, 2447–2452.
- Lander, R.H. (1979a) Fur seal growth. In *Preliminary Analysis of Pelagic Fur Seal Data Collected by the United States and Canada During 1958–74* (eds. H. Kajimura, R.H. Lander, M.A. Perez, A.E. York & M.A. Bigg), pp. 143–147. Unpublished manuscript. (Available National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, USA.)
- Lander, R.H. (1979b) Role of land and ocean mortality in yield of male Alaskan fur seal, *Callorhinus ursinus*. *Fisheries Bulletin*, **77**, 311–314.
- Lander, R.H. (ed.) (1980) *Summary of Northern Fur Seal Data and Collection Procedures*, vol. 1, *Land Data of the United States and Russia (Excluding Tag Recovery Records)*. US Department of Commerce, NOAA Technical Memorandum NMFS F/NWC-3.
- Lavigne, D.M., Innes, S., Worthy, G.A.J., Kovacs, K.M., Schmitz, O.J. & Hickie, J.P. (1986) Metabolic rates of seals and whales. *Canadian Journal of Zoology*, **64**, 279–284.
- Limberger, D., Trillmich, F., Biebach, H. & Stevenson, R.D. (1986) Temperature regulation and microhabitat choice by free-ranging Galapagos fur seal pups (*Arctocephalus galapagoensis*). *Oecologia*, **69**, 53–59.
- Luecke, R.H., Natarajan, V. & South, F.E. (1975) A mathematical biothermal model of the California sea lion. *Journal of Thermal Biology*, **1**, 35–45.
- McClure, P.A. & Porter, W.P. (1983) Development of insulation in neonatal cotton rats (*Sigmodon hispidus*). *Physiological Zoology*, **56**, 18–32.
- McNab, B.K. (1980) Food habits, energetics, and the population biology of mammals. *American Naturalist*, **116**, 106–124.
- McNab, B.K. (1986) Food habits, energetics, and the reproduction of marsupials. *Journal of Zoology*, **A208**, 595–614.
- Matsuura, S.T. & Whittow, G.C. (1974) Oxygen uptake of the California sea lion and harbor seal during exposure to heat. *American Journal of Physiology*, **225**, 711–715.
- Miller, L.K. (1978) *Energetics of the Northern Fur Seal in Relation to Climate and Food Resources of the Bering Sea*. Final report to the US Marine Mammal Commission, Contract MM5AC025. Rep. No. MMC-75/08. National Technical Information Service, Washington.
- Morhardt, S.S. (1975) Use of climate diagrams to describe microhabitats occupied by Belding ground squirrels and to predict rates of change of body temperature. In *Perspectives of Biophysical Ecology* (eds. D.M. Gates & R.B. Schmerl), pp. 303–324. Springer-Verlag, New York.
- Morhardt, S.S. & Gates, D.M. (1974) Energy exchange analysis of the Belding ground squirrel and its habitat. *Ecological Monographs*, **44**, 17–44.
- Odell, D.L. (1974) Behavioral thermoregulation in the California sea lion. *Behavioral Biology*, **10**, 231–237.
- Oftedal, O.T., Iversen, S.J. & Boness, D.J. (1987) Milk and energy intakes of suckling California sea lion (*Zalophus californianus*) pups in relation to sex, growth, and predicted maintenance requirements. *Physiological Zoology*, **60**, 560–575.
- Ohata, C.A. & Miller, L.K. (1976) Recommendations on northern fur seal management based on metabolic and thermoregulatory studies. *Science Alaska*, **27**, 235 (abstr.).
- Ohata, C.A. & Miller, L.K. (1977a) Northern fur seal thermoregulation: thermal responses to forced activity on land. *Journal of Thermal Biology*, **2**, 135–140.
- Ohata, C.A. & Miller, L.K. (1977b) Some temperature responses of northern fur seal (*Callorhinus ursinus*) pups. *Journal of Mammalogy*, **58**, 438–440.
- Ohata, C.A., Miller, L.K. & Kajimura, H. (1977) Northern fur seal thermoregulation: thermal responses to pelagic conditions. *Journal of Thermal Biology*, **2**, 141–143.
- Øritsland, N.A. & Ronald, K. (1978) Aspects of temperature regulation in harp seal pups evaluated by *in vivo* experiments and computer simulations. *Acta Physiologica Scandinavica*, **103**, 263–269.
- Peterson, R.S. (1968) Social behaviour in pinnipeds with particular reference to the northern fur seal. In *The Behavior and Physiology of Pinnipeds* (eds. R.J. Harrison, R.C. Hubbard, R.S. Peterson, C.E. Rice & R.H. Schusterman), pp. 3–53. Appleton-Century-Crofts, New York.
- Peterson, R.S., Le Boeuf, B.J. & DeLong, R.L. (1968a) Fur seals from the Bering Sea breeding in California. *Nature*, **219**, 899–901.
- Peterson, R.S., Hubbs, C.L., Gentry, R.L. & DeLong, R.L. (1968b) The Guadalupe fur seal: habitat, behavior, population size, and field identification. *Journal of Mammalogy*, **49**, 665–675.
- Pierson, M.O. (1987) Breeding behavior of the Guadalupe fur seal, *Arctocephalus townsendi*. In *Status, Biology, and Ecology of Fur Seals* (eds. J.P. Croxall & R.L. Gentry), pp. 83–93. US Department of Commerce, NOAA Technical Report NMFS 51.
- Porter, W.P. & Gates, D.M. (1969) Thermodynamic equilibria of animals with environment. *Ecological Monographs*, **39**, 227–244.
- Porter, W.P., Parkhurst, D.F. & McClure, P.A. (1986) Critical radius of endotherms. *American Journal of Physiology*, **250**, R699–R707.
- Romanenko, E.V. & Sokolov, V.E. (1988) Wettability of the coat of the northern fur seal. *Doklady Biophysics. A translation of the Biophysics Section of Doklady Akademii Nauk SSSR*, **297**, 227–229.
- Roppel, A.Y., Johnson, A.M., Bauer, R.D., Chapman, D. & Wilke, F. (1963) *Fur Seal Investigations, Pribilof Islands, Alaska, 1962*. US Fish and Wildlife Service Special Scientific Report on Fisheries, no. 454.

- Roughgarden, J., Porter, W. & Heckel, D. (1981) Resource partitioning of space and its relationship to body temperature in *Anolis* lizard populations. *Oecologia*, **50**, 256–264.
- Scheffer, V.B. (1950) Winter injury to young fur seals on the northwest coast. *California Fish and Game*, **34**, 378–379.
- Scheffer, V.B. (1962) Pelage and surface topography of the northern fur seal. *North American Fauna*, **64**, 1–206.
- Scheffer, V.B. (1981) Newborn size in marine mammals. *Pacific Discovery*, **34**, 19–26.
- Scheffer, V.B. & Wilke, F. (1953) Relative growth in the northern fur seal. *Growth*, **17**, 35–38.
- Schmitz, O.J. & Lavigne, D.M. (1984) Intrinsic rate of increase, body size, and specific metabolic rate in marine mammals. *Oecologia*, **62**, 305–309.
- Scott, J.R., Tracy, R.C. & Pettus, D. (1982) A biophysical analysis of daily and seasonal utilization of climate space by a montane snake. *Ecology*, **63**, 482–493.
- Spotila, J.M., Soule, O. & Gates, D.M. (1972) The biophysical ecology of the alligator: heat energy budgets and climate spaces. *Ecology*, **53**, 1094–1102.
- Spotila, J.M., Standora, E.A., Easton, D.P. & Rutledge, P.S. (1989) Bioenergetics, behavior, and resource partitioning in stressed habitats: biophysical and molecular approaches. *Physiological Zoology*, **62**, 273–285.
- Spotila, J.M., Foley, R.E. & Standora, E.A. (1990) Thermoregulation and climate space of the slider turtle. In *Life History and Ecology of the Slider Turtle* (ed. J.W. Gibbons) pp. 288–298. Smithsonian Institution Press, Washington.
- Taylor, J.R. (1982) *An Introduction to Error Analysis: The Study of Uncertainties in Physical Measurements*. University Science Books, Mill Valley, California.
- Thompson, S.D., Ono, K.A., Oftedal, O.T. & Boness, D.J. (1987) Thermoregulation and resting metabolic rate of California sea lion (*Zalophus californianus*) pups. *Physiological Zoology*, **60**, 730–736.
- Tracy, C.R. (1982) Biophysical modeling in reptilian physiology and ecology. In *Biology of the Reptilia*, vol. 12 (eds. C. Gans & F.H. Pough), pp. 275–320. Academic Press, New York.
- Trillmich, F. (1984) Natural history of the Galapagos fur seal (*Arctocephalus galapagoensis* Heller). In *Key Environments: Galapagos* (ed. R. Perry), pp. 215–223. Pergamon Press, Oxford.
- Trillmich, F. (1987) Galapagos fur seal, *Arctocephalus galapagoensis*. In *Status, Biology, and Ecology of Fur Seals* (eds. J.P. Croxall & R.L. Gentry), pp. 23–27. US Department of Commerce, NOAA Technical Report NMFS 51.
- Trillmich, F. & Limberger, D. (1985) Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia*, **67**, 19–22.
- Trites, A.W. (1989) Estimating the juvenile survival rate of male northern fur seals (*Callorhinus ursinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1428–1436.
- US Department of Commerce (1987) Comparative climatic data for the US, 1986. NOAA. National Environmental Satellite Data and Information Service. National Climatic Center, Asheville, North Carolina. 1987 ASI microfiche 2154-8.
- Vaz-Ferreira, R. & Palerm, E. (1961) Efectos de los cambios meteorológicos sobre agrupaciones terrestres de Pinnípedios. *Revista de la Facultad de Humanidades Universidad Uruguay*, **19**, 281–293.
- Vaz-Ferreira, R. & Ponce de Leon, A. (1987) South American fur seal, *Arctocephalus australis*, in Uruguay. In *Status, Biology, and Ecology of Fur Seals* (eds. J.P. Croxall & R.L. Gentry), pp. 29–32. US Department of Commerce, NOAA Technical Report NMFS 51.
- Vladimirov, V.A. (1974) The role of climatic factors in the mortality of northern fur seal pups (*Callorhinus ursinus*). *Zoologicheskii Zhurnal*, **53**, 1385–1389.
- Webb, D.R. & King, J.R. (1984) Effects of wetting on insulation of bird and mammal coats. *Journal of Thermal Biology*, **9**, 189–191.
- Webb, D.R. & McClure, P.A. (1988) Insulation development in an altricial rodent: *Neotoma floridana* Thomas. *Functional Ecology*, **2**, 237–248.
- Whittow, G.C. (1987) Thermoregulatory adaptations in marine mammals: interacting effects of exercise and body mass. A review. *Marine Mammal Science*, **2**, 220–241.
- Whittow, G.C., Ohata, F.A. & Matsuura, D.T. (1971) Behavioral control of body temperature in the unrestrained California sea lion. *Communications in Behavioral Biology*, **6**, 87–91.
- Worthy, G.A.J. (1987) Metabolism and growth of young harp and grey seals. *Canadian Journal of Zoology*, **65**, 1377–1382.

Appendix 1. List of symbols and values

Symbol	Quantity		Value	Units
a_s	Short-wave absorbtivity		0.87	Decimal fraction
a_L	Long-wave absorbtivity		0.95	Decimal fraction
A	Surface area of animal	n.f.s. ¹	0.2462	m ²
		g.f.s. ²	0.1808	m ²
A_p	Projected area on a plane perpendicular to solar beam		—	m ²
A_p/A	Fraction of surface area cast as shadow	St. Paul	0.26	Decimal fraction
		San Miguel	0.30	Decimal fraction
		Galapagos	0.30	Decimal fraction
c_p	Specific heat of air		—	J kg ⁻¹ °C
d	Diameter of animal	n.f.s.	0.087	m
		g.f.s.	0.073	m

Appendix 1. (continued)

Symbol	Quantity		Value	Units
E	Water vapour flux density		—	$\text{kg m}^{-2} \text{s}^{-1}$
H	Heat flux		—	W m^{-2}
I	Thermal conductance	wet	25	$\text{W m}^{-2} \text{°C}^{-1}$
		dry	100	$\text{W m}^{-2} \text{°C}^{-1}$
L	Length of animal	n.f.s.	62.0	cm
		g.f.s.	53.0	cm
M	Metabolic rate		Table 2	W m^{-2}
r_e	Parallel equivalent resistance of r_{Ha} and r_t		Table 3	s m^{-1}
r_r	Radiative transfer resistance		Table 2	s m^{-1}
r_{Ha}	Air boundary layer resistance		Table 3	s m^{-1}
r_{Hb}	Coat and tissue layer resistance		Table 2	s m^{-1}
R_{abs}	Absorbed radiation		—	W m^{-2}
S_d	Diffuse solar irradiance	St. Paul	106.9	W m^{-2}
		San Miguel	108.6	W m^{-2}
		Galapagos	108.7	W m^{-2}
S_p	Short-wave flux density perpendicular to beam	St. Paul	1102.7	W m^{-2}
		San Miguel	1138.7	W m^{-2}
		Galapagos	1140.1	W m^{-2}
T_a	Air temperature		Table 1	°C or K
T_b	Deep body core temperature		Table 2	°C or K
T_s	Surface temperature of animal		—	°C or K
u	Wind speed		Table 1	m s^{-1}
W	Mass of animal	n.f.s.	5.4	kg
		g.f.s.	3.4	kg
ϵ	Surface emissivity of animal		0.95	Decimal fraction
ϵ_s	Surface emissivity of surroundings	St. Paul	0.77	Decimal fraction
		San Miguel	0.82	Decimal fraction
		Galapagos	0.84	Decimal fraction
ρ	Air density		—	kg m^{-3}
ρc_p	Heat capacity of air		1200	$\text{J m}^{-3} \text{K}^{-1}$
σ	Stephan-Boltzmann constant		5.67×10^{-8}	$\text{W m}^{-2} \text{K}^{-4}$
λ	Latent heat of evaporation		—	J kg^{-1}
λE	Total evaporative heat loss		0.20 M	W m^{-2}

¹ = Northern fur seal.² = Galapagos fur seal.

Appendix 2. Sensitivity analysis

The thermal budget described by equation 1 represents a linear relationship between air temperature (T_a) and the amount of short- and long-wave radiation exchanged between the pup and the environment (R_{abs}). It can be rewritten as:

$$R_{\text{abs}} = a - b T_a$$

where:

$$a = f(E, T_b, M, d, r_{\text{Hb}})$$

$$= c_1 E T_b^4 - c_2 M + c_3 \frac{(T_b - 273.15)}{\sqrt{d}} - c_4 \frac{M r_{\text{Hb}}}{\sqrt{d}} - c_5 M r_{\text{Hb}} E T_b^4$$

and

$$b = f(d) = \frac{c_3}{\sqrt{d}}$$

with the constants c_i ($i = 1, \dots, 5$) set as follows: $c_1 = 5.67 \times 10^{-8}$; $c_2 = 0.8$; $c_3 = 10.63$; $c_4 = 7.09 \times 10^{-3}$; and $c_5 = 1.51 \times 10^{-10}$.

The slope (b) is a function of the diameter of the pup while the intercept (a) is a function of five parameters (E , T_b , M , d and r_{Hb}). Each of these parameters is measured with errors e_E , e_{T_b} , e_M , e_d , $e_{r_{\text{Hb}}}$. If these uncertainties are independent and random, then error in the estimated slope and intercept will equal:

$$e_a = \sqrt{\left(\frac{\delta a}{\delta E} e_E\right)^2 + \left(\frac{\delta a}{\delta T_b} e_{T_b}\right)^2 + \left(\frac{\delta a}{\delta M} e_M\right)^2 + \left(\frac{\delta a}{\delta d} e_d\right)^2 + \left(\frac{\delta a}{\delta r_{\text{Hb}}} e_{r_{\text{Hb}}}\right)^2}$$

and

$$e_b = \sqrt{\left(\frac{\delta b}{\delta d} e_d\right)^2} = \left|\frac{\delta b}{\delta d}\right| e_d$$

This formulation identifies the contribution of individual parameter errors to overall model uncertainty (Taylor, 1982).

Table A1. Parameter estimates ($\hat{p} \pm e_p$) and solutions of the partial differential equation $\left(\frac{\delta a}{\delta p}\right)$ used to determine the total error (e_a) in the intercept of the energy budget equation. See text for further details.

p	\hat{p}	e_p	$\frac{\delta a}{\delta p}$	$\frac{\delta a}{\delta p} 0.01\hat{p} $	$\frac{\delta a}{\delta p} 0.05\hat{p} $	$\frac{\delta a}{\delta p} e_p $
E	0.95	0.02	361.29	3.43	17.16	7.23
T_b	34.00	1.00	40.96	13.93	69.64	40.96
M	409.00	40.00	-3.06	12.50	62.49	122.22
d	0.087	0.01	-2524.85	2.20	10.98	32.82
r_{Hb}	80.00	10.00	-11.53	9.23	46.13	115.32
e_a				21.26	106.29	176.20

The thermal budget (equation 1) was applied to both dry and wet pups and considered upper and lower lethal limits at four different wind speeds, resulting in 16 unique solutions for the Pribilof Islands (see Fig. 1). Since the response of each model to errors is essentially identical I have chosen to present the sensitivity analysis conducted on the lower combination of air temperatures and radiation levels that are lethal to a wet pup exposed to a wind speed of 7.4 m s^{-1} ($R_{\text{abs}} = 412 - 36 T_a$).

Table A1 shows the estimates of the five parameters and the solutions of the partial differential equations used to estimate e_a . Because the actual errors associated with each parameter were unknown, I examined the effect of uniform errors of 1 and 5%. I also considered errors based on my insight into the maximum uncertainty that might be present for each parameter.

If all five parameters were off by 1%, the intercept a would equal $412 \pm 21 \text{ W m}^{-2}$; at 5% the error in a would be five times higher. If input errors are as high as I have considered, then the uncertainty in the estimate of a could be as much as 176 W m^{-2} . Corresponding estimates of the error associated with the slope b are 36 ± 2 and $36 \pm 10 \text{ W m}^{-2} \text{ } ^\circ\text{C}^{-1}$ for uniform errors of 1 and 5% respectively, and 36 ± 2 when considering maximum uncertainty.

The intercept proved insensitive to errors in the diameter of the pup (d) and to errors in the estimate of surface emissivity (E). The deep body core temperature (T_b), the amount of metabolic heat supplied to the surface (M) and the resistance of the fur seal coat and peripheral tissue layer (r_{Hb}) accounted for over 87% of the uncertainty in a . Of these three parameters, I am most confident in T_b . This means the reliability of the model hinges upon the estimates of M and r_{Hb} .

I feel that the possible errors in the calculation of a and b are within acceptable bounds and that the predictions of the model are reliable. The method employed here is basically a summation of the effects of individual errors and is hence an indication of the maximum possible error that could occur. The actual error in a and b is likely much smaller than I have shown since introducing simultaneous errors into the thermal budget equation can compensate each other such that any new predictions should differ very little from those indicated in Fig. 1.

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