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THERMAL AND ENERGETIC CONSEQUENCES OF OIL CONTAMINATION IN POLAR BEARS

by

RICKI J. HURST

A Thesis presented to the University of Ottawa

in partial fulfillment of the requirements

for the degree of Master of Science in

Department of Biology

Ottawa, Ontario, 1981

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ABSTRACT

The behavioral, metabolic, and temperature responses of 3 sub-adult polar bears (Ursus maritimus) were monitored before and after exposure to a 1 cm slick of Midale crude oil. Body and skin temperatures (T_b and T_s) were measured by surgically implanted radio transmitters, and metabolism by open circuit respirometry.

All bears groomed extensively and showed pronounced shivering in the days immediately following oil contact. Resting metabolic rate increased by 27 percent to 86 percent and averaged 50 percent higher post-oil. Activity metabolism, which was tested in one animal following oil fouling, increased by 24 percent. T_b dropped significantly in one bear but remained stable in 2 of the animals during several days following oiling. T_s of all animals remained abnormally high for approximately one week. All temperatures (T_b and T_s) measured below control values in the following weeks.

Wind tunnel tests of heat transfer through 4 polar bear pelts (in vitro) showed a substantial oil-induced decrease in insulation. The heat transfer coefficient increased following oil contamination by a factor of 2 to 5; the wind coefficient averaged 4.6 times greater; and the solar utilization increased by 28 percent. The most viscous of 3 oils tested had a more consistently negative effect on insulation.

The metabolic and temperature changes induced by oil, and the potential energetic consequences, are discussed in relation to the possible causes including: metabolic compensation for a reduction in fur insulation; a change in the minimum level of energy turnover of body tissues; and a skin reaction to the physical oil coating.

RESUME

Le comportement, le métabolisme et la température de trois ours polaires (Ursus maritimus) sub-adultes furent enregistrés avant et après avoir été exposés à une nappe de pétrole brut Midale, épaisse d'un centimètre. Les températures du corps et de la peau (T_b et T_s) furent mesurées à l'aide de transmetteurs radio implantés chirurgicalement et le métabolisme à l'aide d'un respiromètre à circuit ouvert.

Tous les ours se léchèrent considérablement et frissonnèrent beaucoup les jours suivant le contact avec l'huile. Le taux métabolique au repos augmenta de 27% à 80% et fut en moyenne 50% plus élevé après le traitement. Le métabolisme actif, qui fut mesuré que chez un seul ours, augmenta de 24%. T_b diminua significativement chez un ours mais resta stable plusieurs jours après le traitement chez les deux autres. T_s de chaque animal demeura anormalement élevée pendant à peu près une semaine. Dans les semaines qui suivirent, toutes les températures (T_b et T_s) furent plus faibles que les valeurs contrôles.

L'échange de chaleur à travers quatre peaux d'ours polaire (in vitro) fut déterminé à l'intérieur d'un tunnel à vent et démontra une diminution de l'isolation calorifuge dû au traitement à l'huile. Le coefficient de transfert de chaleur augmenta de 2 à 5 fois à la suite de la contamination; le coefficient vent fut en moyenne 4.6 fois plus élevé; et l'utilisation solaire augmenta de 28%. La plus visqueuse des trois huiles eut un effet négatif plus persistant sur l'isolation.

Les changements métaboliques et de température causés par l'huile, et les conséquences énergétiques sont discutés en fonction des causes possibles: compensation métabolique de la diminution de l'isolation de la fourrure; changement du niveau minimal de l'écoulement de l'énergie des tissus du corps; et la réaction de la peau à l'application physique de l'huile.

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I. GENERAL INTRODUCTION

The polar bear (Ursus maritimus) is a circumpolar species adapted to a semi-marine existence in a cold arctic environment. Extensive travel over sea ice and across open-water leads distinguishes the polar bear as a unique amphibious arctic mammal (Stirling and Kiliaan, 1980; Larsen, 1971, Øritsland, 1969). It also assures a very real possibility of contact with marine contaminants such as crude oil.

Although offshore petro-chemical exploration has recently advanced at an exponential rate (Longhurst, 1980; Gamble, 1979a,b), the potential effect of oil on marine mammals and polar bears remains inadequately known. The suggestion has been voiced that the physiological impact of oil on polar bears could be substantial (Birchard et al., 1978). More frequently, authors have addressed the question as a very important consideration for which there is no data (Stirling and Kiliaan, 1980; McTaggart-Cowan, 1979; Boyd et al., 1978; Milne and Smiley, 1978 and others).

A critical consideration in evaluating the potential of oil contact is the intimate association of polar bears with their primary food source, the ringed seal (Phoca hispida) (Stirling and McEwan, 1975; Tzalkin, 1936). Muller-Willie (1974) reported ringed seals in Hudson Bay completely covered with oil. Moreover, ringed seals have demonstrated rapid absorption of hydrocarbons into body tissue through oil exposure by both immersion and ingestion (Engelhardt, 1978; Engelhardt et al., 1977). Bioaccumulation and magnification of non-hydrocarbon chemicals throughout the food web (Anderson, 1977) may play a serious role in a top carnivore such as

the polar bear. High levels of environmental contaminants such as PCB's, DDT, and mercury have already been documented in polar bears and ringed seals (Bowes and Jonkel, 1975; Smith and Armstrong, 1975; Addison and Smith, 1974 and others). Long term bioaccumulation of hydrocarbons may not be as critical a concern (Varanasi and Malins, 1977).

The potential vulnerability of polar bears to physical oil contact is of considerable concern, particularly during seasonal concentration at limited areas of ice free water (Smith, 1980; Stirling and Archibald, 1977). Polar bears hunt primarily in moving pack ice and areas of ice-bounded open water, termed polynyas (Stirling and Cleator, 1981). The apparently higher productivity, due to upwellings of surface nutrients or other factors (Stirling, 1980; Bailey, 1957), tends to concentrate many marine species in these areas. The result is to effectively 'shrink' the area of critical habitat, making some species particularly vulnerable to marine perturbations.

A reduction in suitable habitat, as a result of unusual ice conditions led to severe reproductive failure of thousands of seabirds in Lancaster Sound (Nettleship et al., 1979). Similarly, a 50 percent drop in the number of ringed seals and bearded seals (Erignathus barbatus) and a reduction in productivity of about 90 percent followed severe ice conditions in the Beaufort Sea (Stirling et al., 1976). As a direct consequence, the population size of polar bears was affected as were the growth rates (Kingsley, 1979; Stirling et al., 1976). Stirling (1980) expressed the concern that offshore petro-chemical exploration might be more difficult, and thus more of a threat to seabirds and mammals, in a year of heavy ice when numbers and reproductive rates were already depressed because of

environmental conditions. The oil industry must take some advantage of areas of high biological productivity. The area in which drilling is concentrated in the Beaufort Sea, for example, is one of the most important feeding areas for polar bears in the Western Arctic (Stirling et al., 1975). Year round ice-breakers, expected to guide traffic through the arctic seas by the late 1980's (Anon, 1980b), will probably make maximum use of polynyas and shore leads to facilitate travel. The effective result could be to reduce the vast expanses of the maritime arctic to a few areas critical to both hydrocarbon resource development and marine mammal populations. The question remains as to the potential implications to the northern environment as well as the value of the individual marine species.

The polar bear is not considered internationally as an endangered species although it has been listed as 'vulnerable' by the International Union for Conservation of Nature (IUCN, 1974). This does not imply total protection. In fact, the allowable quota of polar bears which can be hunted by native peoples of Canada has increased steadily since 1974 to the present level of approximately 600 per year (Smith, 1979; Stirling and Smith, 1976). They are harvested principally by Inuit of NWT and to a minimal extent by natives of Quebec and Newfoundland (Stirling and Kiliaan, 1980). The value of polar bears in terms of their aesthetic and cultural significance is impossible to assess, although such considerations do play a role in marine mammal management. The polar bear represents a substantial component of the economic base of the Inuit people. For example, the sale of hides by Inuit of S. Baffin Islands grossed over $65,000 in 1974 and $50,000 in 1977-78 (Smith, 1979a). As much as $3,000

has been paid for one pelt, while polar bear hides averaged $1,400 each in 1974 (Smith, 1979a,b; Smith and Jonkel, 1975). A limited amount of polar bear meat is also utilized for food by both humans and dogs (Geraci and Smith, 1979; Stirling et al., 1975). Another less obvious benefit is the secondary effect on populations of arctic fox (Alopex lagopus). The dependence of fox on seal carrion left by polar bears may be highly significant to the white fox population and the trapping industry of the north (McLaren Atlantic Ltd., 1978; Stirling and McEwan, 1975). The polar bear is thus of direct economic value to hunters and trappers as well as an important part of a social and cultural heritage.

This report will provide some insight into the severity of impact on one arctic species, the polar bear, in the event of contact with a crude oil spill. I would also like to address the question of the nature and probability of contact by reviewing some of the pertinent literature.

A general concern for the world's oceans is justified, if only from the statistics delineating a spiralling upward trend in oil spillage (Anon, 1980a; Beak, 1974; Blumer, 1971). During 1978, for example, more than 206 million gallons of oil were spilled in 140 major accidents involving more than 20,000 gallons each (Ross, 1980). This compares to a spillage of 93 million gallons in 1959 (Anon, 1970). The 1978 'record' was exceeded in 1979 by oil spills totalling 328 million gallons, an increase in one year of 56 percent (Anon, 1980a).

Canada became the first country to embark upon oil and gas exploration in arctic waters, but was quickly followed by 3 other countries; USA, USSR, and Greenland (Gamble, 1979a,b). Norway began drilling north of

the 62nd parallel in 1980, following a 2 year delay as a consequence of the 1977 disasterous Ekofisk blow-out in the North Sea (Anon, 1980b). The full complement of 5 countries with a population of polar bears are thus involved in arctic drilling, and virtually the entire circumpolar region is now being considered for resource development potential.

Oil exploration and development in arctic waters is a relatively new phenomenon and, to date, large scale discharges have been rare and the extent of oil pollution has been relatively minor. As of 1972, Deslauriers (1975) could find reports of only 24 oil spills in ice-infested waters. The pace of exploration is, however, increasing dramatically. Sixteen artificial islands for drilling rigs had been constructed in the Beaufort Sea by the end of 1979 (Longhurst, 1981). Two recently drilled structures in the Beaufort Sea initially yielded 1,345 and 2,830 barrels of oil per day, and could each contain more than 4 billion barrels of oil (Globe and Mail, Nov. 4, 1981). Estimates of the total reserves for the MacKenzie Delta and Beaufort Sea are 36 billion barrels (Todd, 1981). G. Harrison of Dome Petroleum Ltd. (Lewington, 1981) estimates that the company will spend $500 million on Beaufort Sea drilling in the 1981-1982 season. In sub-arctic waters off east coast Canada, 172 wells have been drilled without mishap (Scarratt, 1981).

The consequences of such exponential development are, however, beginning to emerge. Oil slicks of unknown origin have recently been reported in arctic waters (Barber, 1978; Levy, 1978; Muller-Willie, 1974). A serious tanker spill of 100,000 gallons of Bunker C oil occurred off the coast of Canada, south of Alaska in 1979 (Anon, 1980c) and followed other

less dramatic Alaskan spills (Morris, 1970). In recounting difficulties of petro-chemical exploration in the Beaufort Sea, Stirling (1980) lists a freshwater blowout, gas well blowouts, and a lost oil spill from a service vehicle as but a few of the problems encountered to date.

The potential of a serious accident has received considerable attention, although the projections of the probability of a major northern blowout remain varied and speculative (Topham and Bishnoi, 1980; Milne, 1978; Topham, 1975). World wide statistics suggest a frequency of blowouts exceeding 100 bbl to be about 1 per 100 wells drilled (Scarratt, 1981). Bercha (1977) used a predictive model to estimate a 37 percent chance of a blowout of some kind, a 4.4 percent chance of a sizeable blowout, and a 0.25 percent chance of a major blowout over a ten year period, assuming a drilling rate of 100 offshore wells per year. Day et al., (1979) estimated that if a blowout started in the drilling season and could not be relieved for 8 months, a total of 287,000 barrels or 45,700 cubic meters of oil would be spilled.

Oil spills in the arctic environment present special problems due to the unique conditions of ice, weather and biotic makeup.

Oil-Ice-climate: Perhaps the most unpredictable challenge to petro-chemical development in a generally inhospitable environment is that of ice, which may threaten drilling platforms or transport and effectively reduce the drilling season. Milne and Smiley (1978) determined the median length of drilling season to be 109 days in Lancaster Sound, comparable to the 105 day ice free period in the Beaufort Sea. Oil operations could become

particularly difficult when ice combines with the unpredictable and generally harsh artic conditions. Keliher et al., (1978) found that autumn surface winds exceeded 20 $m.s^{-1}$ almost 10 percent of the time and that 667 cyclones traversed the region of a proposed drill site in Davis Strait during a 20 year study. Although sea ice generally serves to reduce the buildup of waves, wave heights reached 4.5, 5.5 and 11.6 m in three storms analyzed; heights considered potentially serious for drilling operations.

In the event of an accident, arctic ice conditions, with limited areas of exposed water, would modify the pattern of spreading and disappearance of an oil spill (Percy and Mullin, 1975). Oil would be 'herded' by shifting ice and wind against an ice edge or between moving ice flows (Ayers et al., 1974), increasing the depth of a slick to as much as 1 cm (Wadhams, 1976). Alternatively, oil could spread under the ice to be transported by currents and accumulate in pockets at the interface (Day et al., 1979).

Petroleum trapped under the ice does not weather or lose its toxic effect as rapidly as it would in open water. For example, Keevil and Ramseier (1975) demonstrated no difference in toxicity to amphipods between Norman Wells oil which was fresh, and that which had been spilled under ice and recovered 8 months later. Spring breakup or summer melt could cause release of the oil and reintroduction of the toxic components of oil into the water column at the time of greatest biological activity (Craddock, 1977; Percy and Mullin, 1975). Follow-up studies at Chedabucto Bay, Nova Scotia (Thomas, 1973), following the wreck of the Arrow, showed that recurrent release of oil trapped in ice and sediments

caused serious and persistent ecological damage.

Ice may however, play a beneficial role in containing oil by reducing wave size, and by generally mitigating the effects of oil. MacKay (1980) reported that 80 percent of participants at a recent Toronto workshop of oil-gas-and-ice felt that the impact of an oil spill in winter would be less in the Beaufort Sea than in Southern waters for the above reasons.

The length of season, location and weather could seriously hamper cleanup operations, however, particularly in the event of a late seasn blowout. Several months to almost a year could then elapse before a relief well could be drilled and the oil contained. Concern for this 'worst case scenario' has been expressed by many authors (Day et al., 1979; Milne and Smiley, 1978; MacKay, 1977; Pilmott, 1974 and others).

Rate of Degradation: Degradation of oil, by both physical and biological processes, is slow in the arctic as a consequence of less than optimal conditions of temperature and oxygen (Craddock, 1977; MacKay and Shui, 1976; Ottway, 1971). The normal rapid depletion of low boiling aromatics and the eventual neutralization of all toxic fractions is considerably impeded (Harrison et al., 1975; Boesch et al., 1974; Ottway, 1970). The net result would be an effectively extended exposure time to marine mammals and other stages of the food web.

Characteristics of Arctic Life: Low species diversity, slow growth and low reproductive rates would also mean slow recovery in the event of environmental damage (Clark and Finley, 1977; Chia, 1970).

The potential of grand scale population contact wih marine pollution is aggravated by the phenomenon of large seasonal concentrations of cold-climate animals; as documented in polar bears (Smith and Stirling, 1975), seals (Smith, 1980; Smith et al., 1979), seabirds (Nettleship et al., 1979; Divoky, 1978; Bradstreet and Finley, 1977), and many other marine animals. Such concentrations are often at the ice-edge in areas of limited open water, where oil pollution may be most threatening.

Finally, the reduced season and dependence of vast numbers on the climatic factors governing small areas of critical habitat allows little margin for perturbations, either meteorological or industrial. Levy (1980) demonstrated that seabirds, exposed to oil spills on the East Coast of Canada, died after an 'extremely minute' amount of oiling. He suggested that the effects of oil had acted synergistically with the stresses imposed by severe environmental conditions. Geraci and Smith (1976) demonstrated a similar reponse in ringed seals which died on entering an oiled tank, apparently from the effects of oil superimposed on the stress of captivity.

Environmental concern prompted investigations generating considerable information on the effects of crude oil hydrocarbons on lower marine animals (See reviews by Vernberg et al., 1979; Malins, 1977; Wolfe, 1977; Moore and Dwyer, 1974; Straughan, 1971). The death of seabirds has been the most obvious and perhaps dramatic consequence of large scale oil spills, prompting considerable concern and study (See reviews by Holmes and Cronshaw, 1977; Szaro, 1977; Vermeer and Vermeer, 1975).

The question of oil fouling in marine or amphibious mammals has not been addressed nearly as extensively, due in part to the sensitive and

costly nature of such studies. There is also a relative dearth of baseline information on marine mammal physiology to serve as a standard for comparison. This thesis reports on results, obtained both in vitro and in vivo, of the thermal and energetic responses of polar bears following exposure to a simulated slick of crude oil. It also attempts to synthesize some of the control data obtained in this and previous studies towards a more complete understanding of polar bear thermoregulation and energetics.

II. TEMPERATURE AND METABOLIC RESPONSES TO OIL

2.1 INTRODUCTION

Exposure of marine mammals, particularly seals, to crude oil spills is well documented (Baker, 1976; Davis and Anderson, 1976; Anon, 1970). The severity, or in fact manifestation, of physiological impacts from such free-ranging contact remains poorly substantiated (Geraci and St. Aubin, 1980; Brownell and LeBoeuf, 1971). More germane to our understanding of the impact of oil pollution on marine or amphibious mammals are a limited number of controlled studies. These include investigations into the effects of oil on ringed seals (Phoca hispida) and harp seals (Phoca groenlandicus) (Engelhardt, 1978; Engelhardt et al., 1977; Geraci and Smith, 1976), sea otters (Enhydra lutris) (Costa and Kooyman, 1980; Williams, 1978), fur seals (Callorhinus ursinus) (Kooyman et al., 1976), and muskrats (Ondatra zibethicus) (McEwan and Koeling, 1973). Also of relevance are studies on the effects of oil on the insulative value of fur (Kooyman et al., 1977; Øritsland and Smith, 1975).

Marine or amphibious mammals encounter particularly severe and unique thermal challenges in their diurnal or seasonal transitions from air to water. It has been suggested (Kooyman et al., 1977) that mammals which rely on fur to prevent excessive heat loss to the environment would experience more severe oil-induced changes in thermoregulation than those which rely primarily on blubber. Polar bears, although possessing extensive layers of subcutaneous fat (Øritsland, 1970), rely principally on fur

to contend with thermal gradients of as much as 90°C (Scholander et al., 1950a;b).

Crude oil could alter the thermal integrity of the fur itself and jeopardize the thermal balance of an exposed individual. The present study documents some of the thermal and energetic responses of 3 polar bears following controlled exposure to a simulated oil spill.

2.2 MATERIALS AND METHODS

2.2.1 Experimental Animals

Four sub-adult polar bears were captured as 'nuisance bears' in the area of Churchill, Manitoba and held at the Polar Bear Project facilities for 3-4 months prior to experiments. During this time they were fed a diet of beef scraps and ringed seal. Water and/or snow were supplied ad libitum. Bear 1 reacted unpredictably to immobilizing drugs and was, therefore, not used in the oil study. The 3 animals used were of comparable age (2-3 years) and size (110-160 kg). When handled for surgery and movement to and from the respiration chamber, they were immobilized with a jab stick injection of ketaset (ketamine hydrochloride) and rompun (xylazine hydrochloride) each at a weight specific dose of 5.5 $mg.kg^{-1}$. See also Appendix I.

2.2.2 Exposure Procedure

The animals were studied over a 6 week period, each individual monitored through an essentially identical sequence of measurements

designed to use each animal as its own pre-exposure control. The general order of experimentation was bear 2, followed by bears 4 and 3 (Fig. 1). Wind tests and determination of resting metabolism were carried out before and after oil exposure. Mechanical breakdown of the treadmill prevented complete activity testing of bears 4 and 3 post-oil.

A complex of 4 holding cages were interconnected by a series of walkways and sliding doors to each other and to the pool, wind cage, and treadmill (Fig. 2). This afforded easy movement of animals with a minimal number of druggings. The respiration chamber was separate from the cage complex.

2.2.3 Oil Contact

The bears were exposed to a simulated oil slick in a pool measuring 3.7 x 1.5 x 1.5 m and containing 6,800 l of sea water. Oil was introduced to the pool surface in an amount necessary to create a 1 cm slick (57 l) (Wadhams, 1976), 36 hours prior to the first bears' contact. Following exposure, the remaining surface volume was calculated and more oil was added to reconstitute the 1 cm thickness. The oil used was a medium viscosity Midale crude with a specific gravity of 0.89 at 15.6°C, a pour point of 10°C, and a viscosity of 7.43 and 10.24 centistrokes at 50°C and 40°C respectively (Energy, Mines and Resources Canada, 1981). The physical characteristics are generally comparable to Prudhoe crude oil (Beak, 1974). See also Table I. For a more complete analysis of the oil refer to Øritsland et al. (1981, section 5).

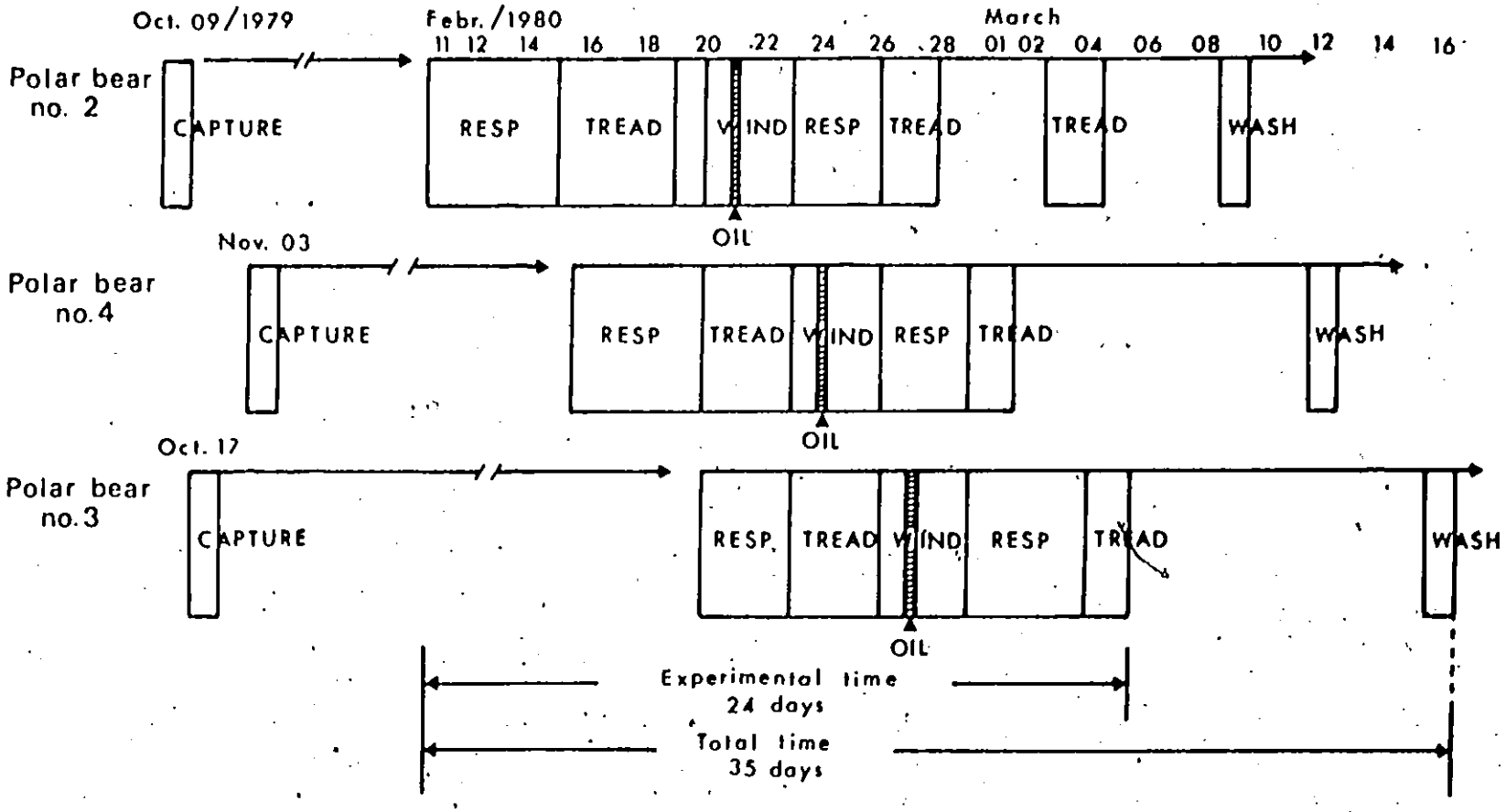
The animal was enticed to the pool edge and a sliding door was closed,

FIGURE 1 Schedule of Experimentation

Each of three polar bears were tested before and after oil exposure, permitting pre-oil values to be used as controls.

FIGURE 2 The Churchill Experimental Complex

The experimental complex used in this study of oil exposure in three polar bears. Connecting passageways, constructed in preparation for the oil project, allowed movement of individuals to the pool, treadmill, etc. without the need of drugging.



EXPERIMENTAL SCHEDULE

Timing w.r.t.- respiration chamber (RESP)
treadmill (TREAD)
wind chamber (WIND)
washing fur (WASH)

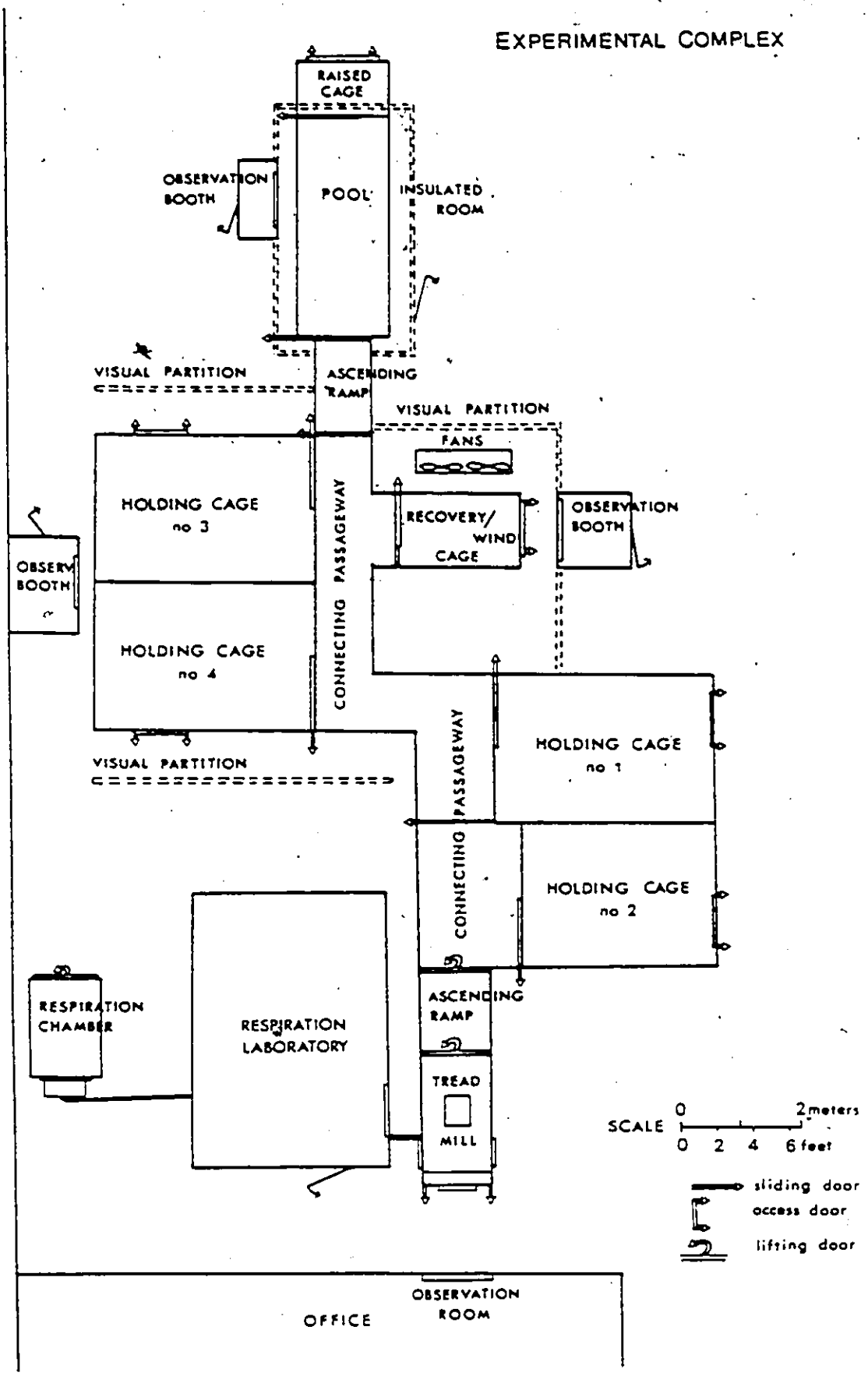

EXPERIMENTAL COMPLEX
RAISED CAGE
POOL
OBSERVATION BOOTH
INSULATED ROOM
VISUAL PARTITION
ASCENDING RAMP
VISUAL PARTITION
FANS
HOLDING CAGE no 3
RECOVERY/ WIND CAGE
OBSERVATION BOOTH
OBSERV BOOTH
CONNECTING PASSAGEWAY
HOLDING CAGE no 4
HOLDING CAGE no 1
VISUAL PARTITION
CONNECTING PASSAGEWAY
HOLDING CAGE no 2
RESPIRATION CHAMBER
RESPIRATION LABORATORY
ASCENDING RAMP
TREAD MILL
SCALE 0 2 meters
0 2 4 6 feet
sliding door
access door
lifting door
OFFICE
OBSERVATION ROOM

TABLE I

PHYSICAL PROPERTIES of CRUDE OILS

ASSAY	VALUE		
	Midale oil[1,2,3]	Prudhoe Bay[4]	Norman Wells[5]
Colour	br.-black-black	-	-
API gravity(16°C)	27.5-37.2	27.0	37.8
Specific gravity	0.890	0.893	0.836
Saybolt Universal Viscosity at 25°C	95	-	-
" 38°C	86	84	42
" 40°C	60	-	-
" 50°C	50	-	-
Pour point, °C	-2.5, 10	-9,-21	-49
Sulfur % wt.	0.58-2.60	0.82	0.45
Carbon residue % wt.	6.9-11.3	-	-

SOFT PROPERTIES - %VOLUME

	Midale[1]	Prudhoe Bay[4]	Norman Wells[5]
Gasoline and naptha	23.7	19.0	35.0
Kerosene	3.9	4.3	5.3
Gas oil	18.0	18.4	19.2
Lub oil	17.6	20.9	17.1
Residium	35.8	36.3	21.2

Sources of data(in brackets): 1,2-assays of Midale crude oil in 1954 and 1981(oil used in this study) by Dept. of Energy, Mines and Resources, Canada; 3-assay of Midale crude in 1971-1972 by Shell Oil Refinery, Sarnia, Ontario; 4-assay of Prudhoe Bay by Oil and Gas Journal, 1971; and 5-assay of Norman Wells by Charbonnier et al, 1969 as cited in Beak, 1974.

forcing the bear into the pool. After a designated time (15 minutes for bear 2, 30 minutes for bear 4 and 53 minutes for bear 3), the entrance door was opened allowing the bear to exit the pool and re-enter the wind cage.

2.2.4 Behaviour

The general behaviour of the study animals was monitored on a daily basis throughout the 6 week period. Intensive observation from booths located adjacent to the wind cage and pool was maintained on a 24 hour basis for the day prior to, during, and for 2 days following oil exposure. This was repeated for a 24 hour period 3 days post washing (i.e. 20 days post exposure). Alternating periods of wind and no wind, each of 4 hour duration, was instituted. Wind at a velocity of 4.9 $m.s^{-1}$ was generated from 2 industrial fans mounted 1.2 m from the wind cage.

All behaviour was recorded including: level of activity, body orientation, position, and response to oil coating. A comparative index of activity was derived by assigning values for the relative costs of each activity as suggested for polar bears by Best *et al.* (1981) on the basis of general metabolic indices (Wunder, 1975; Moen, 1973; Taylor *et al.*, 1970). The assignment of activity coefficients was used as a means of comparing pre and post-oil activity, and followed the format:

Lying-asleep	1.0 x BMR
Lying-awake	1.1 x BMR
Sitting	1.5 x BMR
Standing	1.7 x BMR
Active-restless	2.0 x BMR
Active-aggressive	2.2 x BMR

2.2.5 Metabolism

Indices of resting and activity metabolism were determined using open circuit respiration chambers and calculating the volume of oxygen consumed per unit weight and time. The flow of expired air from the chambers was established by means of centrifugal pumps and determined by a 350 l gasmeter (W.E. Collins Inc.). Flow rates were maintained at approximately 200 l/min and 600 l/min for resting and activity measurements respectively. Oxygen concentration was measured by use of a zirconium oxide oxygen analyzer (Applied Electronics Inc.). Ambient air outside the chamber was recorded before and after each sample period. All values were corrected to S.T.P. of gas. The weight specific oxygen consumption is most often expressed in units of ml $O_2 \cdot g^{-1} \cdot hr^{-1}$. Metabolism is also recalculated to heat production by relating 1 l O_2 (STP) to 4.7 kcal or 20.1 kj, and thus 1 l $O_2 \cdot hr^{-1}$ is equivalent to 5.58 W (Schmidt-Nielsen, 1979; Taylor, 1977). Although the metabolic fuel used in oxidation determines the caloric equivalency of oxygen consumption, the error is at most 6 percent and is considered, for purposes of this study, to be negligible (Schmidt-Nielsen, 1979).

Resting Metabolism: The respiration chamber was a metal cyclinder with a functional volume of 2,300 l which was air-sealed except for intake and air collection openings installed at opposite ends of the chamber. Four weight sensitive load cells (W.C. Dillon Co.), installed under the floor of the chamber and connected to a microvoltmeter, relayed any movement of the animal. Sampling was of 2 hour duration on each of 3 or 4 successive

nights when disturbance factors were minimal. Excessive movement predicated a delay of measurements or rejection of the results.

As the absolute conditions for measuring 'basal metabolic rate' (BMR) (Kleiber, 1975) can rarely be attained, it has been suggested (Pauls, 1981; Bligh and Johnson, 1973) that metabolism during periods of minimal activity should be considered the best possible estimate. Consequently, the term 'resting metabolic rate' (RMR) has been used in this study.

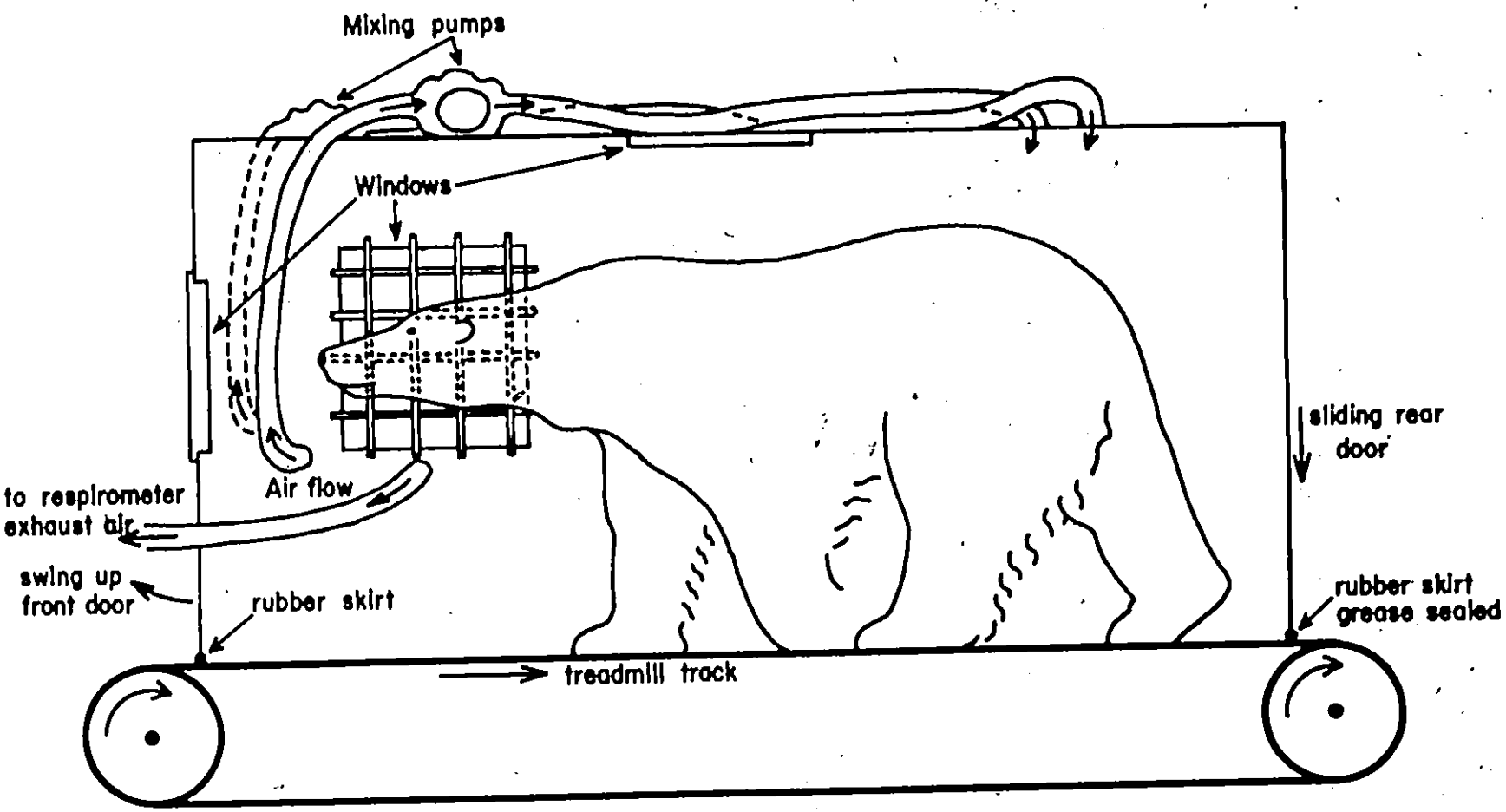
Activity Metabolism: The treadmill used in this study has been described previously (Hurst et al., 1981; Øritsland et al., 1976). It was hydraulically powered and equipped with a variable speed control (Fig. 3). A steel chamber (2.8 x 1.3 x 1.1 m) enclosing the treadmill tract served as an open circuit respiration chamber. Internal air was circulated to avoid stratification. Each animal was run as control for 3 or 4 days at no more than 2 runs per day. All runs were of 30 minute duration at a walking speed of 1.5 m/sec (5.4 km/hr).

2.2.6 Temperature

Body temperatures were determined with temperature sensitive radio transmitters (J. Stuart Enterprises) surgically implanted 2-3 weeks prior to oil contact. Deep body transmitters were implanted mid-ventrally, 20 cm posterior to the sternum and adjacent to the peritoneum, and skin or subcutaneous transmitters were placed just under the skin of the neck. Bear 3 was also implanted with a skin transmitter on the dorsal right side of the rump. Rump temperature readings were subsequently found to be

FIGURE 3 Treadmill Apparatus

An open circuit respiration chamber was mounted on a hydraulically powered treadmill track. Mixing pumps, mounted above the chamber, limited stratification of gases by circulating the internal air.


Mixing pumps
Windows
sliding rear door
to respirometer exhaust air
Air flow
swing up front door
rubber skirt
rubber skirt grease sealed
treadmill track

compromised by contact with the steel bars and cage floor and were discarded, except when the rump was assuredly free of contact. Periodic pulses, convertible to temperature values (±0.01°C), were received and displayed in milliseconds on a digital processor (Telonics). Body temperature was monitored at 15 minute intervals during the wind/observation periods, 5 minute intervals during the determination of resting metabolism and 1 minute intervals during pool immersion and during the testing of activity metabolism. Daily health records also included measurement of body temperatures twice daily, at comparable times, throughout the 4 week observation period.

Ambient air and water temperatures were monitored with standard Tempscribe recorders (Bachard Inst.). Thermistor probes (Y.S.I. Electronics) were used to confirm ambient temperatures and to monitor respiration chamber air temperature. Ambient temperatures ranged from -24 to -16°C during the period and respiration chamber temperatures, higher due to the radiant heat of the animal, were -16 to +3°C. The pool water temperature was maintained at 0°C ± 2°C to best simulate the water temperatures to which a polar bear would normally be exposed (Weller, 1976).

2.2.7 Statistical Treatment

Regressions, elucidating the proportional relationships between different variables, were obtained by determining the best fit of a line by simple linear regression (Zar, 1973). All regressions were considered significant at the $p \leq 0.05$ level using the F test unless otherwise stated.

Students-t tests and analysis of variance were employed for testing both paried and unpaired series of samples (Snedecor and Cox, 1967; pp. 114-116). Statistical significance, unless otherwise stated, was tested at the 0.05 level of significance. Mean values in the text are followed by the value for 1 S.D. (e.g. 1.87 ± 0.13).

Symbols and units used in this thesis conform wherever possible to those recommended by the International Union of Physiological Sciences (Bligh and Johnson, 1973).

2.3 RESULTS

2.3.1 Oil Contact

Oil rapidly contaminated all fur coming in contact with the water-oil surface of the pool. The oil coating was distributed unevenly initially, but became more generally distributed over and into the fur in the days following exposure. Much oil was lost through shaking and grooming and also to sawdust within the respiration chamber.

The oil coating was of a substantial but not fully quantifiable amount. Following each of the first two trials, the thickness of the remaining surface slick was measured. The calculated discrepancies in volume corresponded to a loss of 23 and 28 liters of oil after immersion of bears 2 and 4 respectively. Weight increases as measured from pre oil to 2 days post oil were 9, 21 and 27 kg for bears 2, 3, and 4 respecitvely. At this time they were placed in the respiration chamber to which a quantity of snow and sawdust had been added. The measured weight loss during the 3 days in

the chamber were 14, 25, and 24 kg for animals 2, 3, and 4 respectively (Fig. 4).

2.3.2 Behaviour

Activity: All animals had been habituated to cages and spent most of the time under observation either resting or sleeping. During wind tests, the bears spent more time in a curled, metabolically efficient posture as described by Øritsland (1970). High activity levels were confined to the hours immediately after oil exposure and were followed by a general listlessness. Bear 3 was the most active animal. Although they were generally subdued post-oiling, the bears frequently shifted their position. The net result was that, in the post-washing observation period at least (Table II), all bears spent significantly less time sleeping than prior to oil exposure.

Grooming: The wind cage was cleaned of oil between trials. Enough oil residue remained, however, to cause minor contamination of the paws of the 2nd and 3rd experimental animals. Both of these bears groomed extensively before entering the pool (Fig. 5). After exiting the pool, all animals commenced actively licking oil from their paws, forelegs, and occasionally from the steel floor. They continued intensively ingesting oil for at least 6 hours. Grooming was interrupted frequently by active shaking.

On occasion bear 4 rubbed actively against the cage floor and walls. With this exception, the animals did not use the snow provided to clean their fur. The amount of time engaged in grooming during the 2 day post-

FIGURE 4 Body Weights During the 5 Month Holding Period

The body weights of the 3 polar bears during the 5 month holding and experimental period at the Churchill laboratory. The substantial increase in weight following oil exposure provides a crude estimate of the amount of oil (in kg) taken up in the fur.

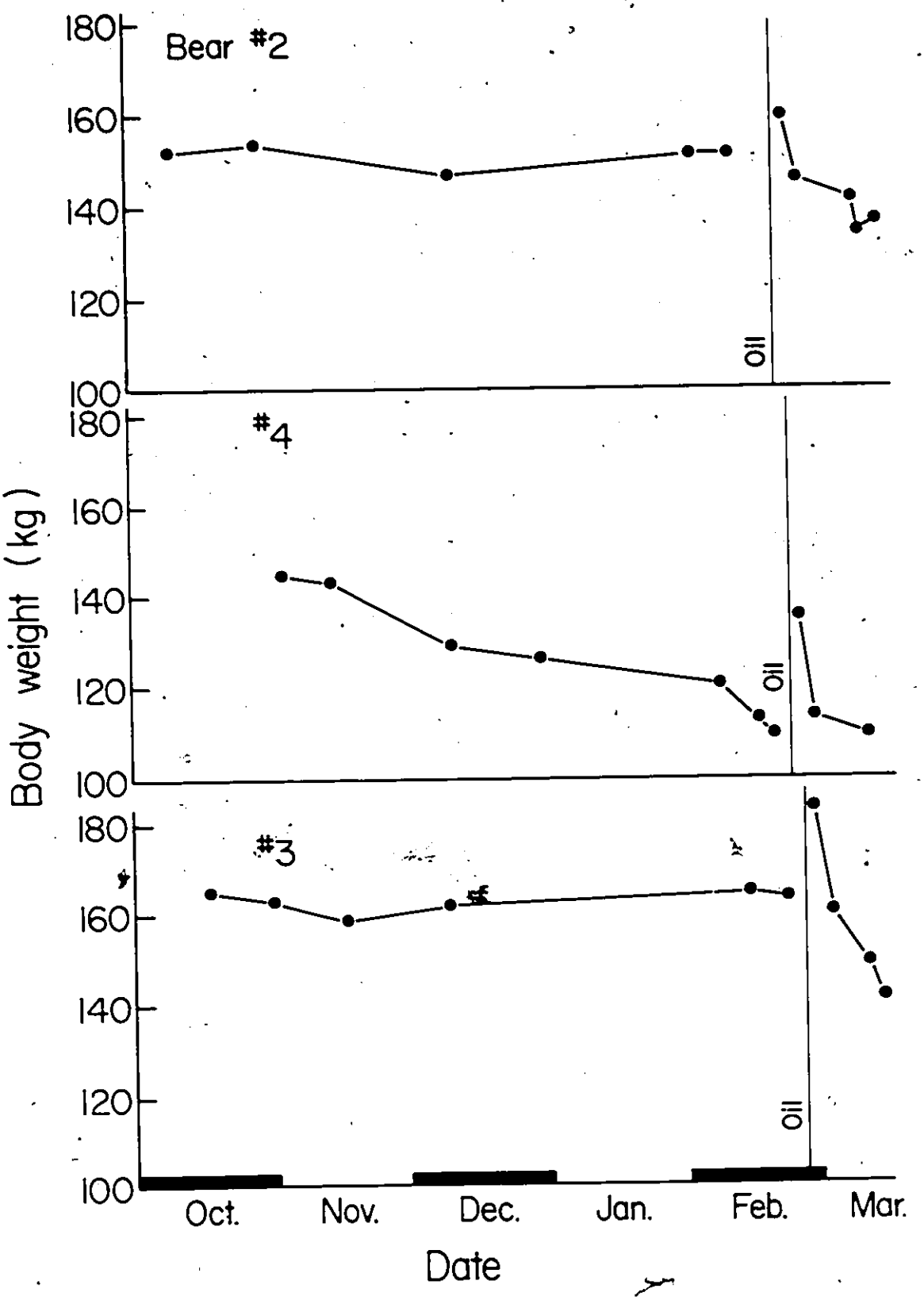

Bear #2
#4
#3
180
160
140
120
100
Oil
Body weight (kg)
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.
Date

TABLE II

WIND CAGE ACTIVITY

	Pre-oil		Post-oil		Post-wash	
Bear	Activity	% sleep	Activity	% sleep	Activity	% sleep
2	1.15 ± 0.27 (96) [a] [b]	54	1.25 ± 0.30 (171)	42	1.19 ± 0.23 (96)	39
4	1.28 ± 0.39 (96)	42	1.25 ± 0.27 (163)	40	1.18 ± 0.20 (96)	22
3	1.30 ± 0.39 (110)	50	1.51 ± 0.31 (155)	16	1.11 ± 0.15 (96)	31
$\bar{X}$	1.24 ± 0.31 (302)	49	1.35 ± 0.35 (489)	33	1.16 ± 0.20 (288)	31

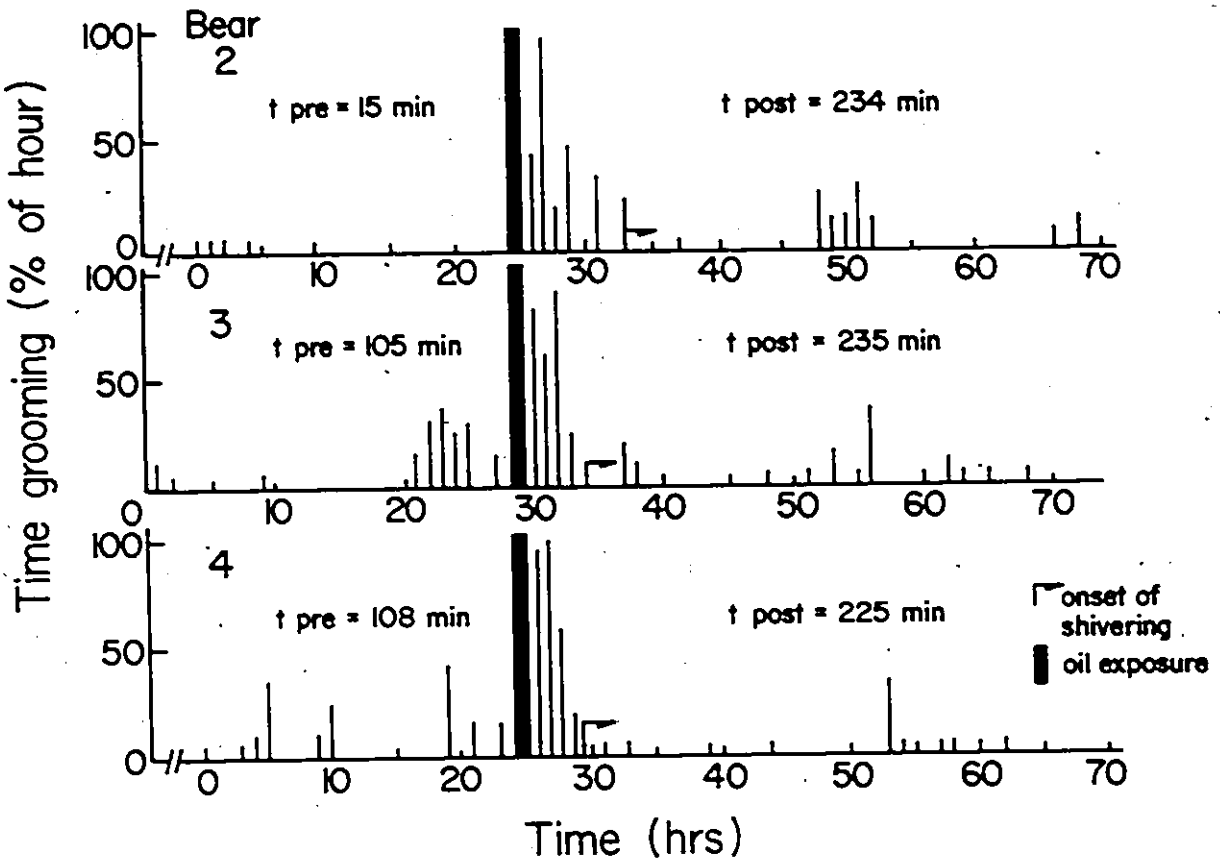
a) activity levels determined from continuous behavioural observations and assignment of activity coefficients ranging from 1.0 (lying, asleep) to 2.2 (active, aggressive).

b) sample size (in brackets) refers to the number of 15 minute intervals under observation.

c) pre-oil observations were made during the 24 to 29 hours immediately preceeding oil contact; post-oil observations were made in the 39 to 43 hours immediately following contact; and post-wash observations were conducted over 24 hours beginning 3 days after washing the fur, or 20 days after oil contact.

FIGURE 5 Grooming Behaviour During Observation in Wind Cage

The grooming behaviour of 3 polar bears during 68 hours of continuous observation in the wind cage. The amount of time spent licking the fur, both pre and post-oil, is indicated in minutes and percent of total time. Oil remnants on the cage structure appeared to influence the time engaged in licking by bears 3 and 4 before oil immersion. Shivering began within 8 hours of exposure and continued throughout the observation period.


Bear
2
t pre = 15 min
t post = 234 min
3
t pre = 105 min
t post = 235 min
4
t pre = 108 min
t post = 225 min
onset of shivering
oil exposure
Time grooming (% of hour)
Time (hrs)
100
50
0
0
10
20
30
40
50
60
70

oil observation period was remarkably consistent. The times were 235 (9.1%), 225 (8.7%), and 234 (10.0%) minutes for bears 2, 4, and 3 respectively. Under 24 hours of observation following washing (20 days post-oil) bears 2 and 4 did not groom at all, while bear 3 licked its front paws for 37 minutes or 2.4 percent of the observation period.

Shivering, which was not noticed in pre-oil observations, began in all bears within 8 hours of oil fouling and continued throughout the observation period. Vomitus and faeces, collected from 12 hours post-oil to the end of observations 4 weeks post-oil, contained large quantities of oil (Engelhardt, 1981). All animals were anorexic for the 4-5 weeks after oil ingestion with some exception in bear 2 which accepted food for the first week only. Activity and muscle co-ordination degenerated until the death of bears 4 and 3 approximately 4 weeks after contamination. Bear 2 recovered only after extensive veterinary care (See Juck in Øritsland et al., 1981).

2.3.3 Metabolism

Resting metabolism: Control values of resting metabolism, determined from the average of minimum daily oxygen consumption rates, were generally comparable with the weight specific basal matabolic rate (BMR) predicted by Kleiber (1975). The mean values of metabolism, using 25 measurements per day, were somewhat higher (Table III). In all cases and with all animals, there was a substantial increase in oxygen consumption following oil fouling. The increase in metabolic rate as a consequence of oiling averaged 50 percent and ranged from 25 percent in bear 2 to 85 percent in bear 4 (Fig. 6).

TABEL III. RESTING METABOLIC RATE

Bear #	Pred. BMR	[a] MINIMUM METAB. RATE (W) Before Oil	After Oil	Factor Change	[b] MEAN METAB. RATE (W) Before Oil	After Oil	Factor Change
2	148	138 ±34 (4)	206 ±06 (2)	1.49	189 ±32 (100)	240 ±16 (50)	1.27*
4	115	133 ±10 (4)	243 ±15 (3)	1.82*	160 ±12 (100)	299 ±51 (75)	1.86*
3	154	210 ±06 (2)	261 ±35 (4)	1.24	263 ±28 (50)	365 ±70 (100)	1.38
$\bar{X}$	-	-	-	1.52 (3)	-	-	1.50* (3)

Resting metabolic rate expressed in watts as determined by indirect calorimetry (ie. oxygen consumption) while enclosed in a respiration chamber.

a) Minimum metabolic rate determined as the mean of the daily lowest recorded MR. n (in brackets) refers to number of days sampled.

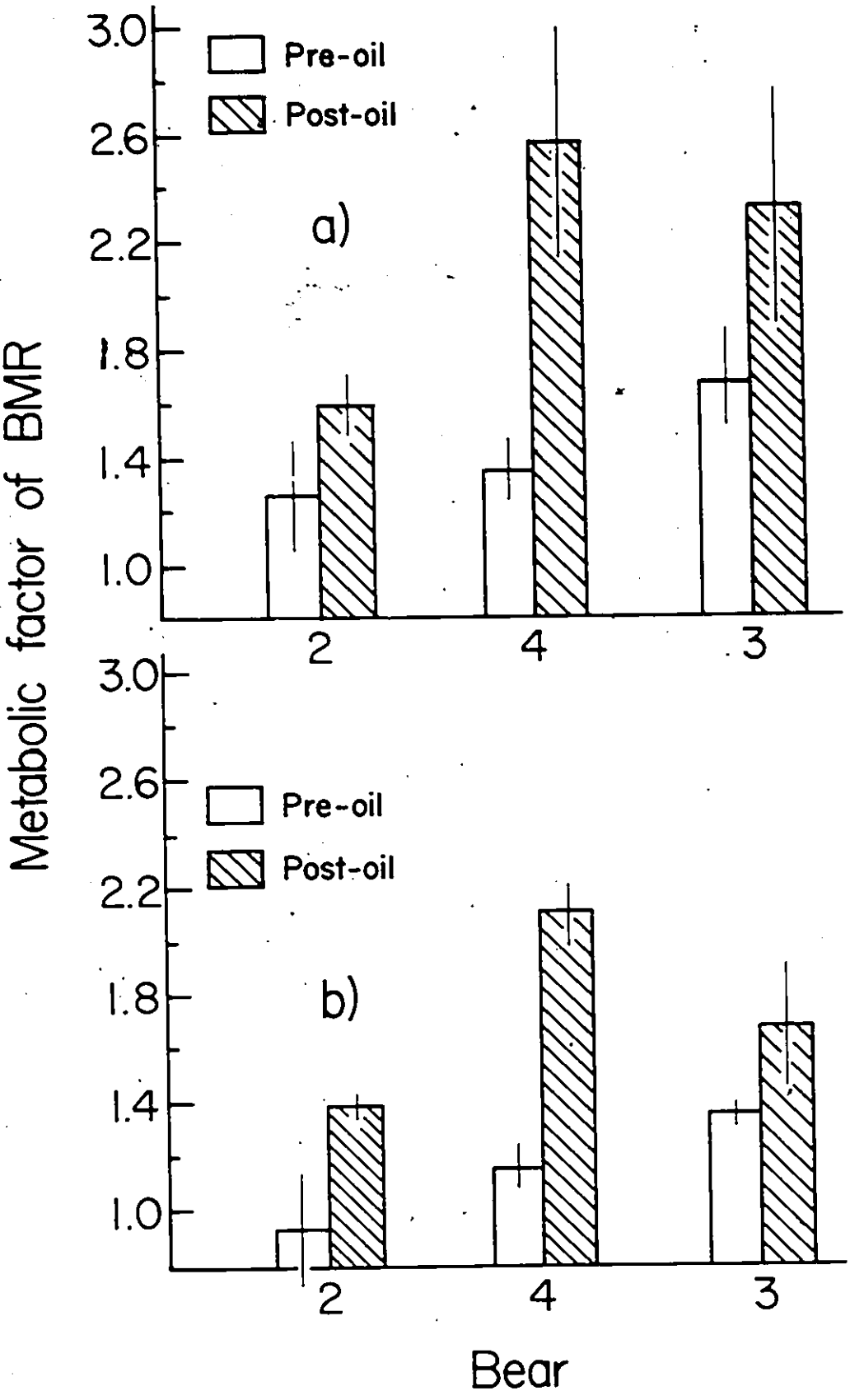
b) Mean metabolic rate determined as the overall mean of recorded MR wherein n (in brackets) refers to the number of samples taken at 5 minute intervals.

FIGURE 6 Resting Metabolic Rate Before and After Oil

Experimental resting metabolic rate (RMR) expressed as a factor of predicted basal metabolic rate (BMR), determined both before and after oil exposure. Vertical lines show 1 standard deviation of the mean.

a) Mean RMR determined over 2 to 4 days per bear at 25 measurements per day.

b) Average of the minimum daily recorded RMR.


Metabolic factor of BMR
3.0
2.6
2.2
1.8
1.4
1.0
Pre-oil
Post-oil
a)
2
4
3
b)
Bear

Activity Metabolism: Results of the weight specific oxygen consumption at a walking speed of 5.4 $km.h^{-1}$ are presented in Table IV. In an attempt to produce a general expression for the energy cost of locomotion of polar bears studied to date, modifications and extrapolations from the available data were made. The procedure was based on the general principles that metabolism increases linearly with walking speed (Taylor, 1977; Taylor et al., 1970) and the oxygen consumption at 0 running velocity (y-intercept) is 1.7 times resting metabolism, representing a postural cost of locomotion (Schmidt-Nielsen, 1972; Taylor et al., 1970).

Values corresponding to 5.4 $km.h^{-1}$ were derived from regression equations (Hurst et al., 1981; Øritsland et al., 1976). Straight lines were drawn from the data points to intersect the y-axis at 1.7 x BMR (Fig. 7). The total cost of locomotion for a range of body weights was then determined by plotting the slope of each line, or 'incremental cost of transport' (Taylor, 1977), against body mass (Fig. 8). This allowed me to develop an equation to predict the amount of energy required to move a unit mass through a unit distance. The slope or incremental cost of walking decreased with increasing body mass in a fashion best fit by the linear regression:

(1) $T_{walk} = 0.505 - 0.00157\ m$ $\quad ml\ O_2.g^{-1}.km^{-1}$

$r=0.98$; see$=0.02$; $p \leq 0.001$

where m is body mass in kg; r is regression correlation coefficient; see is the standard error of estimate; and p is the probability of no correlation.

Metabolic power (Taylor, 1977) is equal to slope times walking speed plus the postural cost of locomotion (y-intercept). The total metabolic

TABLE IV. EXERCISING POLAR BEARS: OXYGEN CONSUMPTION AND BODY TEMPERATURES.

Results were derived from polar bears exercising on a treadmill at a walking speed of 5.4 km.h^{-1}. ΔTb refers to the change in deep body temperature from before to after 30 minutes of walking. Metabolism, measured by open circuit respirometry, was taken as the plateau level of oxygen consumption in the final 10 minutes of each test. n refers to the number of tests. Results of this study (source 1) are compared to those of previous studies conducted with polar bears on the same Churchill treadmill. The y-intercept and 'cost' were derived using techniques described by Taylor (1977) and Taylor et al. (1970).

Age (yrs)	Sex	Mass (kg)	T_a (°C)	V (km.hr^{-1})	At v = 5.4 km.hr^{-1} ΔT_b n	ΔT_b (°C)	Metabolism n	Metabolism (ml O_2.g^{-1}.hr^{-1})	y-int	Cost (ml O_2.g^{-1}.km^{-1})	Source
2	M	110	-17to-13	5.4	4	2.20	4	2.11 ± 0.1	0.325	0.33	1
3	F	154	-19 -11	"	6	1.38	6	1.68 ± 0.04	0.299	0.25	1
2	M	163	-22 -18	"	3	1.50	3	1.77 ± 0.1	0.295	0.26	1
4	F	190	-25 -16	1.8-7.2	28	0.60	19	1.29 -	0.284	0.21	2
4	M	235	-11 -5	2.5-6.0	-	-	13	1.03 -	-	0.14	3
3	M	218	-32 7	4.0-7.9	111	0.61	-	- -	-	-	4
4	M	239	-38 -4	4.0-7.9			-	- -	-	-	4

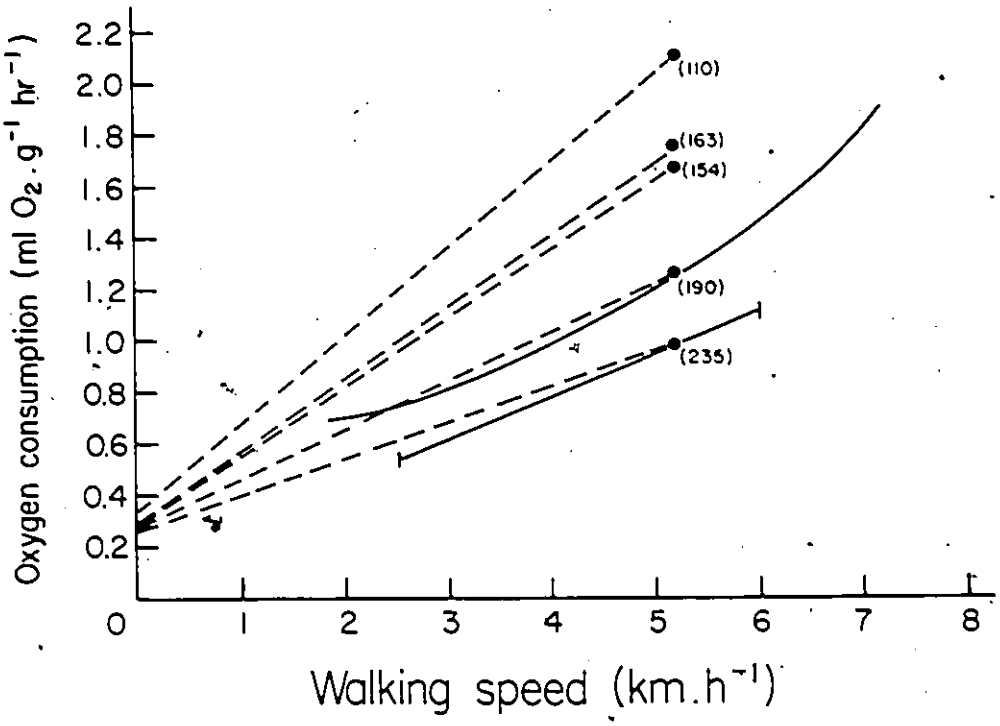
Sources of data: 1- this study; 2- Hurst et al., 1981; 3- Øritsland et al, 1976; 4- Best et al, 1981.

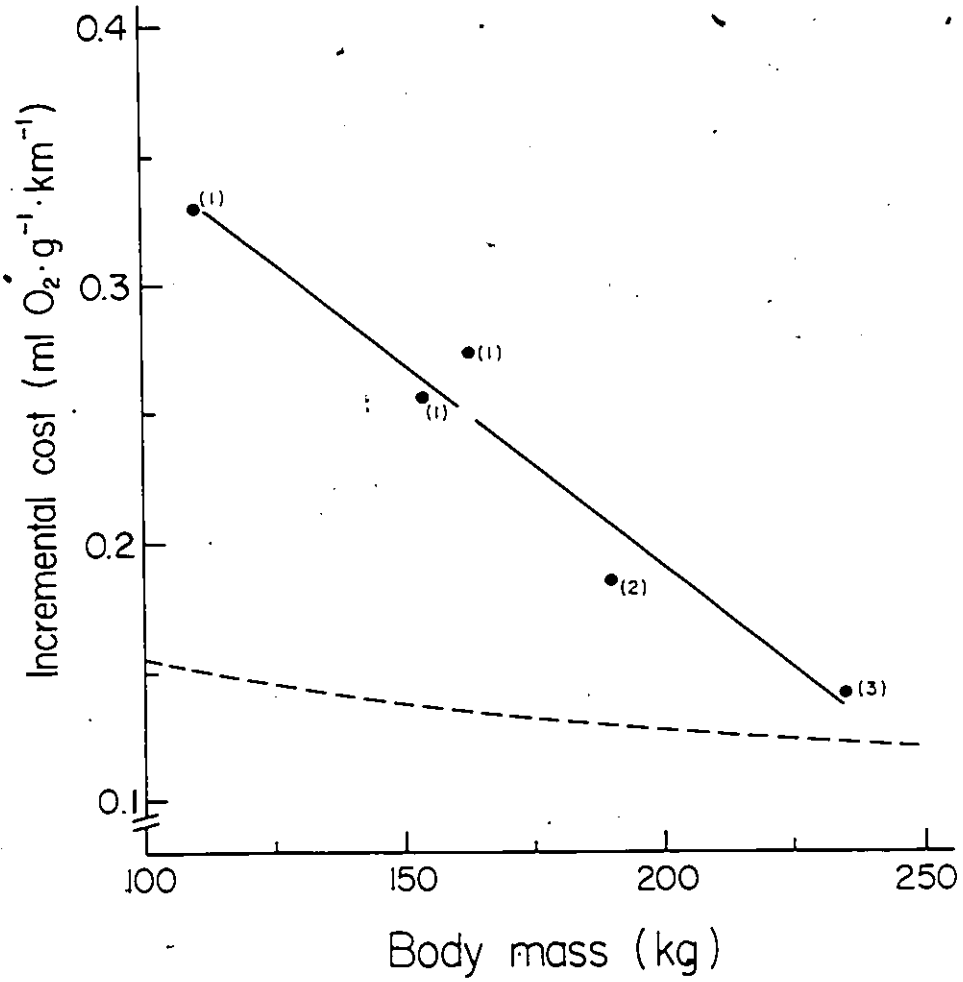
FIGURE 7 Oxygen Consumption vs Walking Speed

Weight specific oxygen consumption plotted as a function of walking speed. Solid lines and points are experimental values. Body weights are placed in brackets and extrapolations to 1.7 times resting metabolism are presented with broken lines. See Table IV for sources of data.

FIGURE 8 Cost of Locomotion vs Body Mass

Incremental costs of locomotion (T_{walk}), or the slopes of the linear relationships between oxygen consumption and walking speed are represented by a solid line. Incremental cost as predicted by Fedak et al., (1979) is represented by the broken line. Sources of data are: 1-this study; 2-Hurst et al., (1981); 3-Øritsland et al., (1976).


Oxygen consumption (ml $O_2 \cdot g^{-1} hr^{-1}$)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
1
2
3
4
5
6
7
8
(110)
(163)
(154)
(190)
(235)
Walking speed ($km.h^{-1}$)


Incremental cost (ml $O_2 \cdot g^{-1} \cdot km^{-1}$)
0.4
0.3
0.2
0.1
(1)
(1)
(1)
(2)
(3)
100
150
200
250
Body mass (kg)

power of walking (W_{walk}) can then be predicted from a bear's body mass and walking speed such that:

(2) $W_{walk} = (0.505-0.00157\ m)v + 1.056\ m^{-0.25}$ ml $O_2.g^{-1}.km^{-1}$

where m is body mass in kg; and v is the walking speed in $km.h^{-1}$.

Comparative results of exercise metabolism, before and after oiling were obtained for bear 2 only. Mean oxygen consumption, as measured in the final 12 minutes of each test, were 1.68 ± 0.4 ml $O_2.g^{-1}.h^{-1}$ versus 2.10 ± 0.2 ml $O_2.g^{-1}.h^{-1}$ pre-oil and post-oil exposure respectively. This constituted an average increase in the energetic cost of walking of 24 percent (Fig. 9). In the initial post-oil treadmill trial of bears 4 and 3, the animals were unwilling or incapable of continuing to walk. Mechanical failure prevented further exercise testing of bears 4 and 3.

2.3.4 Temperatures

Oil Contact: The response in deep body temperature (T_b) during immersion in the pool is presented in Fig. 10. The T_b rose on opening of the cage door, during activity prior to entering the pool, and for the 1st 5 minutes of immersion. This was followed by a rapid and consistent drop in T_b to as low as 34.7°C at a rate of 2.9 to 4.8°C.hr^{-1}. The position of the skin transmitters, in the lateral neck area, assured that the area did not directly contact the water-oil surface. The skin temperature of the rump of Bear 3 (T_r) dropped considerably from 35°C to 20°C during the 53 minute immersion time (Fig. 11).

FIGURE 9 Oxygen Consumption, Exercise Pre and Post-Oil

The weight specific oxygen consumption of bear 2 during 30 minutes of exercise at 5.4 $km.h^{-1}$. Post-oil oxygen consumption values averaged 24 percent higher than pre-oil values.

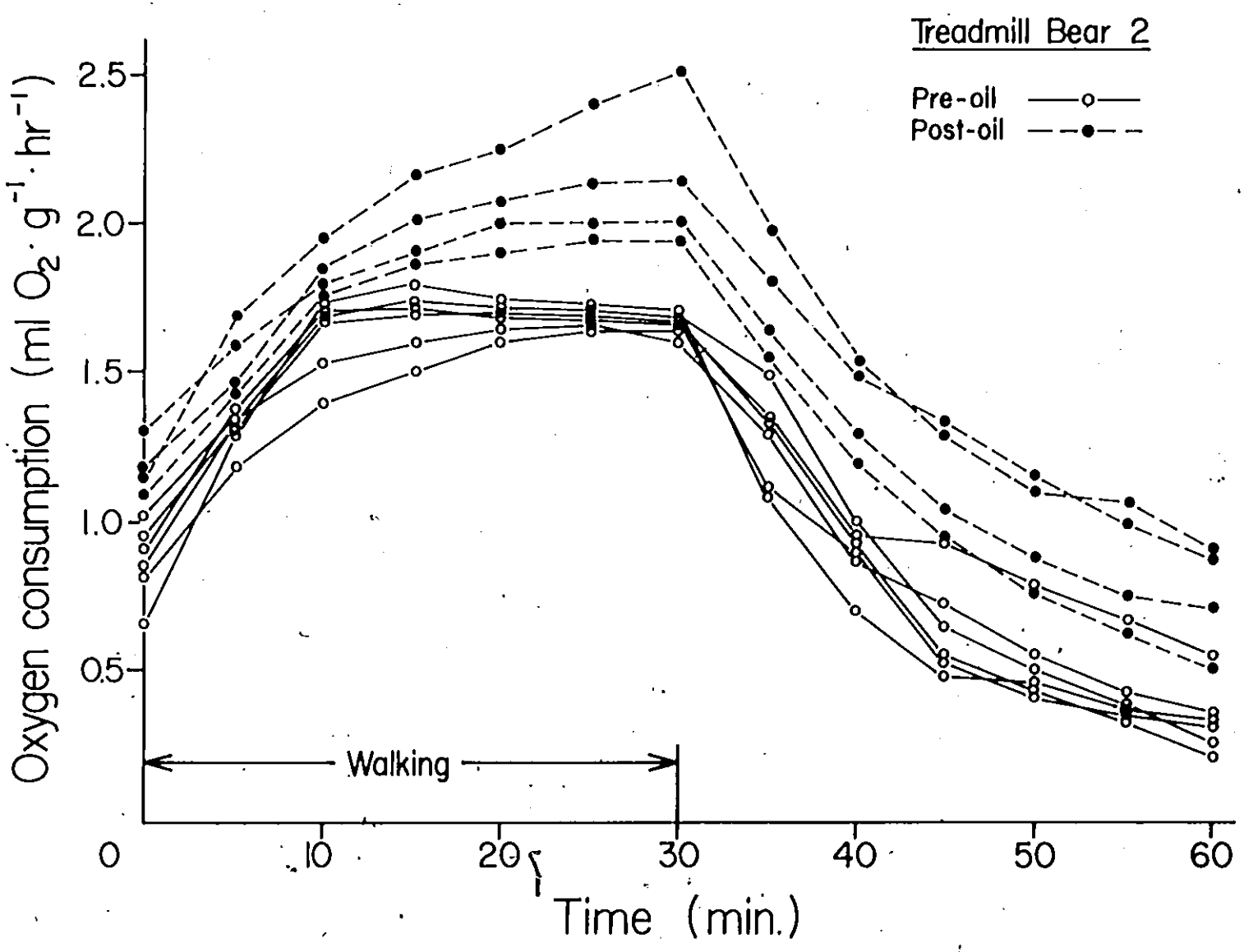
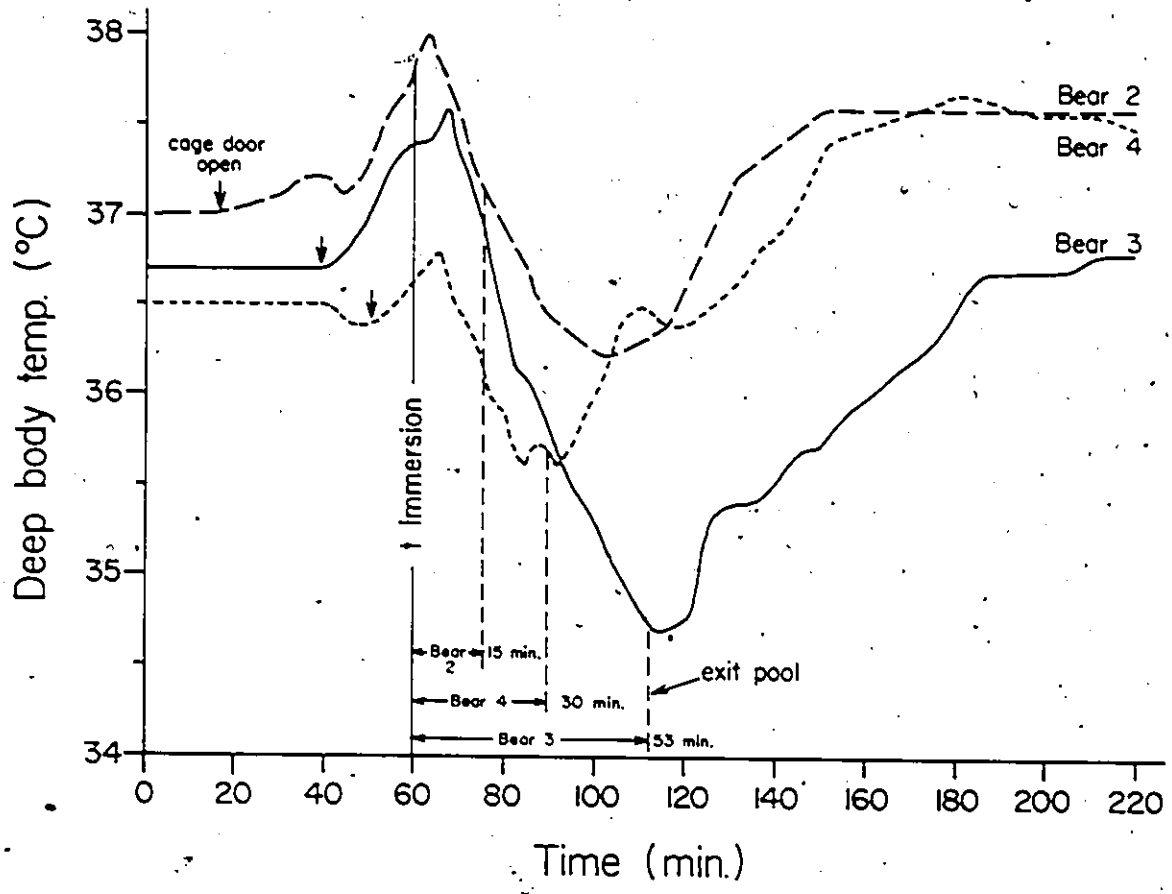

Treadmill Bear 2
Pre-oil
Post-oil
Oxygen consumption (ml $O_2 \cdot g^{-1} \cdot hr^{-1}$)
2.5
2.0
1.5
1.0
0.5
Walking
0
10
20
30
40
50
60
Time (min.)

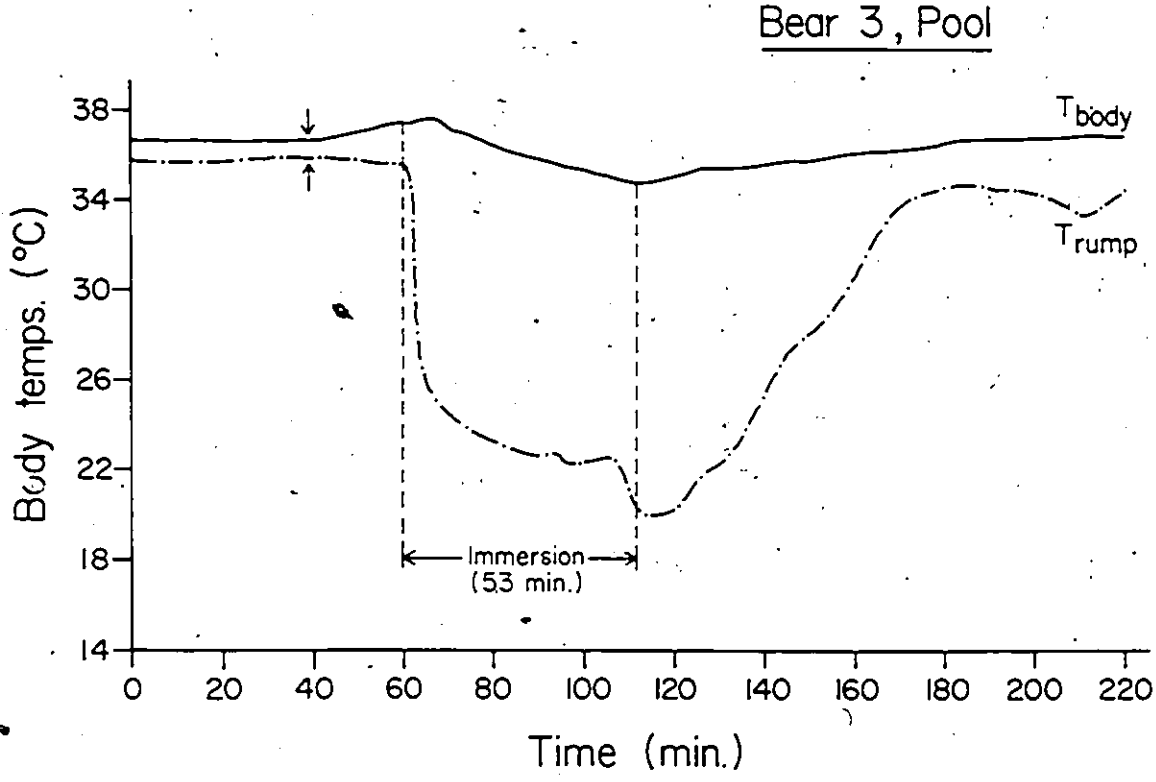
FIGURE 10 Water Immersion, T_b of All Bears

Deep body temperature (T_b) of bears during immersion in a 6,800 l pool. The water was held at a temperature of 0±2°C and was covered with a 1 cm slick of crude oil.

FIGURE 11 Water Immersion, T_b and T_r of Bear 3

Deep body temperature (T_b) and rump temperature (T_r) of bear 3 before, during, and after a 53 minute period in the pool.


Deep body temp. (°C)
38
37
36
35
34
cage door open
Immersion
Bear 2
Bear 4
Bear 3
Bear 2 15 min.
Bear 4 30 min.
Bear 3 53 min.
exit pool
0
20
40
60
80
100
120
140
160
180
200
220
Time (min.)


Bear 3, Pool
Body temps. (°C)
38
34
30
26
22
18
14
Tbody
Trump
Immersion (53 min.)
0
20
40
60
80
100
120
140
160
180
200
220
Time (min.)

Wind: Wind caused a consistent and significant drop in skin temperature in all animals (Table V; Fig. 12). It was most apparent in bear 4. Deep body temperatures of bears 2 and 4 showed no significant change immediately following oil exposure, whereas bear 3 demonstrated a precipitous drop in T_b in the final hours of the observation period (Figs. 13, 14). Skin temperatures of all animals increased significantly following oil contamination.

Only 3 of the 6 implanted temperature transmitters continued to function by the final series of wind cage measurements 20 days after oil contact. In bears 4 and 3 with functioning T_b transmitters, T_b dropped significantly in wind tests by 1.91°C and 0.82°C respectively. Skin temperatures in bear 4 were also lower than in control measurements (Table V).

Resting Metabolism: Deep body temperatures of bears 2 and 4 increased following exposure, whereas bear 3 again showed a signifcant drop in T_b. Skin temperatures increased in all cases following oiling although the rise was less apparent in bear 3. See Table V.

Daily recordings throughout a 4 week period reflected a trend of increased skin and body temperatures for the week after oil contamination, followed by a marked drop during the final two weeks of monitoring (Fig. 15). Bear 3 was an exception in that body temperatures began to drop within 24 hours of oiling and remained low for the remainder of the experiment.

TABLE V. BODY TEMPERATURES WITHIN WIND CAGE

Mean deep body temperatures (Tb) and skin temperatures (Ts) of 3 polar bears. Wind was instituted in alternating 4 hour periods. Observations were made at 15 min intervals in the 24-29 hours immediately preceeding oil contact; the 39-43 hours immediately following contact; and over 24 hours beginning 3 days after washing of the fur, or 20 days after oil contact.

a) WIND vs NO WIND

Bear #	Body Temp. (T_b) No wind	Wind	Change	Skin Temp. (T_s) No Wind	Wind	Change
2	36.9 ±0.35 (151)[a]	36.9 ±0.47 (116)	0	37.1 ±0.70 (151)	36.8 ±0.66 (116)	-0.28*
4	36.7 ±0.37 (132)	36.7 ±0.34 (127)	-0.04	34.7 ±0.72 (116)	32.5 ±2.21 (127)	-2.17*
3	36.1 ±0.82 (137)	35.5 ±1.11 (127)	-0.38*	35.5 ±0.87 (131)	35.3 ±0.78 (103)	-0.22*
$\bar{X}$	36.7 ±0.59 (420)	36.5 ±0.81 (370)	-0.16	35.9 ±1.27 (398)	34.8 ±2.34 (346)	-0.79*

b) BEFORE OIL vs AFTER OIL

Bear #	Body Temp. (T_b) Before Oil	After Oil	Change	Skin Temp. (T_s) Before Oil	After Oil	Change
2	36.9 ±0.21 (96)	36.9 ±0.48 (171)	+0.05	36.4 ±0.69 (96)	37.3 ±0.43 (171)	+0.90*
4	36.6 ±0.29 (96)	36.7 ±0.38 (163)	+0.11	32.9 ±2.09 (96)	34.0 ±1.81 (147)	+1.05*
3	36.8 ±0.28 (110)	35.8 ±1.10 (154)	-1.00*	34.9 ±1.2 (79)	35.7 ±0.43 (155)	+0.77*
$\bar{X}$	36.8 ±0.29 (302)	36.5 ±0.85 (487)	-0.30	34.7 ±2.05 (278)	35.7 ±1.70 (487)	+0.96*

c) BEFORE OIL vs AFTER WASHING

Bear #	Body Temp. (T_b) Before Oil	After Wash	Change	Skin Temp. (T_s) Before Oil	After Wash	Change
2	-	-	-	-	-	-
4	36.6 ±0.29 (96)	34.7 ±0.91 (99)	-1.91*	32.9 ±2.09 (96)	31.4 ±1.81 (89)	-1.50*
3	36.8 ±0.28 (110)	36.0 ±0.43 (71)	-0.82*	-	-	-
$\bar{X}$	36.73±0.22 (110)	35.26±0.73 (170)	-1.47*	32.9 ±2.09 (96)	31.4 ±1.81 (89)	-1.50*

FIGURE 12 Wind Chamber Results, Continuous Recordings of T_s

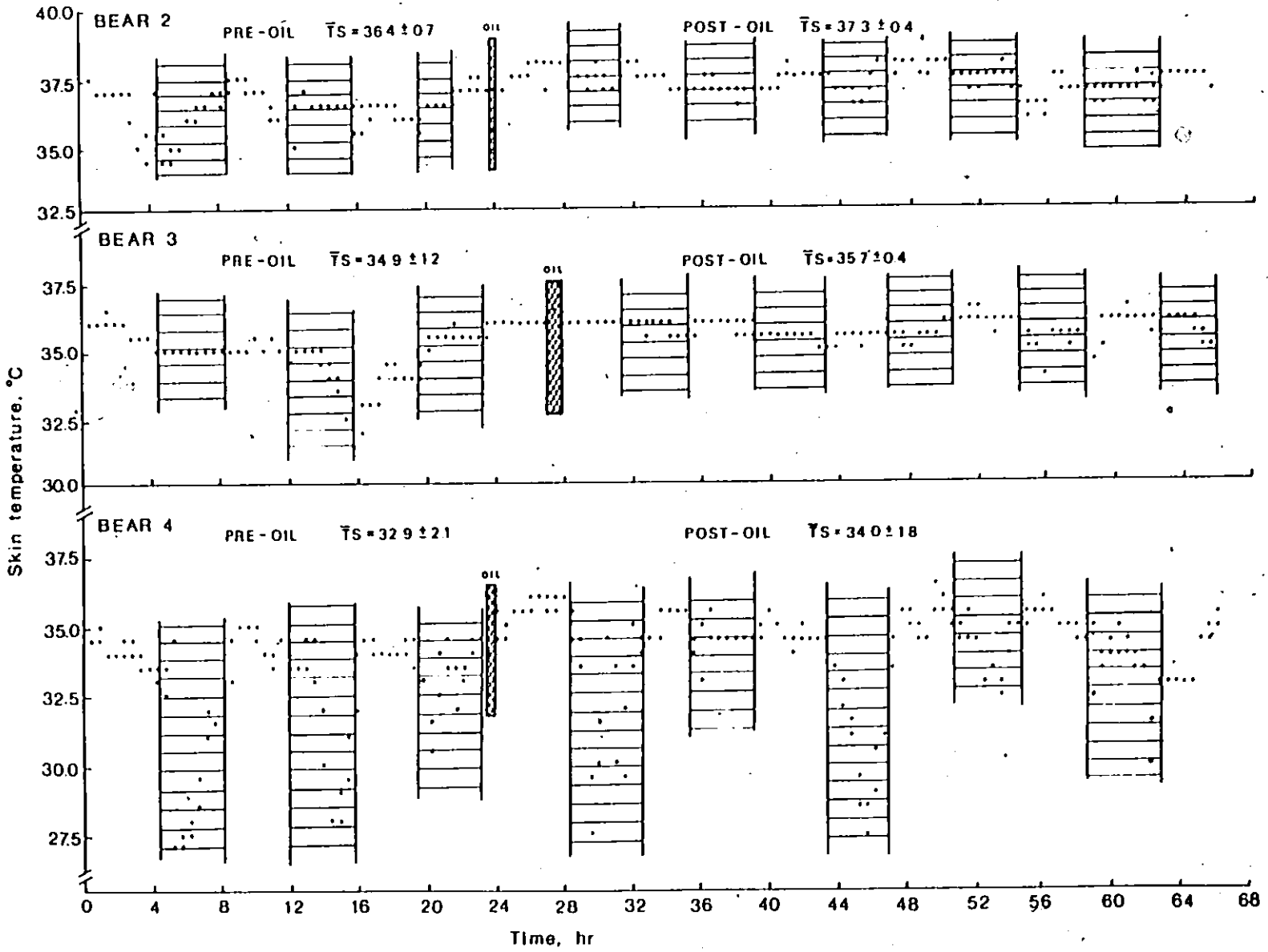
Wind chamber results illustrating fluctuations in skin temperature (T_s) over a 68 hour period, including both pre and post-oil observation. Dots show T_s values recorded at 15 minute intervals. Bears were exposed to 4 hour alternating periods of 5 $m.s^{-1}$ wind (hatched) and no wind (open). Mean temperatures (T_s) and standard deviations (±) are included for both before and after oiling.

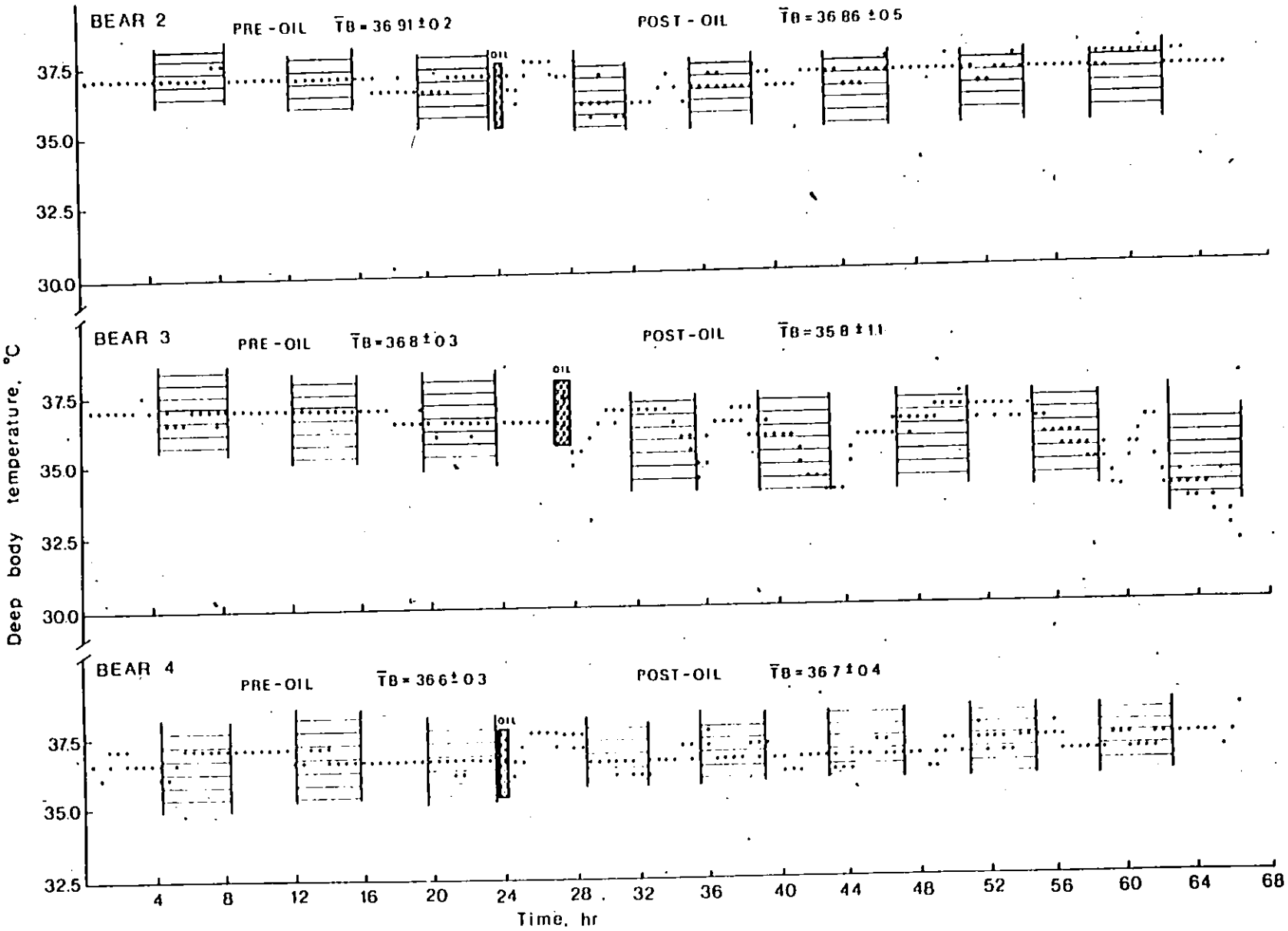
FIGURE 13 Wind Chamber Results, Continuous Recordings of T_b

Wind chamber results illustrating fluctations in deep body temperatures (T_b) over a 68 hour period. Legend is the same as above (Fig. 12).

FIGURE 14 Wind Chamber Results, T_b in Bear 3

Wind chamber results illustrating fluctuations in body temperature (T_b) over a 68 hour period. The results for bear 3 are presented separately to illustrate the precipitous drop in T_b in the final hours of observation.


BEAR 2
PRE-OIL $\bar{T}S = 36.4 \pm 0.7$
OIL
POST-OIL $\bar{T}S = 37.3 \pm 0.4$
BEAR 3
PRE-OIL $\bar{T}S = 34.9 \pm 1.2$
OIL
POST-OIL $\bar{T}S = 35.7 \pm 0.4$
BEAR 4
PRE-OIL $\bar{T}S = 32.9 \pm 2.1$
OIL
POST-OIL $\bar{T}S = 34.0 \pm 1.8$
Skin temperature, °C
40.0
37.5
35.0
32.5
30.0
27.5
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
Time, hr


BEAR 2
PRE-OIL $\bar{T}B = 36.91 \pm 0.2$
POST-OIL $\bar{T}B = 36.86 \pm 0.5$
OIL
BEAR 3
PRE-OIL $\bar{T}B = 36.8 \pm 0.3$
POST-OIL $\bar{T}B = 35.8 \pm 1.1$
OIL
BEAR 4
PRE-OIL $\bar{T}B = 36.6 \pm 0.3$
POST-OIL $\bar{T}B = 36.7 \pm 0.4$
OIL
Deep body temperature, °C
37.5
35.0
32.5
30.0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
60
64
68
Time, hr

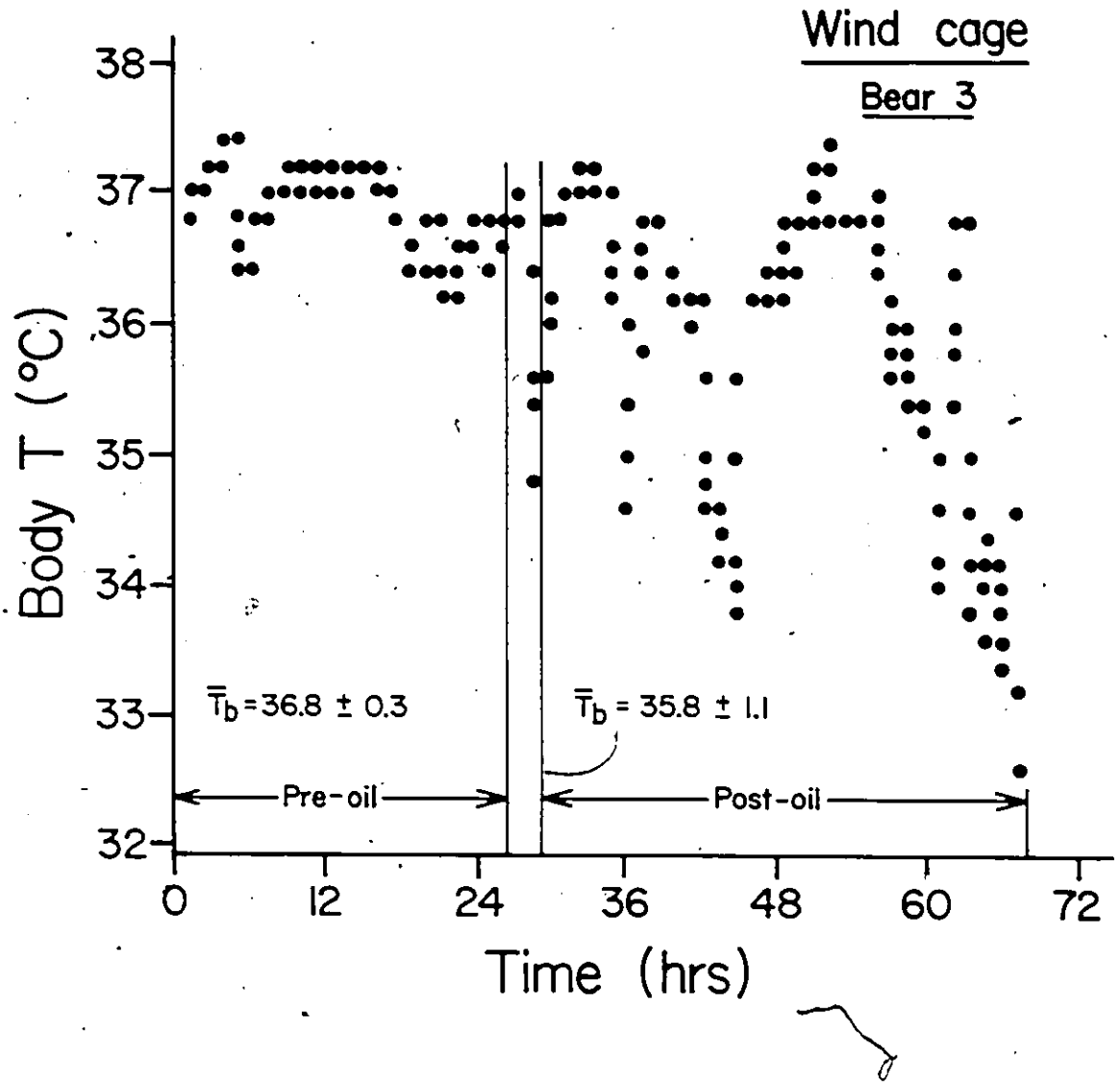
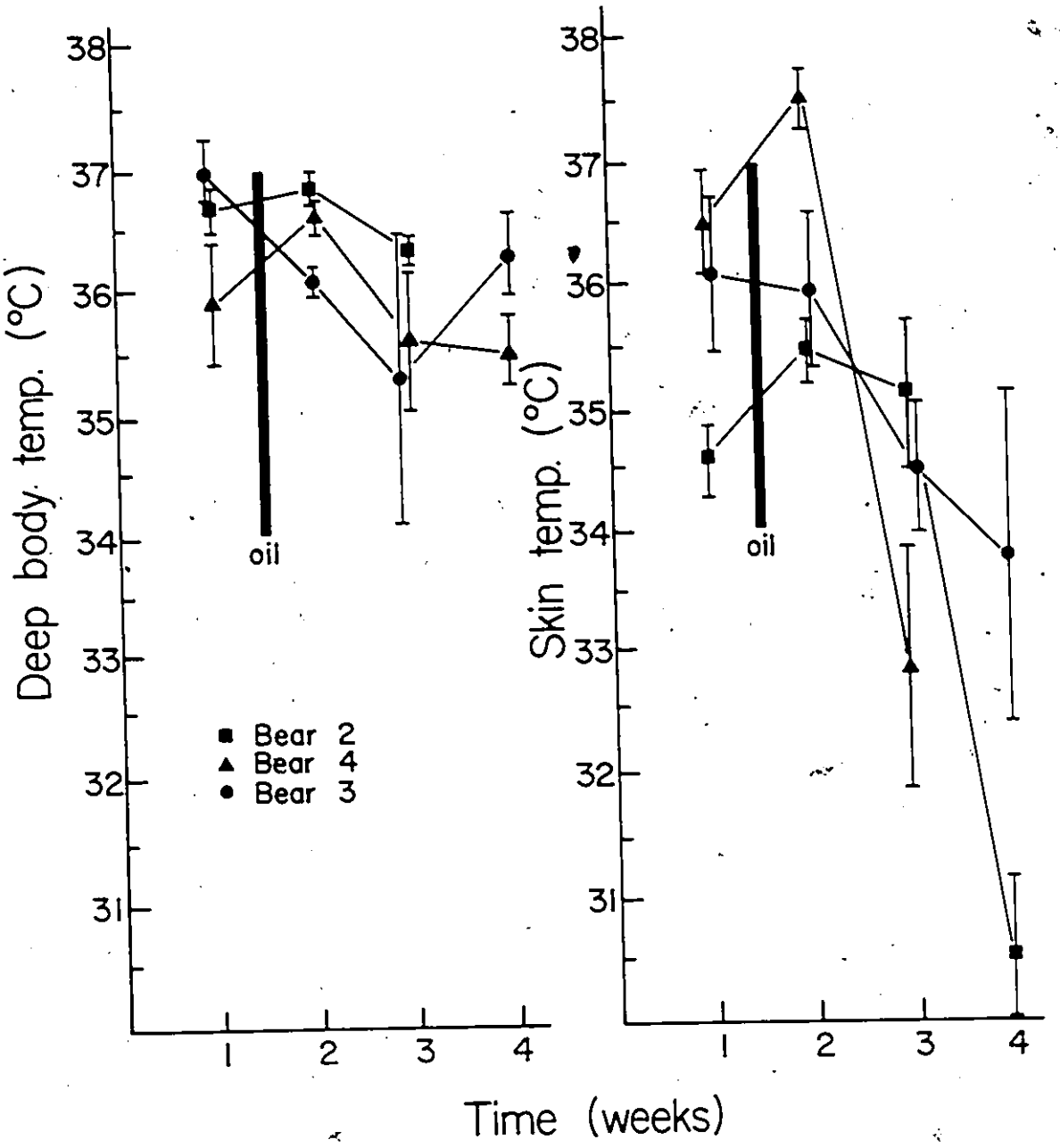

Wind cage
Bear 3
Body T (°C)
38
37
36
35
34
33
32
$\bar{T}_b$ = 36.8 ± 0.3
$\bar{T}_b$ = 35.8 ± 1.1
Pre-oil
Post-oil
0
12
24
36
48
60
72
Time (hrs)

FIGURE 15 T_b and T_s Over a 4 Week Period, All Bears

The deep body temperature (T_b) and skin temperature (T_s) were monitored over a 4 week period. Points represent the mean weekly temperatures calculated from health record measurements taken, at comparable times of the day, twice daily. Vertical lines represent 1 standard deviation of the mean. Only 4 of the 6 implanted temperature transmitters continued to function by week 4.


Deep body temp. (°C)
Skin temp. (°C)
38
37
36
35
34
33
32
31
oil
oil
Bear 2
Bear 4
Bear 3
1
2
3
4
Time (weeks)

Active Metabolism: A regression of oxygen consumption on the increase in T_b was made, using control measurements only, to explore the possible use of body temperature as a correlate of energy expenditure (Gessaman, 1980; Kautz, 1978). Data from other studies (Best et al., 1981; Hurst et al., 1981) was again combined with the results of this study. The increase in deep body temperature as a consequence of walking at 5.4 $km.h^{-1}$ was much less in the larger animals (Table IV, Fig. 16). A regression of oxygen consumption on the increase in T_b yielded the equation:

(3) $W = 0.987 + 0.516T_b$ $\quad ml\ O_2.g^{-1}.h^{-1}$

$r=0.88$; see=0.33; $p \leq 0.001$

where T_b = increase in body temperature as a result of walking (Fig. 17).

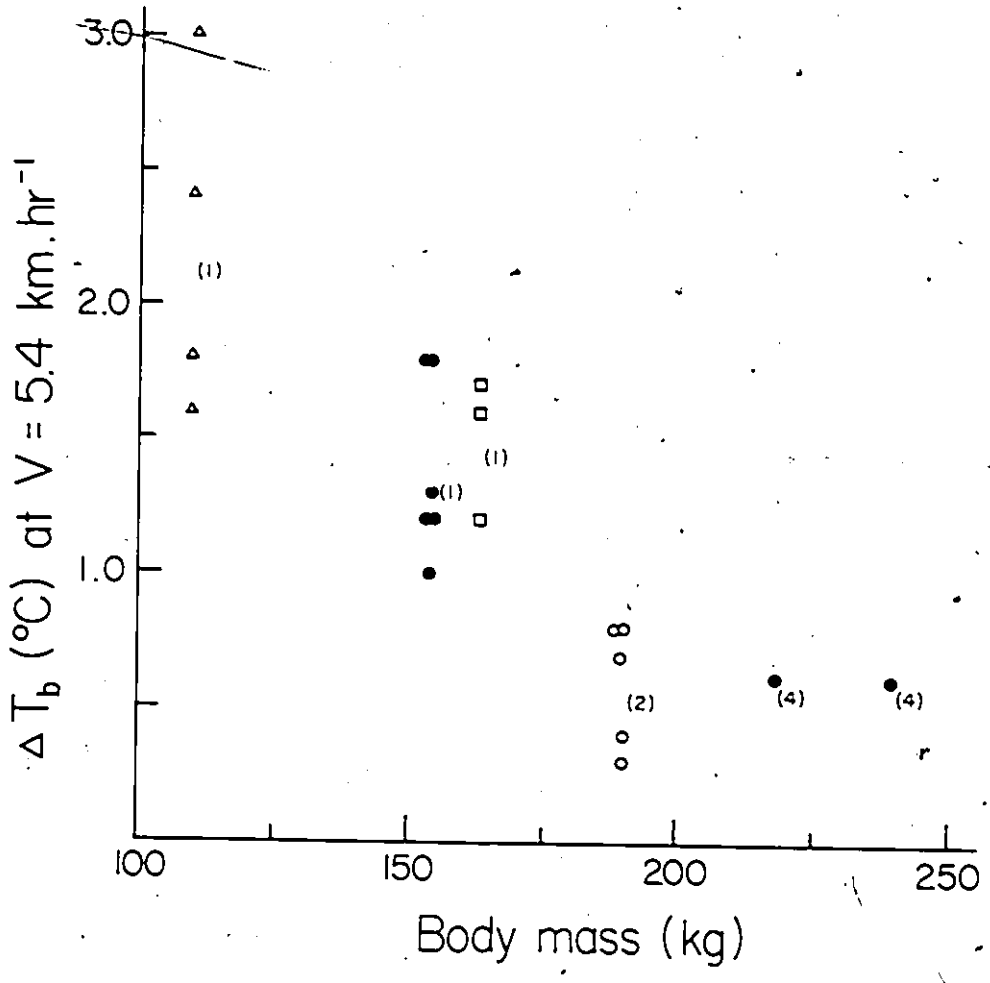
Deep body temperatures in bear 2 prior to exercise averaged slightly higher in the trials after oil contamination. The increase as a consequence of exercise was also higher at 1.92°C post-oil versus 1.34°C pre-oil exposure (Fig. 18). Post-oil skin temperature information, limited to one trial, also demonstrated a higher pre-test value but the increase as a result of exercise was less than controls, reaching approximately the same level. Regressions of skin temperature (T_s) and rump temperature (T_r) on body temperature (T_b) during exercise tests are presented in Table VI and Figs. 19 and 20.

FIGURE 16 Rise in T_b vs Body Mass, During Exercise

The change in deep body temperature (ΔT_b) expresed as a function of body mass. All body temperature changes follow treadmill exercise at a walking speed of 5.4 $km.h^{-1}$. Sources of data (in brackets) are: 1-this study; 2-Hurst et al. (1981); 4-Best et al. (1981).

FIGURE 17 Oxygen Consumption vs ΔT_b, During Exercise

Regression of weight specific oxygen consumption on the change in body temperature (Eqn. 3) as a result of 30 minutes exercise at a speed of 5.4 $km.h^{-1}$. Sources of data, in brackets, are: 1-this study; 2-Hurst et al. (1981).


3.0
2.0
1.0
ΔT_b (°C) at V = 5.4 km.hr^{-1}
(1)
(1)
(1)
(2)
(4)
(4)
100
150
200
250
Body mass (kg)

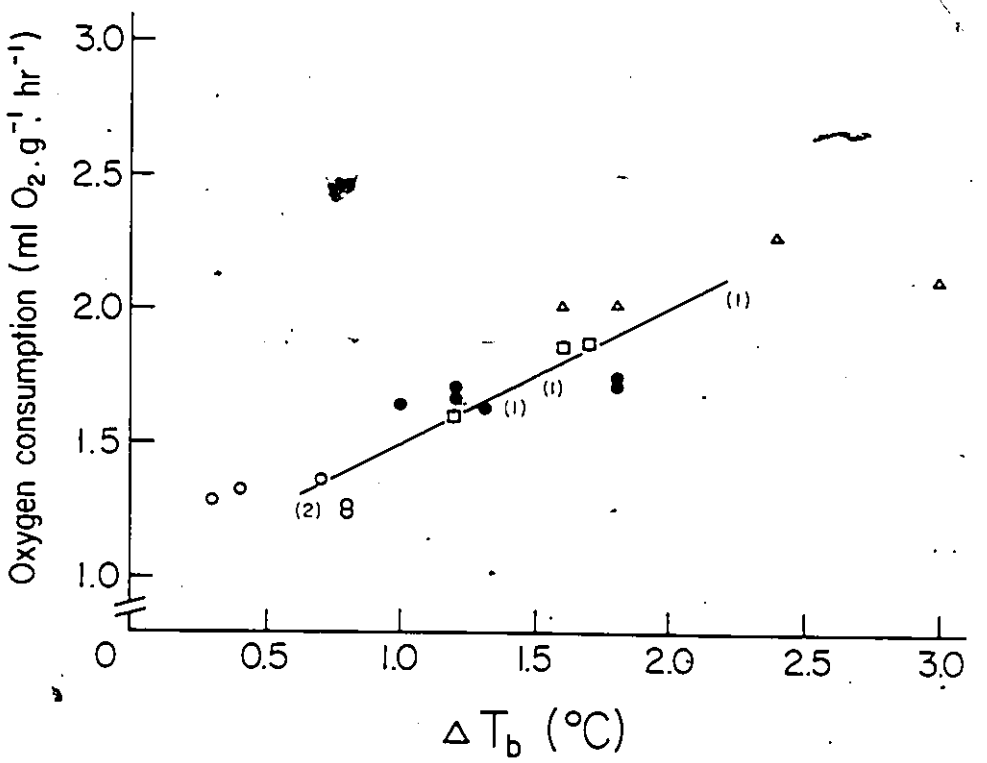

3.0
2.5
2.0
1.5
1.0
0
Oxygen consumption (ml O_2.g^{-1}.hr^{-1})
(1)
(1)
(1)
(2)
0.5
1.0
1.5
2.0
2.5
3.0
ΔT_b (°C)

FIGURE 18 T_b During Exercise, Bear 2 Pre and Post-Oil

Deep body temperature (T_b) of bear 2 recorded at 5 minute intervals before, during, and after 30 minutes of exercise at 5.4 $km.h^{-1}$. Values are presented for before and after exposure to oil.

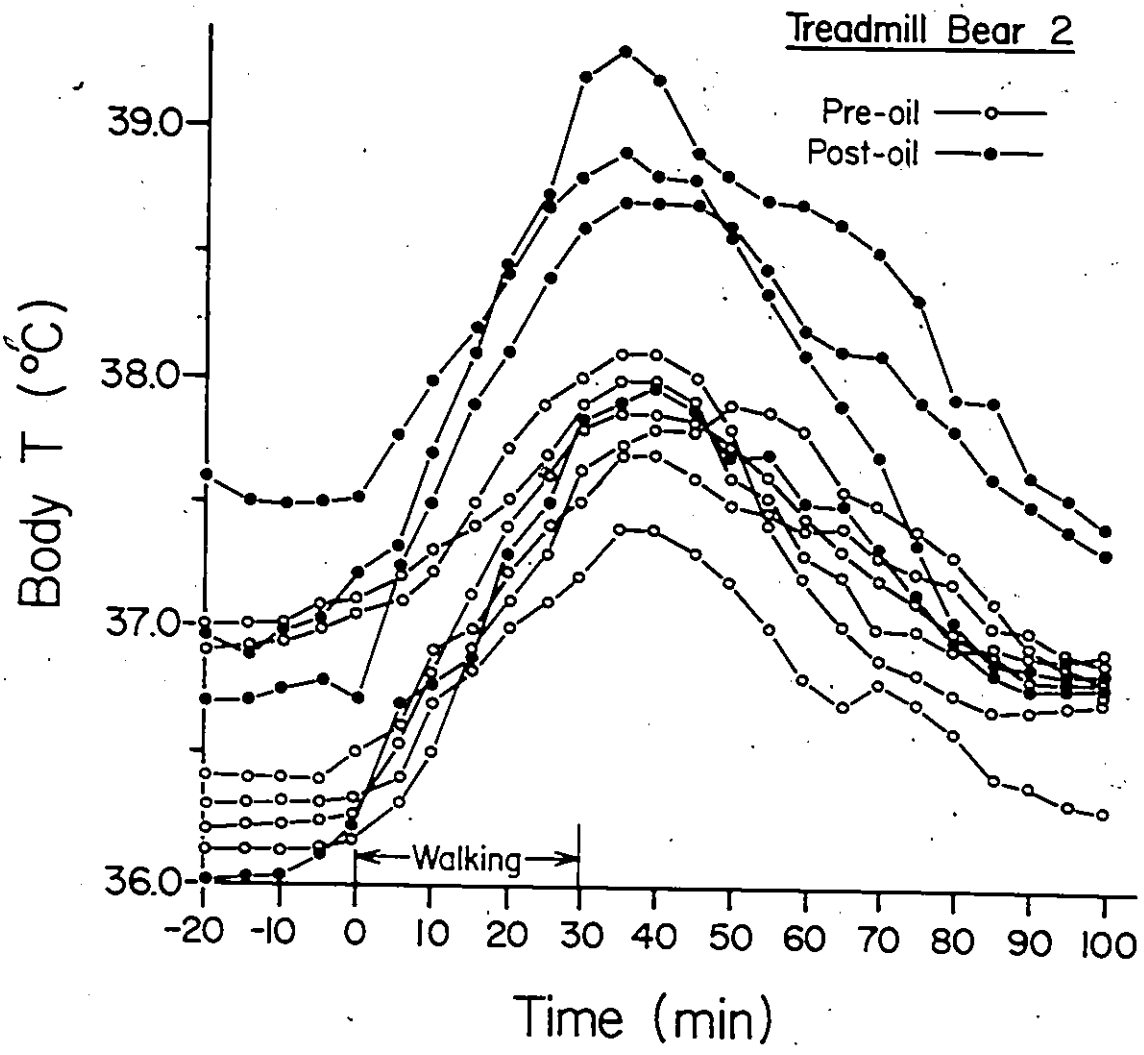

Treadmill Bear 2
Pre-oil
Post-oil
39.0
38.0
37.0
36.0
Body T (°C)
Walking
-20 -10 0 10 20 30 40 50 60 70 80 90 100
Time (min)

TABLE VI. ACTIVITY BODY TEMPERATURES.

Regressions predicting the relationship between skin temperature (Ts) and deep body temperature (Tb); and between rump skin temperature (Tr) and Tb.of 3 polar bears during exercise. n refers to sample size of measurements taken at 5 minute intervals during 30 minute tests at a walking speed of 5.4 km.h^{-1}. r is the regression coefficient, see is the standard error of estimate, and prob. is probability of no correlation.

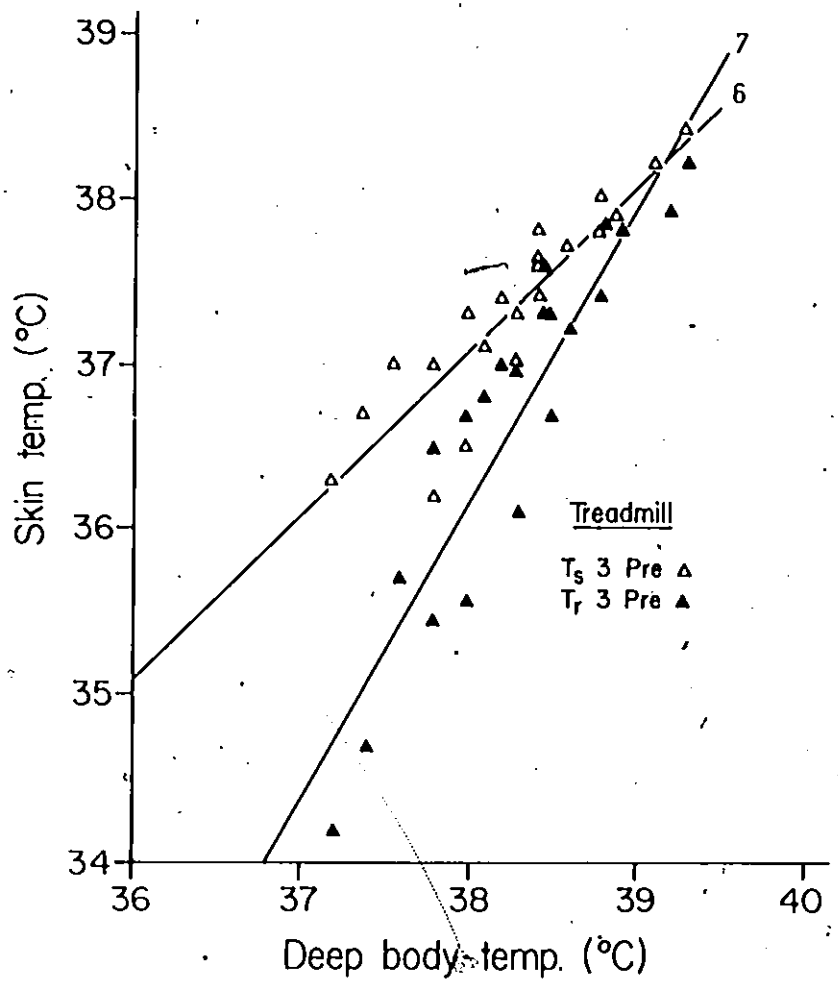
	Bear	Condition	Regr. Function	r	see	n	Prob.
(4)	2	Pre-oil	$T_s = 0.732\ T_b + 9.91$	0.90	0.167	42	$\leq .001$
(5)	2	Post-oil	$T_s = 0.208\ T_b + 29.94$	0.97	2.20	7	"
(6)	3	Pre-oil	$T_s = 0.978\ T_b - 0.10$	0.90	0.265	21	"
(7)	3	Pre-oil	$T_r = 1.780\ T_b - 31.42$	0.91	0.449	21	"
(8)	4	Pre-oil	$T_s = 0.797\ T_b + 5.41$	0.95	0.267	28	"

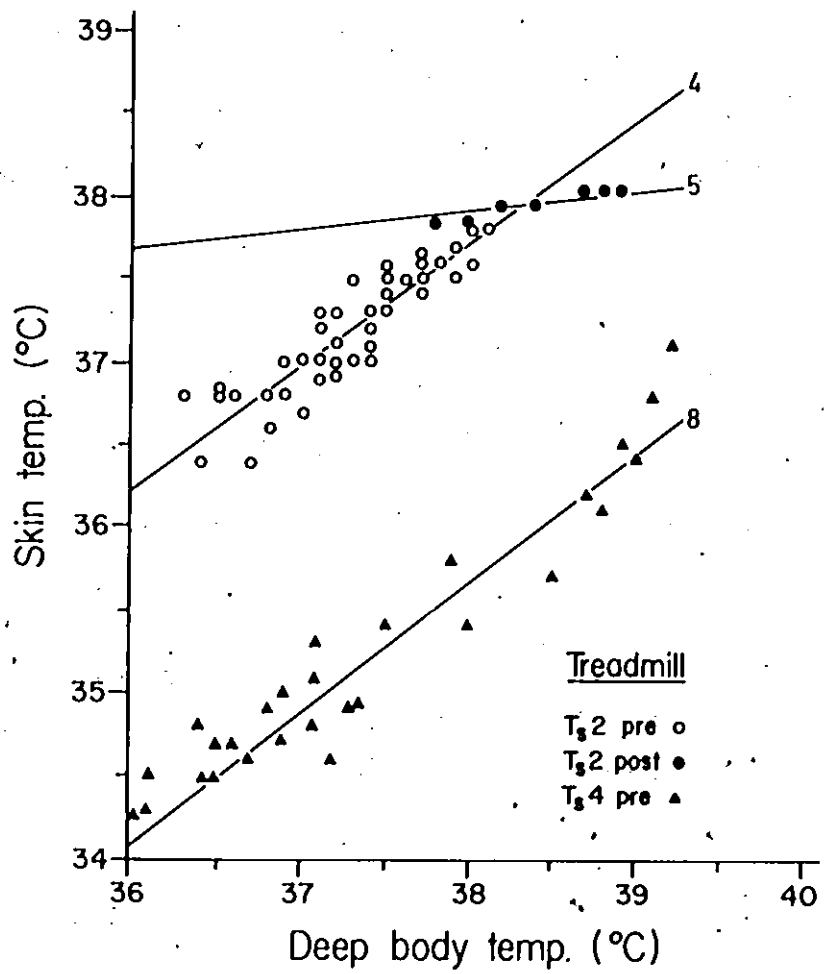
FIGURE 19 Regression of T_s and T_r on T_b; Activity Bear 3

Change in skin temperature (T_s) and rump temperature (T_r) as a function of deep body temperature (T_b) during treadmill exercise of bear 3. T_r, although generally lower than T_s at the beginning of each test, rose to about the same level by the end of each 30 minute walk. Lines represent regressions determined by method of least squares (see also Table VI).

FIGURE 20 Regression of T_s on T_b During Activity, Bears 2,4

Change in skin temperature (T_s) as a function of deep body temperature (T_b) during treadmill exercise of bears 2 and 4. The post-oil regression, determined for bear 2 only, shows the elevation in both T_b and T_s following oil contamination. Lines show regressions determined by method of least squares (See also Table VI).


39
38
37
36
35
34
36
37
38
39
40
Skin temp. (°C)
Deep body temp. (°C)
7
6
Treadmill
T_s 3 Pre △
T_r 3 Pre ▲


39
38
37
36
35
34
36
37
38
39
40
Skin temp. (°C)
Deep body temp. (°C)
4
5
8
Treadmill
T_s2 pre o
T_s2 post ●
T_s4 pre ▲

2.4 DISCUSSION

2.4.1 Oil Contact

Oil adhered to the polar bear fur on contact, suggesting that physical fouling of fur would occur rapidly. Oil distribution was uneven and depended on the point of contact with the water-oil surface. Oil did, however, become more evenly distributed with time as it was worked over and into the fur surface. The results suggest that a polar bear crossing an oil fouled lead would become physically contaminated by a substantial amount of oil.

The experiment was not designed to explore the behavior of the animals under conditions of free choice, and thus we can not address the question of probabilty of contact with any certainty. This would require an experimental design such that free access to oil contaminated water was allowed following a period wherein the bears had become familiar with the structure and water. It might make use of incentive, i.e. seal blubber accessible only through swimming, or of a pool subdivided into oiled and non-oiled surfaces (see for example, Williams, 1978).

2.4.2 Behaviour

Activity: Animals respond behaviourally to individual thermal regimes, altering the balance between heat loss and heat production by changes in posture, orientation, activity or selection of cover. Such 'thermoregularity effectors' are perhaps the most efficient mechanisms of avoiding thermal discomfort and have been reviewed extensively (Chappel

and Bartholomew, 1981; Cabanac, 1974; Dawson, 1972).

During periods of cold ambient temperature, polar bears often assume a 'husky dog', curled posture which closely approximates the ideal surface-to-volume ratio of a sphere (Swan, 1974; Øritsland, 1970). Wind, recognized as the most important factor at low air temperatures (Moen, 1973; This study, Section 3), can also cause a polar bear to orient its well insulated rump relative to the direction of air flow (Stirling, 1974). Both forementioned natural responses were noted more frequently during periods of wind in this study. All animals were also generally less active during wind, as evidenced by a reduction in the mean activity coefficients. The behavioural response to oil was more complex and difficult to interpret.

The estimation of daily energy budgets (DEB) in free-ranging animals has received considerable attention (Chappel and Hudson, 1980; Cabanac, 1974) and will be discussed in detail in Section 4. The narrow confines of the wind cage and the inherently unnatural behaviour of enclosed animals precludes, of course, any extrapolation of the observed DEBs to real world conditions. The calculated values (Table 11) do, however, serve as general indicators of activity, pre and post-oiling. Bear 3 exhibited the most active response to oil, showing a signficantly higher DEB after oil contact. It also slept little in the 2 days post-oil; 16 percent of the time vs 50 percent of the pre-immersion time. Bears 2 and 4 responded with similarly aggressive behaviour for approximately 12 hours after oil contact. They then became subdued and quiet. It is difficult to explain the different response in bear 3 although it became clear that the temperature response in the animal was more dramatic and immediate (see Fig. 14). The higher

activity may have counterbalanced high heat loss but proved insufficient to generate adequate metabolic heat to sustain thermal equilibrium.

Grooming: The most dramatic behavioural manifestation was the duration and intensity with which the polar bears ingested crude oil. Grooming began immediately upon leaving the pool and continued intensively for at least 6 hours (Fig. 5). Licking, concentrated on the forelegs and paws, constituted a means of considerable oil ingestion. The remarkable consistency in the total time engaged in grooming, 234, 225, and 235 minutes for bears 2, 4, and 3 respectively, may have been coincidental or may have reflected some level of saturation.

Although the internal toxic consequences are outside the scope of this study (see Engelhardt, 1981), serious consideration must be given to the critical nature of the first 12 hours or less following oil contact. This would be particularly important in the development of contingency plans.

Grooming occurs normally in mammals that depend on the condition of their pelage for waterproofing, camoflage, or temperature regulation (Tarasoff, 1972). It is of considerable importance to such amphibious mammals as the sea otter (Kenyon, 1974) and fur seal (Scheffer, 1962). Although assumably a normal behaviour, the relative frequency or importance of grooming to polar bears has not been addressed in the literature. It is clear that ingestion of oil by licking the fur is a very real concern in anticipating the consequences to polar bears of contacting an oil spill.

The polar bears in this study, with some exception of bear 4, made little use of snow or the cage structure to physically remove oil from the

fur. This behaviour may or may not be indicative of the response of free-ranging polar bears in natural snow conditions.

Of interest was the uninterpretable behaviour in bears 4 and 3 of apparently seeking out and ingesting oil remnants prior to exposure in the pool. Although it is tempting to consider this in light of scattered but unpublished reports of polar bears scavenging snow machine oil, any confident statement would require study in a more controlled situation.

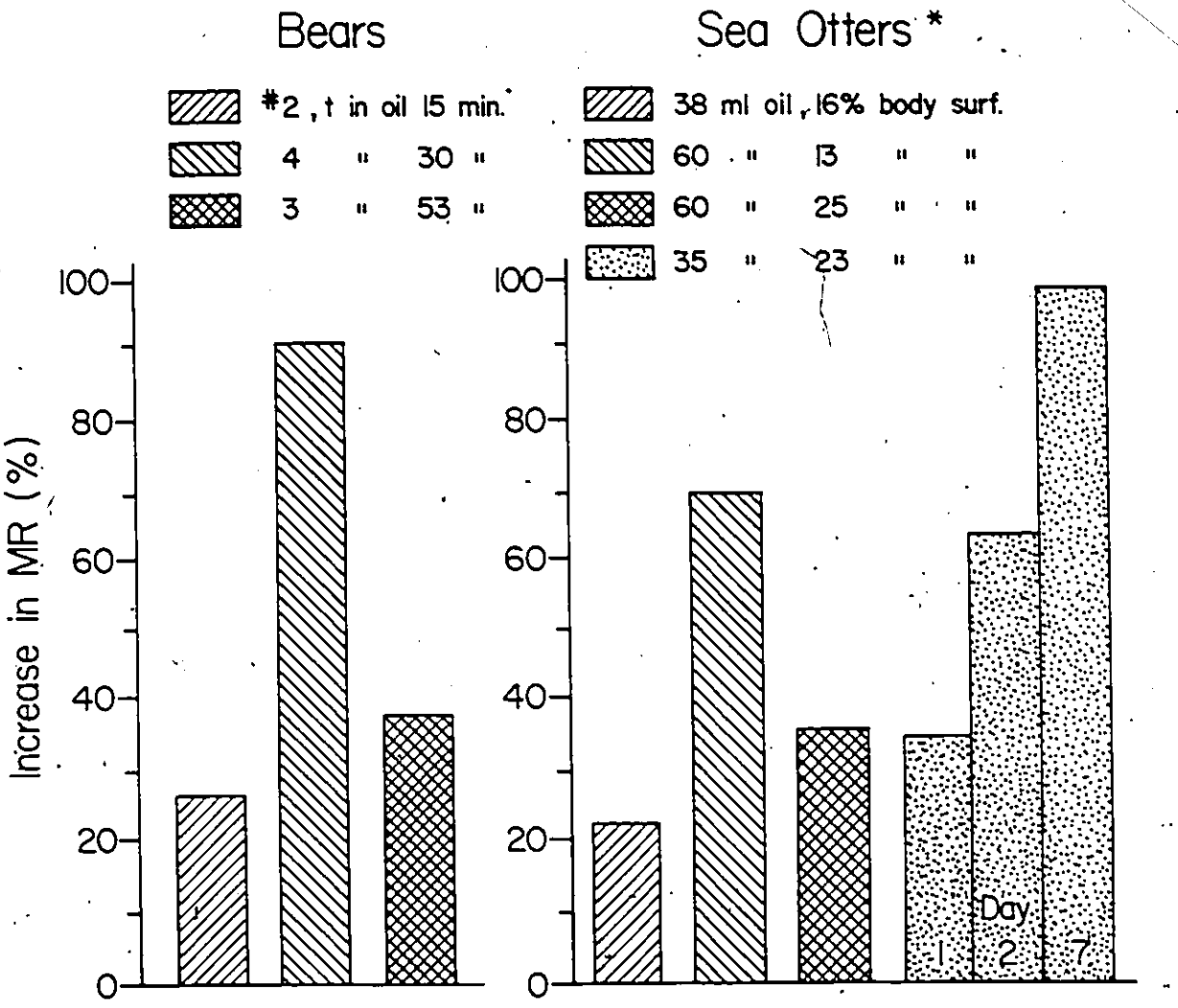
It has been suggested (Costa and Kooyman, 1980), that thermoregulatory stress would increase in time, at least in the sea otter, as an animal continued to groom the oil into its fur. The authors did demonstrate, in fact, a continuing increase in metabolic rate throughout a 7 day period following oil coating (Fig. 21). In this study, grooming did visibly work oil deeper into the fur, assumably further reducing the insulative value. The negative aspects were, however, probably offset by the physical removal of oil by grooming as well as by shaking.

2.4.3 Metabolism

Resting Metabolism: Due to the logistical limitations and the intractable nature of the animal, the resting metabolic rate (RMR) of adult or sub-adult polar bears has not been previously reported. The basal metabolism of polar bear cubs of 12 kg or less has been doucmented (Blix and Lentfer, 1979; Hock, 1968; Scholander et al., 1950b). The higher than predicted values were credited to the age of the study animals. The control results of this study show mean resting metabolic values slightly higher than predicted (Fig. 6). The mean minimal RMR, however, was as generally

FIGURE 21 Resting Metabolic Rates of Polar Bears and Otters

The change in resting metabolic rate (RMR) as a consequence of oil contamination. Weight specific oxygen consumption was determined for polar bears in air (this study) and sea otters in water (Costa and Kooyman, 1980). One otter was monitored over a 7 day period post-oil exposure and demonstrated an increasing RMR with time.


Bears
Sea Otters *
#2, t in oil 15 min.
4 " 30 "
3 " 53 "
38 ml oil, 16% body surf.
60 " 13 " "
60 " 25 " "
35 " 23 " "
Increase in MR (%)
100
80
60
40
20
0
Day
1
2
7

predicted (Kleiber, 1975). Although some semi-aquatic mammals may have acquired metabolic rates higher than those of similar sized terrestrial mammals as a compensation for high heat loss (Grant and Dawson, 1978; Iversen, 1972; Hart, 1964), there is no support for such a strategy in polar bears.

The increase in resting metabolic rates (RMR) of the polar bears as a consquence of oil fouling was consistent and substantial (See Table III; Fig. 6). The change in heat production suggests a metabolic compensation for a reduction in body insulation. Comparable metabolic elevations, attributed to insulative changes of the fur or feathers, have been noted in oil contaminated ducks (Lambert and Peakall, 1981; McEwan and Koelink, 1973; Hartung, 1967) and marine mammals (Costa and Kooyman, 1980; Kooyman et al., 1976; McEwan et al., 1974). Crude oil may, in fact, alter the sensitive balance between heat production and heat loss and thereby jeopardize the basic requirement of homeothermy. The general strategies for altering heat retention and/or heat production will be discussed in detail in Section 4.

Activity Metabolism: The cost of locomotion of all animals tested was higher than that predicted from general expressions scaling the energy costs of locomotion (Fedak and Seeherman, 1979; Taylor, 1977). Such unpredictably high costs have also been documented in lions (Chassin et al., 1976); man (Margaria et al., 1963), and in other animals (Pedley, 1977). The calculated cost of walking in polar bears was in reasonable agreement with that predicted by Fedak and Seeherman (1979) for body

weights approaching 200 kg (Fig. 8). It was, however, much higher for polar bears of smaller size and suggests that this species attains maximum efficiency of walking, i.e. low energy consumption, as adults. It also implies an energetic pressure on sub-adult polar bears to develop optimally efficient hunting strategies (Stirling and Latour, 1978).

The relationships between many biological functions and body mass are best defined by allometric equations (Hoppeler et al., 1980; Kleiber, 1932; Huxley, 1924). General equations for predicting the cost of locomotion as a function of body mass are logarithmic for quadrupeds (Taylor et al., 1970); bipeds (Fedak et al., 1974); and quadrupeds and bipeds as a group (Fedak and Seeherman, 1979). Such equations predict a relatively small difference in the cost of running over the range of body weights used in this study (Fig. 8). The straight line relationship between body mass and slopes of weight specific oxygen consumption during walking (Eqn. 1; Fig. 8) appears statistically justified. A linear relationshp is unexpected, however, as is the very high cost in smaller polar bears. It is realized that linear change such as described by Eqn. 2 becomes biologically nonsensical when extrapolated; i.e. a 322 kg polar bear would theoretically not increase its metabolism with walking. The present equations should thus not be used outside the range of body weights investigated to date (110 to 235 kg). It must also be recognized that measurements have been confined, by necessity, to a relatively low range of walking speeds.

The walking heat production prior to oiling was more than 9 times BMR. From a thermoregulatory viewpoint, the work load would generate excess heat. Thus, a post-oil metabolic increase to counteract cold induced

by changes in the insulative value of the fur was entirely unexpected. The degeneration of motor co-ordination, particularly evident in the later weeks of observation and suggested by the unwillingness or inability of bears 4 and 3 to complete their single post-oil trials, implies a possible change in the mechanical efficiency of walking. Although this may have accounted for the 24 percent increase in oxygen consumption, a stress or toxicity induced metabolic elevation should not be dismissed.

Stirling (1974) found that free-ranging polar bears under observation in the high arctic spent 29 percent of their time walking. An increase in the cost of walking as a consequence of oiling could lead to changes in hunting strategies and/or an acceleration of the exhaustion of body energy stores.

2.4.4 Temperatures

Water-Oil Immersion: The cooling rate of the body core for all 3 animals during the period of water-oil immersion was unexpectedly high (Fig. 10, Table VII), particularly when compared to a previous study of polar bear thermoregulation in water (Øritsland, 1969). The present study was not designed to include a control period of water immersion and, thus, no definitive statements on the effect of oil can be made. The subject does, however, deserve some consideration.

Water, due to its high conductivity, has a cooling potential about 25 times that of air of the same temperature (Weast, 1971). Aquatic or semi-aquatic mammals must therefore either prevent or compensate for high rates of heat loss, or tolerate a degree of hypothermia (Fanning and Dawson, 1980).

TABLE VII. BODY COOLING RATE IN WATER

Results of this study (source 1) are compared to those of previous studies of polar bears (sources 2,3) and other mammals. Body temperature changes (Tb) were measured during immersion in water.

Species	Age	Mass (kg)	T_{water} (°C)	Rate of change in T_{body} ($\Delta T_b \cdot hr^{-1}$)	($\Delta T_b \cdot hr^{-1} \cdot °C^{-1}$)	Source
Polar Bear (Ursus maritimus)	3 yr	154	0 2	4.8	0.13	1
" "	2 "	110	"	2.9	0.08	"
" "	2 "	163	"	4.0	0.11	"
" "	$\bar{X}$	-	"	3.9	0.10	"
" "	3 mo	13	"	17.4	0.46	2
" "	8 mo	80	"	-3.3	-0.09	3[a]
Weddell seal (Leptonychotes wedelli)	8 hr	-	-1.8	7.8	0.20	4
	9 day	-	"		0	"
Harp seal (Phoca groenlandicus)	< 7 day	7-12	0	5.0	0.14	5
	≥ 8 day	15	"	0	0	"
Muskrat (Ondatra zibethica) summer	adult	-	6	8.2	0.22	6
winter	"	-	"	5.3	0.14	"
Water rat (Hydromys chrysogaster)	adult	-	5	11.3	0.31	7
100% active						
50% "	"	-	"	6.6	0.18	"
0% "	"	-	"	4.5	0.12	"
Man (Homo sapiens)	adult	69	10	2.7	0.10	8
	"	"	0	4.7	0.13	"[b]
	"	-	10	3.0	0.11	9

Sources of data: 1-this study; 2-Blix and Lentfer(1979); 3-Øritsland(1969); 4-Elsener et al.(1979); 5-Davydov and Makarova(1964); 6-MacArthur(1979); 7-Fanning and Dawson(1980); 8-Hayward et al.(1975a); 9-Hayward et al.(1975b).

a) T_b actually rose during water immersion to 38.5°C.

b) The cooling rate for man is estimated from an equation.

The fur of polar bears is long but relatively sparse and accordingly permits rapid penetration of water to the skin. The thermal conductance of polar bear pelts in water can increase by a factor of 20 to 25 over that in air (Scholander et al., 1950a), reaching values of 60 to 70 $W \cdot m^{-2}$ in calm water, and significantly more in agitated water (Frisch et al., 1974). Scholander et al. (1950a) postulated that heat loss during swimming is reduced by peripheral vasoconstriction and is compensated for by high heat production. Øritsland (1969) confirmed some form of compensation in that the T_b of an unrestrained 80 kg sub-adult polar bear actually increased to 38.5°C following as much as 80 minutes of swimming at water temperatures of 0-2°C and 12.5°C.

Øritsland (1970) suggested that sub-cutaneous fat deposits measuring as much as 11 cm could play an important role in thermoregulation of polar bears, although less than that in phocid seals (Elsener et al., 1977; Davydov and Makarova, 1964). In another study, Blix and Lentfer (1979) demonstrated a rapid drop in the T_b of a 12.5 kg polar bear cub in ice water. The latter response was largely, if not wholly, attributable to the high surface to volume ratio and lack of subcutaneous fat in the very young study animal. The aforementioned two studies constitute the extent of information on the T_b of swimming polar bears. This makes comparisons difficult, particularly considering the disparities in age and body size.

The subcutaneous rump temperature, T_r, of bear 3 decreased from 35°C to 20°C during 53 minutes of water-oil immersion (Fig. 11). A drop from 35°C to 25°C was previously documented in an adult polar bear restrained in a 12°C water bath (Øritsland, 1970). Such a reponse, considered normal,

is advantageous in deepening the insulative shell to assist in heat retention. The process, referred to as "regional hypothermia", has been documented in a host of mammals, both in air (Henshaw, 1978; Irving, 1972; Irving and Krog, 1955), and in water (MacArthur, 1979; Steen and Steen, 1965; Hart, 1962).

The slight but consistent rise in T_b immediately after entering the pool (Fig. 10) may be attributed to a rapid rise in metabolic heat production before peripheral cooling had affected the body core. Such a response has been noted elsewhere (Fanning and Dawson, 1980). Bear 2 continued to cool for 30 minutes after exiting the pool (Fig. 10). The slow rewarming may be an indication of peripheral cooling during the brief 15 minutes of swimming, followed by a period of time to stabilize tissue temperatures throughout the body as suggested by Øritsland (1969).

The rate of change in T_b documented in this study was equal to that of naked, terrestrial man (Hayward et al., 1975a,b). The results suggest several alternative explanations or a combination of each.

Polar bears may in fact be able to tolerate a significant drop in body temperature during occasional swims through ice-water leads. Smaller semi-aquatic mammals such as the muskrat (Hart, 1962) and others (Fanning and Dawson, 1980) show a drop in T_b at water temperatures as high as 25°C. Although the animals must rely extensively on food gathering in cold water, they can cope by altering the length of the 'swimming bouts', elevating T_b before entering the water, and tolerating a limited degree of hypothermia (Fanning and Dawson, 1980; Fish, 1979; MacArthur, 1974). Polar bears have often been observed to enter ice-water during periods of

high ambient temperature (Hochbaum, 1973), or after chases by man (Øritsland, 1969). This is presumably used as a means of reducing T_b and heat stress. Physiological mechanisms called into play under colder environmental conditions may be insufficient to prevent a drop in T_b.

The size of the pool and restrictions on swimming activity may have reduced the amount of heat generated by exercise metabolism. Although activity does increase heat loss by maximizing both the amount of surface area exposed to water and the convective heat loss (Hayward et al., 1975b; Frisch et al., 1974), metabolic heat can also reduce or compensate for heat loss (Blix and Lentfer, 1980; Costa and Kooyman, 1980; MacArthur, 1974). The animals may also have possessed very little subcutaneous fat, and thus an ineffective barrier against passive heat loss.

Finally, the oil may have reduced the insulative effectiveness of the fur, causing a higher than normal rate of heat loss. Frisch et al., (1974) showed that a layer of stagnant water trapped in the underfur of polar bear pelts acted as an important barrier to heat loss in water. Oil has been shown to compromise the thermal integrity of the fur of semi-aquatic mammals and to reduce the insulation both in air (This study, Section 3; MacEwan et al., 1974) and in water (Costa and Kooyman, 1980; Kooyman et al., 1977; Wragg, 1954). Oil-contaminated polar bear fur has not been examined in water although extreme changes in the insulating capacity of fur-seal and sea otter pelts have been documented (Kooyman et al., 1977).

Unfortunately, due to the lack of specific control values, it is

impossible to resolve the water-oil immersion results of this study. Contributing the unpredicted results to crude oil contact would be unjustified.

Resting Temperatures: The respiration chamber results show that a 38 percent rise in the metabolic rate of bear 3 was insufficient to sustain T_b at the normal pre-oil level (Table V). Bears 2 and 4 demonstrated body temperatures of normal or above normal levels for approximately one week following oiling. It appeared that all animals were unwilling or incapable of sustaining normal body temperatures in the later weeks of observation (Fig. 15). Hypothermia, defined as a drop in T_b more than 1 standard deviation below normal levels (Bligh and Johnston, 1973), was experienced to varying degrees by all 3 study animals after oil fouling.

The different thermal strategies between oil exposed individuals (Table V; Fig. 13) may reflect a difference in the degree of oiling, the energetic condition of the animals, or other factors. It must be emphasized that the maintenance of normal T_b in oil-fouled animals, particularly arctic homeotherms, may occur concurrently with severe thermal stress. This may be accomplished by utilizing peripheral body tissues as insulation, although there is then the potential of freezing injuries. The alternative response, an obligatory rise in metabolism as noted in this and other studies, is 'paid for' by an acceleration of the exhaustion of energy stores.

Wind, and its attendant cooling effect, caused a consistent drop in skin temperature particularly in bear 4. (Fig. 12). The response indicated a reduction of blood flow to the periphery and subsequent use of sub-skin

insulation to reduce heat loss (Henshaw, 1978; Irving and Krog, 1955). Normally healthy bears would compensate for a reduction in fur insulation by reducing their peripheral blood circulation, causing a corresponding increase in tissue insulation and decrease in skin or sub-cutaneous temperatures. The transitory skin temperature rise, therefore, indicates a skin reaction to the topical coating of oil or a more generalized malfunction of the thermoregulatory system. These possibilities and the attendant energetic implications will be discussed in detail in Section 4.

Activity Temperatures: Developments in long range biotelemetry have advanced the use of physiological parameters as indices of an animal's activity level and metabolism (Pauls, 1981; Robins et al., 1979; Kautz, 1978; Gessaman, 1980; 1973). Best et al. (1981) rejected the use of body temperature as an index in polar bears, however, since the relationship between walking speed and core temperature was strongly curvilinear; whereas general predictions (Taylor et al., 1970), and a preliminary study with one polar bear (Øritsland et al., 1976), suggested that metabolic rate increased in a linear fashion with increasing walking speed. A more recent examination (Hurst et al., 1981), in which body temperature and metabolism were measured simultaneously, showed a markedly curvilinear increase in both deep body temperature and oxygen consumption, and prompted this re-evaluation of polar bear walking energetics.

It is generally recognized that during muscular work, rectal temperature stabilizes at a level dependent upon the intensity of exercise (Nielsen, 1970, 1966; Saltin, 1970; Saltin and Hermansen, 1966) and independent of a

wide range of ambient temperatures (Nielsen, 1970; Lind, 1963). Best et al. (1981) suggested such an independence of ambient temperature in active polar bears over a range of -38°C to 7°C. There was no apparent difference in body temperature as a function of ambient temperature in this study. This strengthens the suitability of body temperature as a correlate of energy expenditure. The strong correlation between the change in T_b and oxygen consumption (Eqn. 3; Fig. 17) suggests the use of T_b as a correlate of energy expenditure.

There may be limitations, however, to the use of body temperature. Pre-exercise body temperature as manifested by the circadian rhythm of body temperature, for example, may affect thermoregulation associated with exercise (Hagan and Horvath, 1978). Ideally, reliable estimates of energy expenditure would require extensive laboratory correlation with body temperature, preferably with the individual animal, prior to interpretations from a free-ranging individual (Wunder, 1975; Pauley, 1971; Berggren and Christensen, 1950). Due to the frequent technical difficulties experienced with heart rate devices in polar bears (Best et al., 1981), T_b may be used alone or as a companion index of activity metabolism. Considering the lack of information for energy expenditure in free ranging bears, body temperature may serve as a valuable, if as yet inexact, correlate of activity.

The general elevation in T_b and the greater rise in T_b during post-oil exercise (Fig. 18) was not predictable from an insulative viewpoint, but may conform to a fever response. Fever is produced by an upward displacement of a central 'reference point' temperature controlling the rate of

metabolism (Stitt et al., 1974; Dubois, 1948). The general consequences of fever are an increase in heat production accompanied by an elevation of T_b and often T_s (Palmes and Park, 1965). The greater rise in T_b during post-oil exercise conforms with findings of fever in humans wherein there was a greater rise in T_b during the rising phase of fever than during the afebrile state (See Bligh, 1973, p. 235; Grimby, 1962).

The documented rise in T_b in all animals was, however, less than that of a true pyrogen induced fever. Exercise tests, post-oil, were also limited to one polar bear. Although the experimental evidence for oil acting as a pyrogen is limited (See also Øritsland et al., 1981), the subject deserves consideration in that normally acceptable techniques of polar bear capture by helicopter could cause dangerous overheating in oil stressed individuals.

Crude oil contamination appeared, on the basis of the live animal study, to have a deleterious and potentially fatal effect on polar bears. The simultaneous exposure to oil by both immersion and ingestion, however, precludes any definitive analysis of the thermal consequences of fouling of the fur. In an attempt to gain more insight, it was decided to investigate the effect of oil on such quantifiable physical parameters as thermal conductance, wind chill and solar utilization. Complementary studies were thus undertaken to delineate the changes in heat transfer through polar bear pelts under controlled laboratory conditions.

III. FUR INSULATION

3.1 INTRODUCTION

The remarkable ability of large northern mammals to maintain a thermoneutral state under conditions of extemely low environmental temperatures can be largely attributed to insulative adaptations. Retaining the thermal integrity of the fur itself allows arctic species such as the polar bear to contend with thermal gradients, between animal and environment, of as much as 90°C (Scholander et al., 1950a,b). The adherance to certain physical tendencies or 'laws' (Kreith, 1965; Gates, 1962) makes in vitro fur studies of heat flow applicable to interpreting this aspect of live animal thermoregulation.

The relative contributions of factors such as conduction, convection, and radiation to heat transfer were delineated largely through studies on the fur of domestic mammals (Cena and Monteith, 1975; Hutchinson and Brown, 1969; Bennett and Hutchinson, 1964). The pioneer work of Scholander and co-workers (1950a,b,c) generated an interest in the physiology of arctic animals, prompting studies of thermoregulatory strategies in individual species (Jacobsen, 1980; Stevens, 1972; Moote, 1955), and studies on the comparative aspects of fur as related to the distribution of species (Øritsland and Ronald, 1978; Hammel, 1956).

Polar bear fur is of relatively poor insulative value for its thickness, yet is comparable in overall insulative value for example, to that of the red fox (Vulpes fulva) or husky dog (Canis sp.) (Øritsland, 1976; Hart, 1956;

Scholander et al., 1950a). The apparent importance of fur prompted concern that physical exposure to crude oil may alter the thermal integrity of the pelt and compromise the energetic balance of a polar bear.

Limited observations (Davis and Anderson, 1976; Geraci and Smith, 1976) suggest that short haired marine mammals, such as phocid seals, can recover from simple surface contact with oil. Fur-bearing marine mammals such as the fur seal (Callorhinus ursinus) and sea otter (Enhydra lutris), however, appear to be more susceptible and may die from such oil contact (Costa and Kooyman, 1980; Williams, 1978; Kooyman et al., 1976). The polar bear may use a thick layer of subcutaneous fat as a partial or secondary insulative defence (Øritsland, 1970) but, unlike a hair seal (Miller et al., 1976; Irving and Hart, 1957), relies on heavy fur for most of its thermal protection. In this study, I have used pelt samples to examine the effect of different oils on the insulative value of polar bear fur in air.

3.2 MATERIALS AND METHODS

3.2.1 Fur Samples

Pelts from 3 polar bears were obtained through the co-operation of the Manitoba Department of Renewable Resources and the Department of Wildlife, NWT. Bears 1 (NWT#87) and 2 (NWT#101) were 1 year old syblings shot in Clyde River, NWT on October 2, 1978. Bear 3 was a 2 year old bear which died in Churchill during October of the same year. Two 50 x 50 cm squares were taken from the dorsal area of each animal. They were fleshed and frozen without chemical treatment until use in the summer of 1980.

3.3.2 General Design

The wind tunnel facility, housed in a greenhouse in Oslo, is presented diagramatically in Figs. 22 and 23. Fur samples measuring 30 x 30 cm were mounted over a heat flow disk, positioned in a layer of viscous grease and over a steel chamber through which water was continuously circulated. Water temperature was maintained at 38°C ± 0.2°C by thermostat control. Skin temperature (T_s) was measured by a thermosensor inserted from the underside of the skin, while ambient temperature (T_a) was derived from a second thermosensor positioned to one side and below the fur. Temperatures were expressed on a digital thermocouple thermometer, and heat flow on a D.C. millivoltmeter. Solar radiation, recorded on a compensating recorder, was measured with an Epply solarimeter mounted parallel to the fur surface.

Wind speeds of 4 $m.s^{-1}$ or less were generated by a variable speed industrial fan which pulled air across the fur by suction (Øritsland and Smith, 1975). Speeds were measured with a hot-wire anemometer. The fur sample was positioned at an angle to the direction of wind in order to compensate for the spherical nature of an animal's body (Lentz and Hart, 1960; Larose, 1947).

3.2.3 Theoretical Considerations

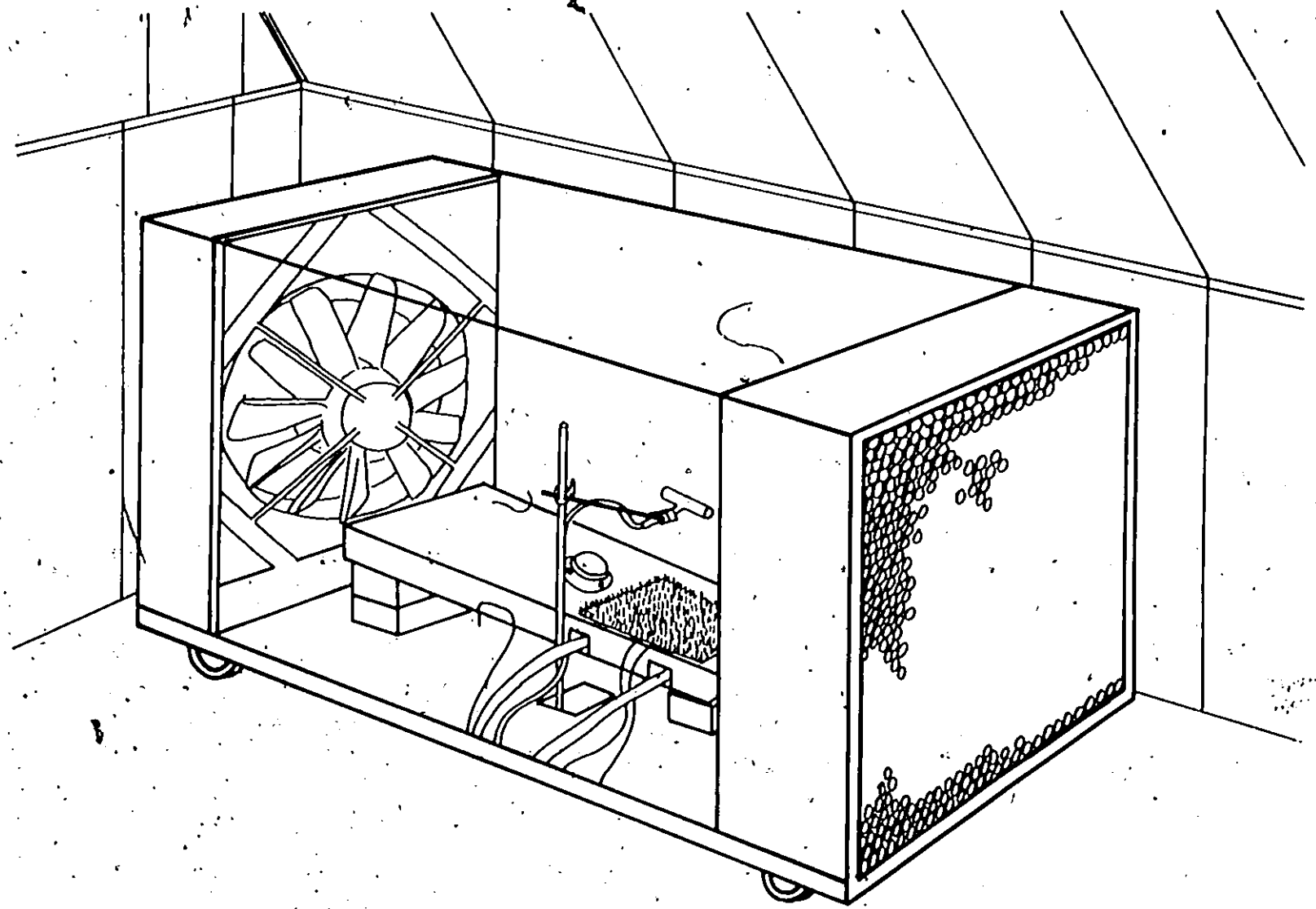
The amount of heat flow through a fur is determined by the nature of the fur and the temperature gradient in the following manner:

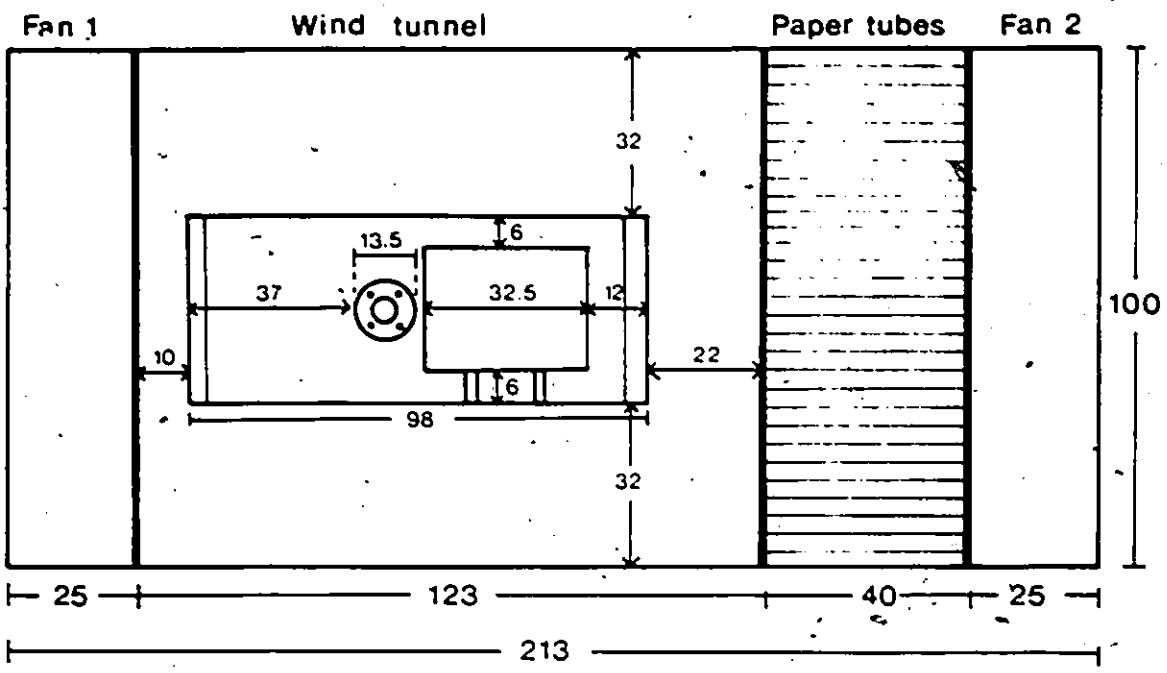
(9) $HF = h_c(T_s - T_a)$

where HF = heat flow ($W.m^{-2}$), h_c = convective heat transfer coefficient

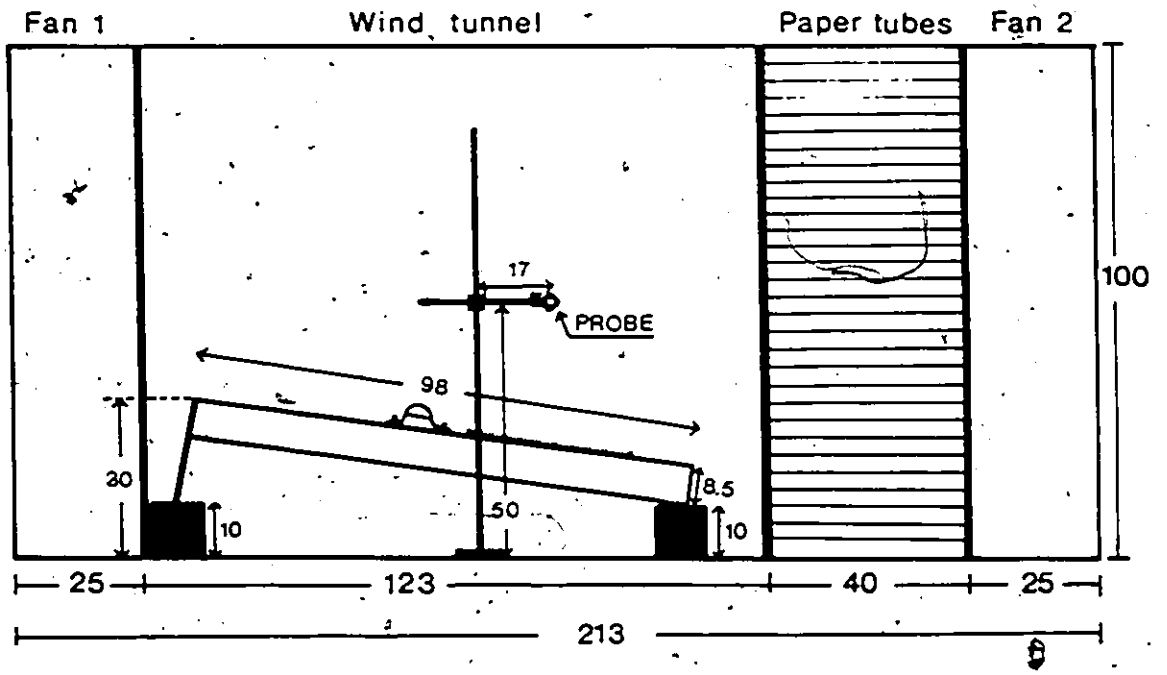
FIGURES 22 and 23 Wind Tunnel, Fur Insulation Study

Wind tunnel used in this study of heat transfer through polar bear fur. Air was pulled across a fur sample by a variable speed industrial fan and turbulence was minimized by a latticework of tubing at the point of air inflow. The tunnel iteslf, measuring 2.1 x 1.0 x 1.0 meters, was enclosed in a greenhouse to allow direct exposure to solar radiation.





Top view



Side view

($W.m^{-2}.°C^{-1}$), and T_s and T_a are skin and air temperatures (°C) respectively.

Thermal conductance is also a function of wind speed such that:

(10) $h_c = h + bV^c$

where h = calm air conductance ($W.m^{-2}.°C^{-1}$), V = wind speed ($m.s^{-1}$), and b and c are experimentally determined factors.

Heat load at skin level per unit of solar radiation may be expressed as a solar utilization factor (U) of the individual fur (Øritsland, 1974; Øritsland and Ronald, 1973) such that:

(11) $U = HF/SR$

where HF is the difference in heat flow with and without solar radiation ($W.m^{-2}$), and SR is the measured incoming solar radiation ($W.m^{-2}$).

3.2.4 Oil

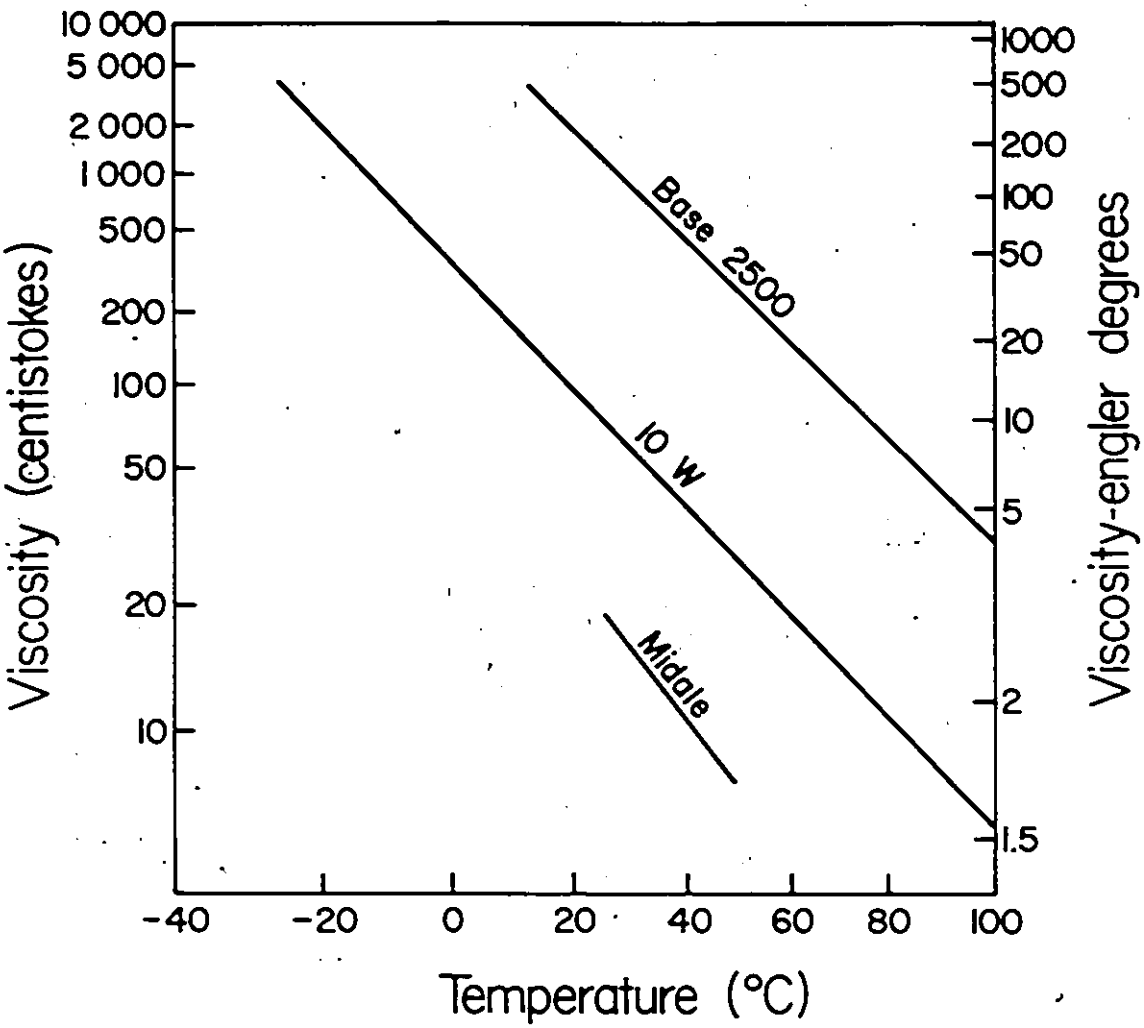
Three types of oil were investigated. These were Midale crude as used in the live animal study (See Section 2; Table 1), and 2 oils of different viscosities; 10W motor oil (Shell) and Stanco Base 2500 (Norske-Esso). See viscosity Figure 24.

Control values of heat transfer were established over a period of days for each of 4 fur samples. Thirty minutes was allowed between individual measurements for stabilization of heat flow. Measurements were carried out at 4 wind speeds, in both darkness and natural sunlight.

Application of oil was achieved by immersing the fur in a 15-20°C water bath, covered with a 1 cm slick of oil. (See also Wadhams, 1976). The fur

FIGURE 24 Oil Viscosity-Temperature Diagram

Oil viscosity-temperature diagram of the three oils used in this study. The oils were of various viscosities and included Midale crude (Dept. Energy, Mines and Resources, Canada), 10 W motor oil (Shell) and the comparably viscous Base 2500 (Norske Esso).


10 000
5 000
2 000
1 000
500
200
100
50
20
10
Viscosity (centistokes)
1000
500
200
100
50
20
10
5
2
1.5
Viscosity-engler degrees
Base 2500
10 W
Middle
-40
-20
0
20
40
60
80
100
Temperature (°C)

was agitated for 5 minutes and allowed to 'soak' for another 25 minutes in the oil-water mixture, while taking care to avoid contact with the skin side of the pelt. Measurements of thermal conductance and solar utilization were repeated for approximately 4 days per pelt in the manner outlined above.

3.3 RESULTS

3.3.1 Conductance

Conductance equations experimentally determined for both control and oiled pelts are presented in Table VIII. The average control calm air conductance value for the 4 pelts was 1.75 ± 0.2 $W.m^{-2}.°C$. Values obtained on the day of oiling (Day 1) were 10.4, 8.9 and 9.0 $W.m^{-2}.°C^{-1}$ for pelts treated with Midale, 10W and Base 2500 oils respectively. Because of the presence of water, and the unstable nature of the oiled fur on day 1, values from days 2 and 3 were averaged for presentation in Fig. 25.

3.3.2 Wind

Wind caused a change in the insulative value of control furs in a manner described by the wind coefficient (b) of 0.11 ± 0.06V, where V is wind speed in $m.s^{-1}$. The post-oiling wind coefficients increased considerably and averaged 0.50 ± 0.19.

TABLE VIII. HEAT TRANSFER THROUGH POLAR BEAR FUR; WIND TUNNEL

PUR	CONDITION	DAY	n	Y-INTERCEPT (h)	E/C_h	SLOPE (b)	E/C_b	R^2	s.e.e.	SOLAR UTILIZATION n	SU	E/C_{SU}
1A	Control	-	20	1.95	-	0.13	-	35	0.19.	18	0.19	-
1B	Control	-	18	1.42	-	0.17	-	77	0.10	11	0.10	
2	Control	-	12	1.77	-	0.13	-	89	0.06	12	0.12	
3	Control	-	32	1.86	-	0.02	-	5	0.09	13	0.12	
Mean			4	1.75	±0.2	0.11	±0.06			4	0.11	±0.01
1A	Midale oil (with sun)	1	8	5.82	2.98	0.07	0.54	38	0.13			
	" "	2	10	4.54	2.33	0.24	1.85	93	0.08			
	" "	3	12	4.32	2.22	0.36	2.77	94	0.11	20	0.15	1.5
Mean of day 2 + 3				4.43	2.27	0.30	2.30					
1B	Base 2500	1	16	8.96	6.31	0.19	1.12	54	0.41			
	" "	2	16	6.34	4.46	0.81	4.76	91	0.30			
	" "	3	12	5.97	4.20	0.68	4.00	94	0.20			
Mean of day 2 + 3				6.17	4.34	0.74	4.41					
2	10 W 30	1	22	8.94	5.05	0.84	6.46	40	1.23			
	" "	2	12	4.92	2.78	0.49	3.77	97	0.14			
	" "	3	12	3.58	2.02	0.68	5.23	93	0.25	18	0.16	1.33
Mean of day 2 + 3				4.25	2.40	0.55	4.23					
3	Midale oil	1	16	10.40	5.59	5.50	275	69	4.30			
	" "	2	16	6.95	3.73	0.43	21.5	68	0.35			
	" "	3	16	3.25	1.75	0.34	17	18	0.89	10	0.14	1.16
Mean of day 2 + 3				5.10	2.85	0.39	19.5					
All oils Mean of day 2 + 3			4	4.98 ±0.87	2.85	0.50 ±0.19	4.6			3	0.15	1.28

Conductance or heat transfer through polar bear pelts as measured in a wind tunnel. Conductance takes the form:

$$h_c = h + bV - (SU \times SR) \qquad W.m^{-2}.{}^{o}C^{-1}$$

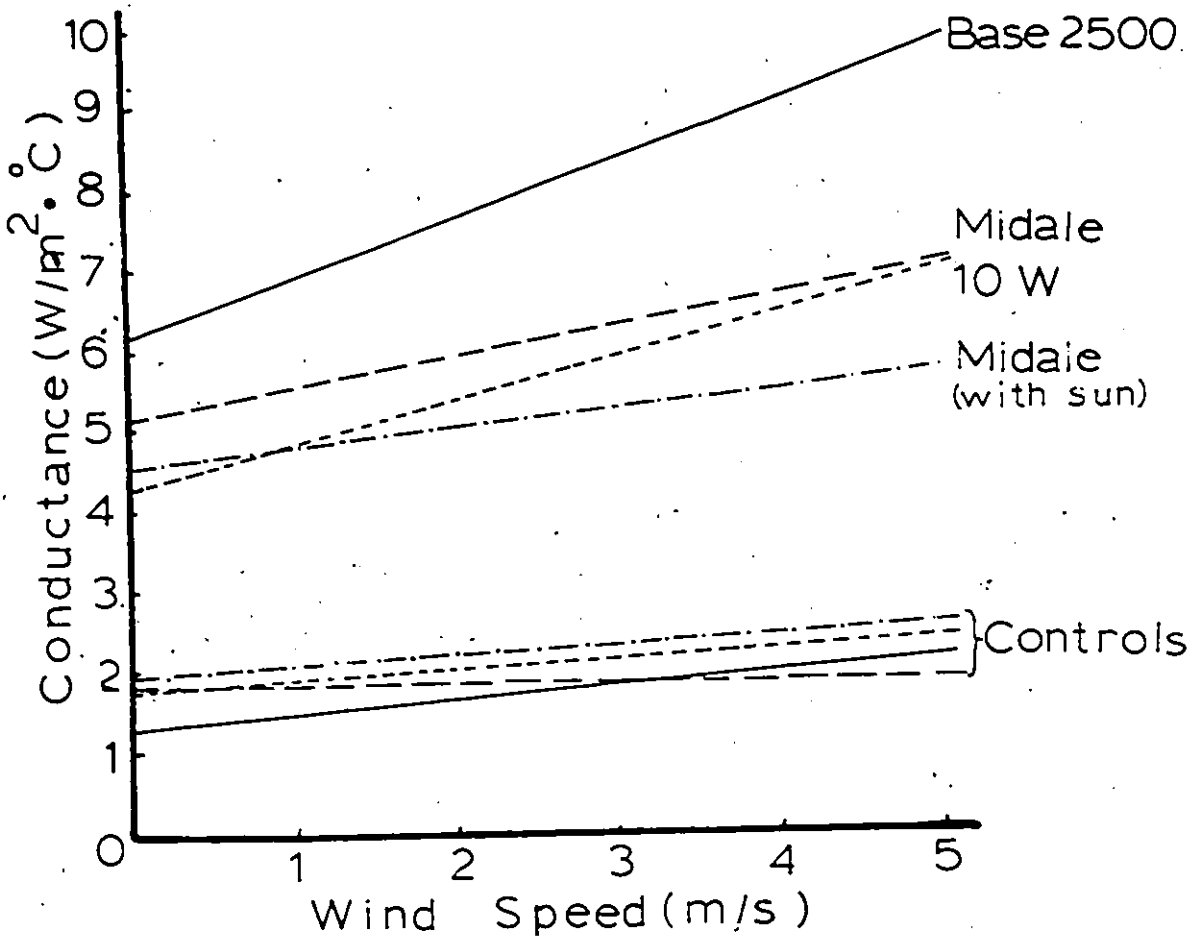
where h is calm air conductance ($W.m^{-2}.{}^{o}C^{-1}$); b is the wind coefficient or slope; V is the wind speed ($m.s^{-1}$); SU is the solar utilization fraction; and SR is the solar radiation striking the fur ($W.m^{-2}$).

a) fraction of experimental(post oil) over control(pre oil).

b) n refers to the number of measurements taken at 30 minute intervals.

FIGURE 25 Fur Conductance vs Wind Speed

Polar bear fur heat transfer or thermal conductance (the inverse of insulation) expressed as a function of wind speed. Lines were derived from regressions of the total heat transfer both before oil (controls) and from the average of days 2 and 3 after exposure to a slick of one of 3 types of oil. Midale with sun refers to a fur exposed to sunlight immediately after oil contamination.


Base 2500
Midale
10 W
Midale
(with sun)
Controls
Conductance (W/m² • °C)
Wind Speed (m/s)
0
1
2
3
4
5
6
7
8
9
10

3.3.3 Solar Radiation

Solar utilization factors, determined for 3 control pelts, averaged 0.11. Solar utilization increased in all cases following oiling and averaged 0.15, representing a mean increase of 28 percent.

3.4 DISCUSSION

3.4.1 Conductance

Control values were very comparable among pelts from each of the three polar bears (Fig. 25). The calm air conductance values of this study were between the range previously reported for polar bear summer fur (Øritsland, 1976) and winter fur (Scholander et al., 1950a). The minimal intraspecific variability was predictable from the similarity in age and size of the animals and season of collection of the fur samples. Seasonal moulting (Jacobsen, 1980; Dawson and Brown, 1970) is an important adaptation in large mammals since heat dissipation in warm weather could be as severe a problem as heat retention in cold weather. Hart (1956) noted a 32 percent seasonal change in the insulation of polar bear fur and a 50 percent change in that of black bear (Ursus americanus) fur. Topographical differences over the body surface may explain the lower calm air conductance of fur 1B (Table VIII) which was taken from a more posterior section of the back. Such a distribution, recognized but not previously quantified for polar bear fur, has been documented in other species (Jacobsen, 1980; Dawson and Brown, 1970).

The effect of oil on insulation was dramatic, with substantial

conductance increment factors of 2-5 recorded for all oiled furs (Table VIII). The change can be explained by physical properties of heat transfer. Heat passes through fur mainly by way of the trapped air between the hairs and not the hairs themselves, and thus the efficiency of fur as an insulator depends largely on its ability to trap air (Tregear, 1965; Hammel, 1955). There is an optimum hair density for trapping a layer of still air, beyond which heat transfer through the fur shafts reduces the overall insulating value. Compression of hair will, for similar reasons, increase the rate of heat loss (Moen, 1973).

Moisture is also critical in determining heat flow. Since the conductivity of water is about 25 times that of air (Weast, 1971), even a small amount of moisture can substantially increase thermal conductance (Alexander, 1962). For example, many mammals, particularly marsupials in hot environments (Dawson et al., 1974), use saliva spread over their fur as an important means of heat dissipation. Lentz and Hart (1960) demonstrated that spraying water on caribou fur increased heat transfer by up to 100 percent.

Polar bear fur, in contrast to fur of some other aquatic mammals such as sea otters and muskrats (Morrison et al., 1974; Johansen, 1962), allows water to penetrate to the skin surface dislodging all air (Frisch et al., 1974). Water is normally shed easily upon shaking, however, so that insulation is readily restored (Scholander et al., 1950a). Oil of course is not so easily removed. Oil acts much like water in effectively minimizing the insulation of polar bear fur. The persistence of oil in altering the thermal integrity of fur is of paramount concern.

This *in vitro* study fails to account for polar bear behaviour, however, particularly shaking and grooming. Such responses could significantly alter the thermal effect on a living animal either by displacing oil, or by working surface oil deeper into the fur (Section 2.4.2).

3.4.2 Wind

Wind of even a relatively low velocity normally causes a substantial drop in the insulative value of fur by wiping away the boundary air layer and increasing the convective heat loss. Such forced convection, combined with a physicial buffetting and flattening of the fur, significantly alters the rate of heat transfer (Davis and Birkebak, 1975; Tregear, 1965). The 500 percent increase in the wind coefficient, b, as a consequence of oiling, implies an extreme effect on an oiled polar bear inhabiting an environment where wind speeds of 10 $m \cdot s^{-1}$ and even 20 $m \cdot s^{-1}$ are common (Keliher *et al.*, 1978; Boughner and Thomas, 1962). A severe windchill factor (Øritsland, 1974) would radically increase the rate of heat loss and/or alter the normal behaviour of an oil-fouled polar bear.

3.4.3 Solar Radiation

Solar radiation is a potentially overwhelming source of energy to animals. When exposed to bright sunshine, the amount of solar radiation striking the surface of an animal coat will often exceed 500 $W \cdot m^{-2}$. A utlization coefficient of 0.11 implies a source of heat comparable to, or greater than, the basal metabolic rate of a homeotherm such as the polar bear. Absorption of radiant energy as a metabolic heat sparing mechanism during

cold exposure has been reported for birds (Hayes and Gessaman, 1980; DeJong, 1976; Lustick, 1969) and mammals (Øritsland and Ronald, 1973). The thermal consequences of solar radiation depend on a host of factors such as orientation of the body, meteorological variables, and coat colour and microstructure; each of which has received considerable attention (Lustik et al., 1980; Øritsland and Roland, 1978; Cena and Monteith, 1975).

The observed increase in solar utilization following oiling could have a metabolic sparing effect under bright sunny conditions. Polar bear range, however, predicates low intensity and duration of sunlight during the colder months. The oblique solar angle at a lattitude of 65°N, for example, reduces the intensity of the brightest winter sun to 70-280 $W \cdot m^{-2}$ (Hardy and Stoll, 1954), thus minimizing the contribution to thermoregulation. Higher intensities of sunlight approaching 1000 $W \cdot m^{-2}$ parallel increasing daylight, but also coincide with high ambient temperatures. During summer, the higher solar utilization could put an extra burden on heat dissipation (Schmidt-Neilsen, 1964) at a time when polar bears often seek shelter from heat in tundra pools or earthen dens (Hochbaum, 1973; personal observation). A change in solar utilization of the magnitude documented in this study would, in itself however, probably be of minimal importance to a free-ranging polar bear. Of potentially more importance is the effect of solar radiation on the oil-fur layer.

3.4.4 Oil

— Normally conduction, expressed as a function of temperature gradient, is essentially independent of ambient temperature. There is a slight positive relation between the conductivity of air and air temperature, such that the k value of air at -40°C is about 3/4 of the value at 50°C (Kreith, 1965). More importantly, it became apparent in the course of this study that oil introduces new considerations, primarily because oil viscosity is temperature dependent (Fig. 24). Thus, solar radiation and ambient temperature, in combination with sub-skin temperature determine the physical characteristics of the oil coating. Since the physical matting of the fur appeared to be directly related to viscosity, consideration must be given to not only the amount and nature of the oil, but also to the temperature of the oil-fur surface.

There was also a temporal consideration since a fraction of oil 'melted' from the fur with time at the temperatures of this study (16°C to 35°C). Pelt 1A had a conductance closest to control as a result of exposure to sunlight, and its attendant melting effect, immediately after oil treatment (Fig. 25). The viscous Base 2500 oil remained relatively unaltered with time and caused a more consistently high heat flow through the fur. Such a thick oil best approximates a potential natural encounter since most oils are very viscous at the water and air temperatures to which a polar bear is normally exposed. Such physical considerations could be better controlled by performing fur-oil conductance measurements at low environmental temperatures.

Øritsland (1976) and Øritsland and Smith (1975) found that a spray of

Norman Wells oil caused relatively little change in heat transfer through the pelts of polar bears and ringed seals respectively. Both studies were carried out at high experimental temperatures wherein the normally low viscosity Norman Wells oil was even thinnner than would probably be encountered by either species. Øritsland (1976) recognized that the failure of the oil to matt down the fur was a critical and perhaps unrealistic phenomenon. In the only comparable study on marine mammals (Kooyman et al., 1977), the thermal conductance of the fur of the sea otter and several species of pinnipeds were determined during water immersion after oiling and cleaning. Oil caused little or no change in furs of phocid seals (Erignathus barbatus, Leptonychotes weddelli) or the sea lion (Zalophus californicus). The authors did, however, demonstrate a profound change in oiled furs of a sea otter pup and sub-adult fur seals in which conductance increased 2.1, and 1.7 to 2.0 times respectively. The results support the generalization that oil has a profound effect on aquatic mammals which rely primarily, if not wholly, on fur for insulation. Oil is probably less critical to the thermoregulation of mammals which have sparsely furred, wettable pelts and depend on subcutaneous fat deposits for insulation (Kooyman et al., 1976; Tarasoff, 1974).

Whole body thermal conductance has been estimated from body temperature and metabolism of live animals following exposure to oil. Heavy oiling increased the thermal conductance, C, of muskrats (Ondatra zibethicus) by as much as 122 percent (McEwan et al., 1974), similar to increases of 74 percent for oiled mallard (Anas platyrhyncha) and 98 percent for scaup (Athya marila) (McEwan and Koelink, 1973). See Section 4 for a more

extensive discussion of thermal conductance.

When confronted with thermal cold stress, a homeotherm may respond by reducing heat loss through behavioural or physiological means, or by increasing metabolic heat production. Compensatory adjustments would have to be sizable at low ambient temperatures to counteract the suggested decrease in polar bear fur insulation caused by oil exposure. Such an oil induced change represents a potentially serious stress to the animals' heat balance and thermoregulatory stability.

IV. GENERAL DISCUSSION

4.1 THERMOGENIC RESPONSES

Thermoregulatory reponses to changing environmental or physiological conditions include both behavioural and autonomous effector mechanisms. A general discussion of the mechanisms and strategies in maintaining homeothermy can be found in Schmidt-Nielsen (1979), Moen (1973), and Hart (1964). Three thermogenic strategies potentially responsible for the observed increase in heat production following oil fouling can be considered separately.

Activity can serve as a means of counteracting low environmental temperatures and maintaining homeothermy. As a result of the mechanical inefficiency of muscle, activity causes an increase in heat production which is partly, or wholly dissipated as internal heat (Tucker, 1975; Bligh, 1973; Schmidt-Nielsen, 1972). An increase in body activity to maintain homeothermy is not generally a feasible short-term solution because of alteration of behaviour patterns and metabolic limits. In the long-term, there are energetic consequences and limits imposed on the amount of weight loss that can be physiologically tolerated (Moen, 1973).

Activity may have caused the slightly higher than predicted control values for RMR. Respiration chamber results suggest, however, that activity was probably not responsible for the increase in RMR following oiling. For example, all measurements were conducted at the same time of night and the animals appeared generally subdued within hours of oil

fouling. Finally, no experimental difference in activity, as reflected by a response of the weight-sensitive load cells, was noted. It is therefore concluded that the sizable metabolic increase following oil (Table III; Fig. 6) was real and reflected an increased thermogenic response.

Limitations on maximal thermogenic capacity, discounting exercise, have been addressed recently (Wickler, 1981) in reference to thermogenesis in birds (Carey et al., 1978) and cold acclimated hares (Feist and Rosenmann, 1975) and rats (Wang, 1978). Small eutherians, in particular, increase their ability to produce heat in the cold through a process known as non-shivering thermogenesis (NST). The process has been reviewed extensively by Wallis (1979) and Jansky (1973). NST via oxidation of brown fat has also been documented in young animals, including marine mammals (Grav and Blix, 1976), and less convincingly in newborn polar bear cubs (Blix and Lentfer, 1979). It is generally reduced or absent, however, in large adult mammals (Jansky, 1973; Brück et al., 1969). There is little reason to suppose that non-shivering thermogenesis would be a significant factor in the heat balance of polar bears.

Shivering thermogenesis, on the other hand, was probably of considerable importance in the animals of this study. As described previously, all animals began shivering within 8 hours of oil contact. Shivering varied in intensity but continued essentially throughout the 5 week post-oil period. Shivering was also observed in comparable studies of oil-fouling in furred amphibious mammals, including muskrats (McEwan et al., 1974) and sea otters (Costa and Kooyman, 1980; Williams, 1978). The observed shivering could have increased heat production at the

expense of an increase in metabolic rate, as suggested by the 27 percent to 86 percent rise increase in oxygen consumption recorded for the oil fouled polar bears of this study.

4.2 THERMAL CONDUCTANCE

Adaptation to an arctic environment involves control of heat loss mechanisms designed to contend with the extreme thermal gradient between animal and environment (Wallis, 1979; Bligh, 1973; Scholander et al., 1950a,b,c). It is now possible to compare the rates of heat flow through fur, as determined in Section 3, with that calculated for the live study animals.

Heat loss in biological systems is often described by 'Newton's Law of Cooling' which states simply that the rate of heat loss from a body is the product of a proportionality coefficient, C, and the temperature difference or gradient between the object and its environment such that:

(12) $dH/dt = C(T_b - T_a)$

where T_b is the temperature of the object and T_a is the ambient temperature. Although there is some controversy as to the suitability of designating C as a constant (Bakken and Gates, 1974; Tracy, 1972), the equation remains useful and generally accepted (Pauls, 1981; Bartholomew, 1977; Kleiber, 1972; Wunder, 1970). Whole body thermal conductance can be calculated simply at any given T_a by rearranging equation 12, assuming that a steady state condition is maintained, to:

(13) $C = MR/(T_b - T_a)$

where MR is the weight specific metabolic rate. Thermal conductance, C, may be expressed in terms of rate of heat loss per unit surface area and temperature gradient, i.e. $W \cdot m^{-2} \cdot {}^{\circ}C^{-1}$ (Bligh and Johnson, 1973). The procedure relies, however, on accurate estimates of surface area (Walsberg and King, 1978; Webster, 1971). A general weight vs surface area equation for polar bears has been formulated by Best (1976). C is expressed more frequently in terms of weight specific oxygen consumption; i.e. $ml\ O_2 \cdot g^{-1} \cdot hr^{-1} \cdot {}^{\circ}C^{-1}$.

Overall thermal conductance is inversely related to body weight in mammals (Gettinger, 1975; Morrison, 1960; Scholander et al., 1950c), due in part to the smaller surface to volume ratio in larger animals. A general allometric equation relating conductance to body weight was formulated by Herreid and Kessel (1967). The expression was generated, however, from information of only 24 species within the narrow range of 30-80 g and led to many subsequent deviations from the predicted values (McNab, 1978; Hudson et al., 1972). A comprehensive re-examination (Bradley and Deavers, 1980), including values from 192 species of mammals, led to the equation:

(14) $C = 0.760\ W^{-0.426}\ ml\ O_2 \cdot g^{-1} \cdot hr^{-1} \cdot {}^{\circ}C^{-1}$.

The equation has excellent predictive powers, although it also suffers from poor representation of large animals.

Although thermal conductance, or convective heat transfer, has been determined for polar bear fur in vitro (See Section 3), metabolism and body temperatures of resting polar bears were not previously available for a calculation of C. The results of this study (Table IX; Fig. 26) show an

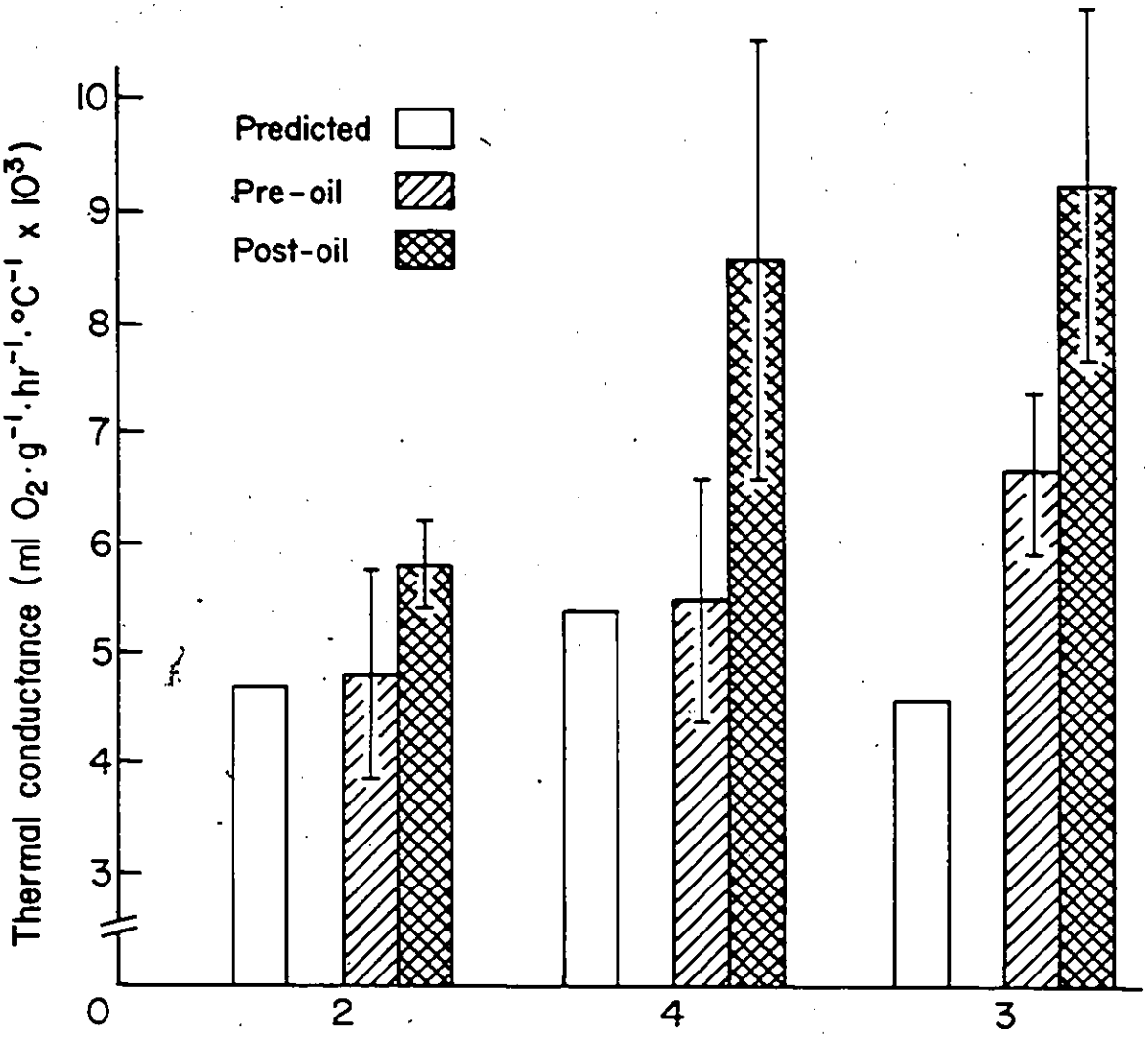
TABLE IX WHOLE BODY THERMAL CONDUCTANCE (C)

Bear	Mass (kg)	A_b[b] (m^2)	T_b-T_a (in ^oC) Bef.	Aft.	C (in ml $O_2.g^{-1}.hr^{-1}.{}^oC^{-1}x10^3$) Est(E)	Bef(B)	Aft(A)	Ratios[a] B/E	A/E	A/B	C (in $W.m^{-2}.{}^oC^{-1}$) B	A	A/B
2	154	2.59	45	49	4.7	4.8	5.8	1.02	1.24	1.21	1.55	1.86	1.21
4	110	2.07	44	52	5.4	5.5	8.6	1.02	1.59	1.55#	1.56	2.50	1.60#
3	163	2.69	45	44	4.6	6.7	9.3	1.46	2.03	1.39#	2.22	3.08	1.38#
$\bar{X}$	-	-	-	-	-	-	-	1.17	1.62	1.38#	1.78	2.49	1.40#

Whole body thermal conductance calculated from oxygen consumption under resting conditions; and the temperature gradient between animal and environment (T_b-T_a).
a) calculations are made both before(B) and after(A) oil exposure and comparisons are then made to predicted or estimated conductance(E) (See Bradley and Deavers, 1980).
b) A_b is the total surface area of the bear as predicted from body mass(See Best, 1976).

FIGURE 26 Whole Body Thermal Conductance

Whole body thermal conductance, C, calculated from the oxygen consumption and temperature gradient (T_b-T_a) of bears under resting conditions. Calculations were derived from measurements made before and after oil contamination of fur. Comparisons were made to values predicted from body mass (Bradley and Deavers, 1980).


Predicted
Pre-oil
Post-oil
Thermal conductance (ml $O_2 \cdot g^{-1} \cdot hr^{-1} \cdot °C^{-1} \times 10^3$)
10
9
8
7
6
5
4
3
0
2
4
3

excellent correlation between control and predicted values, particularly for bears 2 and 4. The mean control value of 1.78 $W \cdot m^{-2} \cdot {}^{\circ}C^{-1}$ is also in good agreement with the mean thermal conductance value of 1.75 determined for the fur samples in Section 2. The agreement is, in part at least, coincidental.

The in vitro conductance values were derived from fur of the mid-dorsal region, a region known to have low conductance relative to areas of the body such as the legs and head (Jacobsen, 1980; Øritsland and Lavigne, 1976; Dawson and Brown, 1970). This consideration is counterbalanced by the fact that the curled posture effectively reduces the surface area and minimizes heat loss from sparsely furred areas. Furthermore, a circumpolar species such as the polar bear would be expected to possess superior heat loss mechanisms to contend with severe environmental conditions of the arctic (Wallis, 1979; Kleiber, 1975; Bligh, 1973). Effective C could, therefore, have been expected to be somewhat lower than the 'predicted' C. The documented 'high' values may be explained by the young age and relatively small subcutaneous fat deposits of the study animals.

The increase in thermal conductance as a consequence of oiling was dramatic in bears 4 and 3, averaging 39 percent and 55 percent respectively. It was less so in bear 2, wherein C increased by 21 percent (Fig. 26). Since this expression takes into consideration both the metaboloic rate and the thermal gradient between animal and environment, it confirms the assertation of Section 2; oil fouling does indeed cause a reduction in the overall insulation of polar bears. The increase cannot

necessarily be attributed entirely to changes of the pelt. The single expression, C, does not attempt to partition heat loss according to its different pathways. It serves as a general expression of all the thermoregulatory effectors at an animal's disposal including the insulative value of fur, tissue, and blubber, and changing blood flow (Henshaw, 1978; Porter and Gates, 1969; Irving and Krog, 1955).

4.3 FUR INSULATION

The *in vitro* results of this study (Section 3) confirm the premise that physical fouling by crude oil causes a substantial decrease in the insulative value of fur. It was apparent, both intuitively and statistically, that oil acts in a persistently negative manner in changing the effectiveness of fur as an insulative heat barrier.

The response of homeotherms contacting crude oil strongly supprts the probability of metabolic compensation in response to a reduction in insulation. Hartung (1967) demonstrated that the elimination of entrapped air from between the feathers led to a loss of insulation in ducks exposed to oil. In a similar controlled study with ducks, McEwan and Koeling (1973) showed an oil-induced shift in the lower critical temperature from 12°C to 25°C. Depending on the extent of oiling, the metabolic rate in air increased by 1.7 and 2 times the resting value in mallard and scaup (McEwan and Koelink, 1973) and 2 to 2.4 RMR in dabbling ducks (Hartung, 1967). Holmes and Cronshaw (1977) speculated that dramatic changes in metabolism of oil soaked birds were due entirely to physical changes of the plumage

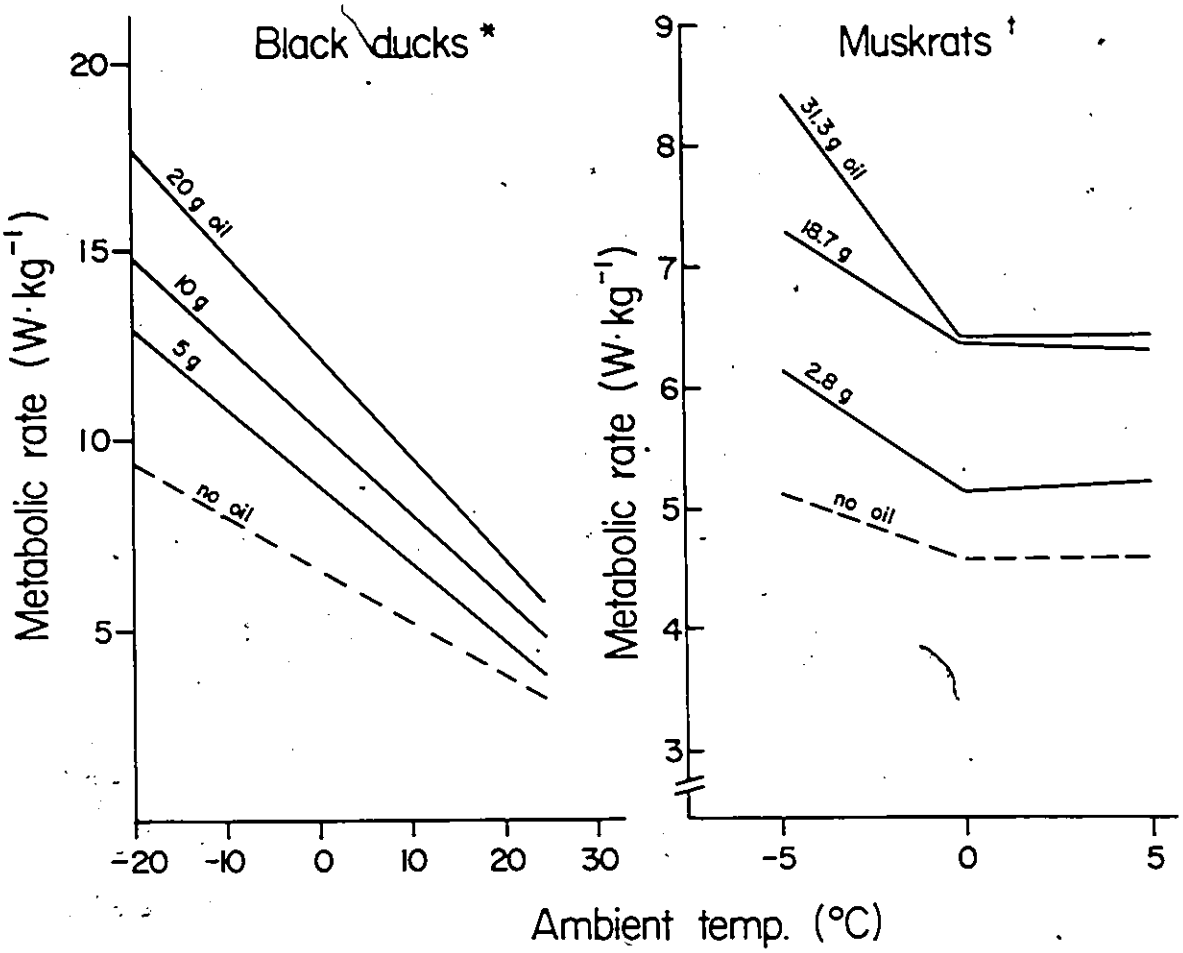
and not due to systemic toxicity or irritation of the skin. See Fig. 27. McEwan et al. (1974) demonstrated a comparable response in muskrats, wherein the metabolic rate was dependent on the degree of oiling and increased by 120 percent following heavy fouling of the fur (Fig. 27).

Davis and Anderson (1976) reported a lower peak weight in naturally oiled harbour seal pups, but cautioned that the difference may have been partly attributable to the greater experimental disturbance suffered by oiled pups. In a controlled study, Costa and Kooyman (1980) found that oiling of 13 percent of the fur surface caused a 70 percent increase in metabolic rate of sea otters in 15°C water (Fig. 21). The authors calculated that oiling of the entire fur surface would cause a 3 fold increase in metabolism. Similarly, Kooyman et al. (1976) showed that light oiling of 30 percent of the fur surface resulted in a 50 percent increase in MR of fur seals immersed in water.

Alteration of the insulative value of polar bear fur is considered a potentially serious consequence of physical contact with crude oil. The oil may also have caused a skin or peripheral tissue vasodilation reaction, resulting in enhanced heat loss from the body. Since external and internal oil exposure were not experimentally independent, I will also address the possibility of a toxicity induced systemic elevation of metabolism or a general malfunction of the thermoregulatory system.

FIGURE 27 Metabolic Rate of Black Ducks and Muskrats

The metabolism of black ducks and muskrats are presented as a function of ambient temperature following topical application of various amounts of oil. Figures were re-drawn from data of black ducks by Hartung (1967), and muskrats by McEwan et al. (1974).


Black ducks *
Muskrats †
Metabolic rate (W·kg⁻¹)
Metabolic rate (W·kg⁻¹)
20 g oil
10 g
5 g
no oil
31.3 g oil
18.7 g
2.8 g
no oil
20
15
10
5
9
8
7
6
5
4
3
-20
-10
0
10
20
30
-5
0
5
Ambient temp. (°C)

4.4 SYSTEMIC RESPONSES

The actual mechanisms of detoxification of hydrocarbons and the metabolic consequences are poorly understood at this time. Rice et al. (1977) speculated that the increased breathing rate observed in oil exposed fish was coupled with an increased energy demand for detoxification and elimination of hydrocarbons from the body tissues. The actual anabolic or catabolic reactions involved in neutralizing or clearing oil fractions from the body tissues have not yet been described. Since the polar bears of this study took up considerable quantities of oil (Engelhardt, 1981), a toxicity induced metabolic elevation cannot be rejected. It would be premature and outside the scope of this report, however, to speculate on the potential metabolic pathways involved in such detoxification of oil in polar bears.

There is also the possibility that oil acted as a pyrogen in inducing fever in the study animals. As discussed previously (Section 2.4.4), the manifestations of fever include an increase in metabolism and an attendant rise in T_b and often T_s (Stitt et al., 1974; Palmes and Park, 1965). However, since the experimental evidence was limited and derived principally from activity testing of one animal, no definitive statements of the probability of a systemic fever response can be made.

4.5 SKIN IRRITATION

The elevation of skin temperatures following oil exposure (Table V, Figs. 12, 19) was not predictable from a thermogenic viewpoint and

prompted consideration of alternative explanations.

As discussed by Hodgins (1977), petroleum acts like many microbial invaders in inducing an inflammatory reponse of the skin tissues of the host as an immunological attempt to establish a micro-environment unfavourable for microbial growth. A number of fish species, for example, responded to topical hydrocarbon exposure by inflammation and severe hyperplasia of the skin (Reichenbach-Klinke, 1965), with mucous cells becoming dilated and numerous (Waluga, 1966).

Laboratory mammals demonstrated an inflammatory skin reaction to petroleum hydrocarbons, with attendant hyperplasia and hyperkeratosis (Nau et al., 1966), as has man (Truhaut, 1967; Treon et al., 1943). The skin of mice appeared thick, dry and scaly following topical application (Nau et al., 1966). Similar application of kerosene also caused hair loss in the horse and severe dermatosis and hematuria in cattle (Blood et al., 1979; Smith et al., 1972).

The literature thus supports the hypthesis that the unexpectedly high post-oil subcutaneous temperature documented in this study could reflect a skin reaction and perfusion of blood to the skin. More germane to this study are the companion studies concerning hydrocarbon uptake and clearance as well as the necropsy results for the two polar bears which died 4 weeks following oil contact.

Engelhardt (1981), in a comprehensive assessment of the accumulation and clearance of the Midale oil fractions, documented extensive hydrocarbon loading of polar bear body fluids and tissues. The author suggested that inhalation and skin absorption contributed to this hydrocarbon

accumulation. The dynamics of the uptake were, however, masked by the extensive hydrocarbon loading through ingestion by grooming. Juck (in Øritsland et al., 1981) recorded during necropsy an oil covered epidermis which had a fine, crusty appearance that was most evident in a large, almost completely hairless patch along the mid back of bear 3. Hair could easily be pulled out in patches from a 30 x 30 cm area. More detailed microscopy of skin samples from bear 4 revealed that 'the dermis formed variably hyperplastic and acanthotic, hyperkeratotic epidemis and ... epithelial degeneration and cleft formation with some inflammatory cells in the epithelium and the submucosa.' The crusty, dry and swollen skin of both polar bears supports the contention of an extreme skin reaction to the oil.

Since the rate of oil absorption depends on the rate of blood circulation through the skin (Tagami and Ogino, 1973), an increase in blood flow as implied by the higher skin temperatures would increase cutaneous absorption of hydrocarbons. Such absorption could suppress immune responses and resistance, thereby increasing morbidity and mortality from infectious disease (Hodgins et al., 1977).

Hunter (1968) showed that enough gasoline was absorbed through the skin of humans to cause renal damage, while other investigations into mammalian systems (Sims and Grover, 1974), demonstrated that polycyclic hydrocarbons absorbed by the skin were metabolized to potentially mutagenic and carcinogenic compounds.

There is little precedent in the area of marine mammals. Van Haaften (1973) found harbour seals (Phoca vitulina) with patches of oil on their

fur, below which were inflamed areas of skin and, in a few cases, skin lesions. Engelhardt et al. (1977) reported rapid absorption of hydrocarbons into body fluids and tissues of ringed seals when exposed to Norman Wells crude oil by both immersion and ingestion. Costa and Kooyman (1980) demonstrated that the subcutaneous temperature beneath the oiled fur of sea otters dropped 5-10°C. This localized reduction in peripheral circulation was followed, however, after several days of oil contact or following a washing episode by an unexpected increase in subcutaneous temperature to that approaching body temperature. The authors speculated that there may be a limit to how long or extensively an otter can maintain peripheral vasoconstriction. It is possible, partly on the strength of the present study, that the oil caused a delayed irritation, and the soap solution a more immediate effect on the skin temperature and heat loss to the environment (Fig. 21).

The thermal implications are serious. Thermoregulatory demands generally play a significant role in the distribution of blood flow between the body core and periphery. The reduced temperature of the skin and extremities is recognized as an important, if not essential, prerequisite of mammalian life in a northern environment (Henshaw, 1978; Henshaw et al., 1972; Irving and Krog, 1955). The apparent elevation of skin temperature of polar bears documented in this study compares with that of some tropical species at cold temperatures (Baust and Brown, 1980) which must, as a consequence, pay the price of tremendous heat loss to the environment. Such an ineffective circulatory response could compound the effects of increased fur conductance and thereby augment an already potentially serious thermal imbalance.

4.6 ENERGETIC IMPLICATIONS

The estimation of energy budgets is of considerable value in behavioural and ecological studies of free ranging animals (Chappel and Hudson, 1980, 1979; Gessaman, 1980, 1973). A particularly timely application is the recent assessment of the energetic impact of harrassment (Miller and Gunn, 1981, 1979; MacArthur et al., 1979). It seems appropriate at this time, considering the present information on changes in metabolic rates of oiled polar bears, to extend the concept to the potential energetic consequences of marine oil pollution.

The rationale follows the preliminary thesis of Best et al. (1981) and Best (1977). The authors attempted to estimate the daily energy budget (DEB) of polar bears by applying literature values of the time spent on each activity per day (Stirling, 1974; Knudsen, 1973), multiplied by the estimated metabolic cost of each activity (Wunder, 1975; Taylor et al., 1970). The results may also be applied to the hunting demands or nutritional needs of the individual animal.

By way of clarification, we should consider the unique nutritional strategy of polar bears. Polar bears depend predominantly on ringed seals for their caloric intake and maintenance of metabolic energy stores. Young, inexperienced seals between the age of 0.5 and 2.0 years are easier prey, yield an energy value in caloric density equivalent to adult seals (Stirling and McEwan, 1975), and form the largest proportion of a polar bear's diet (Stirling and Archibald, 1977). Blubber is consumed preferentially and may form up to 80 percent of the total food intake (Best, 1976).

The apparent digestibility of seal blubber by polar bears is also very high at 97.9 percent; making the metabolizable energy of a seal carcass approximately 86 percent of the gross energy content (Best, 1977). The effective result is an ideal food source with a compact energy content of 34-39 $kJ \cdot g^{-1}$ (Stirling and McEwan, 1975).

Polar bears may have between 8-41 percent of their total weight as body fat (Lønø, 1970) which serves as a general energy source. Blubber also serves as an insulative layer in itself (Øritsland, 1970). Fat stores must often sustain activity through the summer when the energy intake is reduced, particularly in the south where the available food is mostly vegetation and not highly digestible (Russell, 1975, 1971). Of critical concern is the extended period of fasting endured by adult females during parturition of cubs. The implications of an oil-induced change in metabolism can be assessed in energetic terms.

Best (1977) presented an example, demonstrating that a sub-adult seal would sustain a 200 kg polar bear, at a DEB of 2 times BMR, for approximately 6.4 days. Application of the metabolic results of this study reduce the estimated sustenance time for an oiled bear to less than 5 days (Appendix 2). A slightly more complex treatment, using activity budgets determined by Stirling (1974) and by this study, suggests an energetic cost for a non-oiled bear higher than that predicted by Best (1977). Oil-induced metabolic increases would necessitate an even higher hunting efficiency in order to sustain body weight. The unexpectedly high cost of walking (Section 2.3.3) radically influences the DEB of sub-adult animals. A further consideration is that young, inexperienced polar bears are

generally poor hunters (Stirling and Latour, 1978; Stirling, 1974). The suggestion that immature members of a population are generally most vulnerable to severe environmental conditions (Stirling, 1980; Siniff et al., 1978), was recently confirmed for polar bears. Following a year of severe ice conditions in the Beaufort Sea, sub-adult animals appeared most affected and showed the most significantly reduced growth rate (Kingsley, 1979; Stirling et al., 1976). It is reasonable to predict that sub-adult polar bears would also be most affected by an oil spill encounter. Pregnant or lactating females, by virtue of their normally increased energetic demands, could also be particularly susceptible to oil contact.

It was demonstrated by McEwan et al. (1974) that muskrats responded to a higher oil-induced metabolic demand by increasing their food consumption by as much as 400 percent over control values. This consideration would become meaningless if, in a real oil spill situtation, the affected animals responded with anorexia as documented in this study. The degeneration of nervous and muscular co-ordination could also detract from hunting success. Hartung (1967) suggested the term 'accelerated starvation' to describe the response when sharply increased metabolic demands combine with reduced food intake. This may be a consequence of oil-induced changes in behaviour, in physiology or in hunting success.

Starvation may then be a valid scenario following oil contact. Best (1977) calculated that a normal 200 kg polar bear could be expected to sustain life for approximately 45 days on fat reserves of 20 percent of the body weight, assuming a DEB of 2 times BMR. The question could be more confidently addressed by use of a computer starvation model such as that

developed by Øritsland (1976b). See Appendix 2 of this study. The metabolic results of this study suggest a reduction in the estimated survival time from 45 days to about 30 days. Young or unfit animals could die in an even shorter time particularly under severe environmental conditions.

4.7 CONCLUSIONS

The metabolic and body temperature changes in polar bears following oil contamination may have been due to:

1. a normal metabolic compensation for a reduction in fur insulation (as further substantiated by fur studies, Section 3);
2. a direct effect on the minimum level of energy turnover of the tissues or a general systemic metabolic response;
3. a skin rection in combination with the effects of reduced fur insulation; or
4. a combination of all three mechanisms.

Regardless of the specific partitioning of heat loss, it has become apparent that oil causes a substantial reduction in the overall ability of polar bears to conserve heat. The results of this study suggest that oil-induced thermoregulatory stress could lead to serious alterations in activity patterns, hunting strategies, and ultimately survival.

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APPENDIX I

DRUG IMMOBILIZATION SUMMARY

IMMOBILIZATION SUMMARY - BEAR #2

DATE	DRUG(S) DOSAGE (mg)	METHOD OF INJECTION	ROUTE	INJECTION SITE	TIME TO EFFECT (min)	IMMOBILIZATION TIME (min)	PURPOSE
Oct. 09/79	Phencyclidine HCl 150 Promazine HCl 150	jab stick	I.M.	-	17	-	Capture and transfer from snare.
28	^Ket. HCl 750 ^^Xyl. HCl 350	"	"	shoulder	4	100	Transfer within the lab. and blood collection
31	Ket. HCl 190 Xyl. HCl 190	"	"	neck	7	54	Transfer within the lab.
Dec. 10	Ket. HCl 850 Xyl. HCl 850	"	"	"	6	120	Blood collection
Feb. 02/80	Ket. HCl 820 & 200 Xyl. HCl 820 & 300	"	"	"	21	230	Surgery
11	Ket. HCl 530 Xyl. HCl 680	"	"	"	18	in den	Placed in respiratory chamber
15	Ket. HCl 710 Xyl. HCl 800	"	"	"	25	130	Moved to treadmill blood collection
23	Ket. HCl 720 Xyl. HCl 720	"	"	rump	20	in den	Placed in respiratory chamber blood collection
26	Ket. HCl 730 Xyl. HCl 500	"	"	neck	10	148	Moved to treadmill
Mar. 09	Ket. HCl 800 & 900 Xyl. HCl 800 & 700	"	"	"	20	69	Washing for three hours
11	Ket. HCl 800 Xyl. HCl 800	"	"	shoulder	23	73	Blood collection
15	Ket. HCl 800 Xyl. HCl 400	"	"	rump	18	88	Blood collection
25	Ket. HCl 760 Xyl. HCl 760	"	"	neck	5		Transportation to Winnipeg

^Ketamine hydrochloride ^^Xylazine hydrochloride

IMMOBILIZATION SUMMARY - BEAR #3

DATE	DRUG(S) DOSAGE (mg)	METHOD OF INJECTION	ROUTE	INJECTION SITE	TIME TO EFFECT (min)	IMMOBILIZATION TIME (min)	PURPOSE
Oct. 17/79	Phencyclidine HCl 180 Promazine HCl 150	jab stick	I.M.	shoulder & Neck	6	70	Transfer to L-9 lab. and blood collection
Oct. 31	*Ket. HCl 720 **Xyl. HCl 720	"	"	back leg	6	72	Blood collection
Nov. 16	Ket. HCl 300 & 100 Xyl. HCl 200 & 100	"	"	neck	8	90	Blood collection
Dec. 10	Ket. HCl 850 Xyl. HCl 850	"	"	neck	8	90	Blood collection
Feb. 15/80	Ket. HCl 900 Xyl. HCl 900	"	"	shoulder	12	120	Surgery-radio transmitter implantation
20	Ket. HCl 900 Xyl. HCl 900	"	"	rump	20	not recorded	Moved to respiratory chamber
23	Ket. HCl 700 Xyl. HCl 700	"	"	neck	30	120	Moved into treadmill blood collection
29	Ket. HCl 875 Xyl. HCl 525	"	"	rump	24	60	Moved into respiratory chamber blood collection
Mar. 04	Ket. HCl 850 Xyl. HCl 425	"	"	neck	10	100	Moved into treadmill blood collection
11	Ket. HCl 850 Xyl. HCl 850	"	"	rump	11	not recorded	Moved to saw dust cage blood collection
15	Ket. HCl 825 & 1600 Xyl. HCl 825 & 1200	"	"	neck	5	80	Four-hour washing
25	Ket. HCl (Not known)			- not known -			

*Ketamine hydrochloride **Xylazine hydrochloride

IMMOBILIZATION SUMMARY - BEAR #4

DATE	DRUG(S) DOSAGE (mg)	METHOD OF INJECTION	ROUTE	INJECTION SITE	TIME TO EFFECT (min)	IMMOBILIZATION TIME (min)	PURPOSE
Nov. 13/79	Phencyclidine HCl 200 Promazine HCl 150	jab stick	I.M.	neck	13+	60	Transfer to L-9 Lab.
16	*Ket. HCl 300, 100 & 200 **Xyl. HCl 300, 100 & 200	"	"	"	6	100+	Blood collection
Dec. 10	Ket. HCl 800 Xyl. HCl 800	"	"	"	10	120	Blood collection
Feb. 08/80	Ket. HCl 750 & 300 Xyl. HCl 750 & 300	"	"	neck rump	7	83+	Surgery - radio transmitter implants
16	Ket. HCl 650 & 200 Xyl. HCl 675 & 200	"	"	neck	20	90	Moved to respiratory chamber
20	Ket. HCl 650 Xyl. HCl 650	"	"	"	17	-	Moved to treadmill blood collection
26	Ket. HCl 625 Xyl. HCl 310	"	"	"	12	-	Moved to repiratory chamber blood collection
29	Ket. HCl 600 Xyl. HCl 300	"	"	"	7	80	Moved to treadmill blood collection
Mar. 12	Ket. HCl 600 & 1050 Xyl. HCl 600 & 1050	"	"	shoulder	5	60	Washing and blood collection

*Ketamine hydrochloride
**Xylazine hydrochloride

APPENDIX 2

COMPUTER MODEL SIMULATIONS OF POLAR BEAR THERMOREGULATION, ENERGY NEEDS, AND STARVATION: PRE AND POST OIL CONTAMINATION

I. POLAR BEAR THERMOREGULATION MODEL

INTRODUCTION

Thermoregulation is defined simply as the maintenance of body temperature within a restricted range by automatic and behavioral means (Bligh and Johnston, 1973). It was initially treated as a system by Burton (1941) and Wyndham et al. (1952). Analytical models, used extensively in the physical and biological sciences, were developed and modified to describe thermoregulation particularly since the introduction of accessible computer systems. Thermoregulation is well suited to modelling in that parts of the overall system obey relatively simple physical laws which can be readily linked together in quantitative form. Consequently, thermal physiology models have been developed using engineering concepts and adapted terms such as 'set point' and 'reference signal' derived from cybernetics and control theory.

The majority of heat balance models have dealt with humans (See reviews by Werner, 1980; Mitchell, 1978). More recent applications of modelling to other animal systems include temperature balance in domestic animals (Bakken, 1981; Cabanac, 1975), poikilotherms (Spotila et al., 1973), and hibernating marmots (Luecke and South, 1972). Marine or amphibious mammals encounter particularly severe and unique thermal challenges in their seasonal or diurnal transitions from air to water. The incorporation of biothermal information into a comprehensive model of thermoregulation has been done for very few marine mammals. These include the California sea lion Zalophus californicus (Luecke et al., 1975)

and the harp seal Phagophilus groenlandicus (Øritsland and Ronald, 1978). The present work makes use of a dynamic model of the temperature regulation of polar bears developed by Øritsland (Øritsland et al., 1981). The model, implemented in the language of APL (Hellerman and Smith, 1976), is an expansion of the principles presented by Øritsland (1974) and Øritsland and Ronald (1978).

Homeothermy is achieved by a balancing of heat production against heat loss. The aim of a temperature regulation model is to accurately simulate responses in heat loss or production to changing environmental conditions. All mammals, tropical or arctic, have essentially identical deep body temperatures and weight dependent heat production (Irving and Krog, 1954; Morrison and Ryser, 1952). Heat loss mechanisms are sufficiently different particularly in respect to body insulaton, however, to compensate for the extreme difference between tropical and arctic climates (Wallis, 1979; Bligh, 1973).

A homeotherm must possesss a sensitive means of interpreting thermal information and of integrating the thermoregulatory effector mechanisms in response to changing conditions. Temperature sensitive elements may be heterogeneously distributed throughout the body, although the predominant areas are the spinal cord, hypothalymus and skin (Bligh, 1978, 1973). The central nervous system (or controller) dictates the responses to changing environmental conditions through behavioral and autonomous effector mechanisms. Avoidance behavior may include seasonal migration and changes in patterns of daily activity (Moen, 1973; Hart, 1964). It may also involve changes in body position and posture to alter the amount of

surface area exposed to wind, sun or extreme temperatures (Withers and Jarvis, 1980; Øritsland, 1969). Autonomous effectors include heat production by metabolism, skin blood flow via vasomotor activity, and evaporation via respiration (Werner, 1980; Wunder, 1975; Schmidt-Nielsen, 1964).

The purpose of this, or any model, is to make a comparison of a concept with the real world and to simulate experimental effort and new data. In this way an interplay between facts and imagination can be maintained (Hardy, 1972). In the context of the oil-polar bear study, the model is used for comparison with experimental results, extrapolation to physical and environmental parameters outside the scope of the live animal study, and for the generation of better defined thermoregulatory predictions.

MODEL DESCRIPTION

General Description: The present model of heat balance in polar bears was developed entirely by N. Øritsland and has been described in detail elsewhere (Øritsland et al., 1981). I have included a general description of the design and physiological basis to facilitate an understanding of the simulations presented in this report. Minor adjustments of the design, justified in predicting the potential effect of oil on polar bears, are presented in the text.

The model utilizes the principle (Øritsland, 1974) that a total heat balance expression may be constructed by combining the formulas of Kleiber (1975) and Meeh (Hemmingson, 1960) for heat production and body

surface respectively with the thermal properties of a plane fur sample. The model mimicks the effect of curvature (Øritsland, 1976) without representing an animal body as a cylinder as done elsewhere (Porter and Gates, 1969). The model attempts to maintain the body temperature within a normal range through comparing body temperatures via a controller, and implementing changes in heat production and loss through effectors.

Controllers: The controller operates by comparing the simulated body temperature simultaneously with a set point (TBS) and three other reference temperatures (TBSM, TBSH, TBEVS). Although the present model uses the term 'set point', the controller is more complex than a conventional proportional controller. It acts as a filter and possesses some of the properties of a null point described by Bligh (1978). The sensitivity or magnitude of response in heat production or loss is determined by the difference between the simulated body temperature and reference temperatures. Adjustments are made toward bringing the body temperature back to normal. See Fig. 1.

Effectors: There are three major thermal states: 'too cold', 'too warm' or 'neutral'. The controller responds via effectors to minimize heat production to a basal level (Kleiber, 1975) or increase it proportional to the demand. It will also change the level of the heat dissipation through the following three routes:

1) the appendages, where the heat loss is regulated by the skin temperature with the fur acting as a permanent insulator;

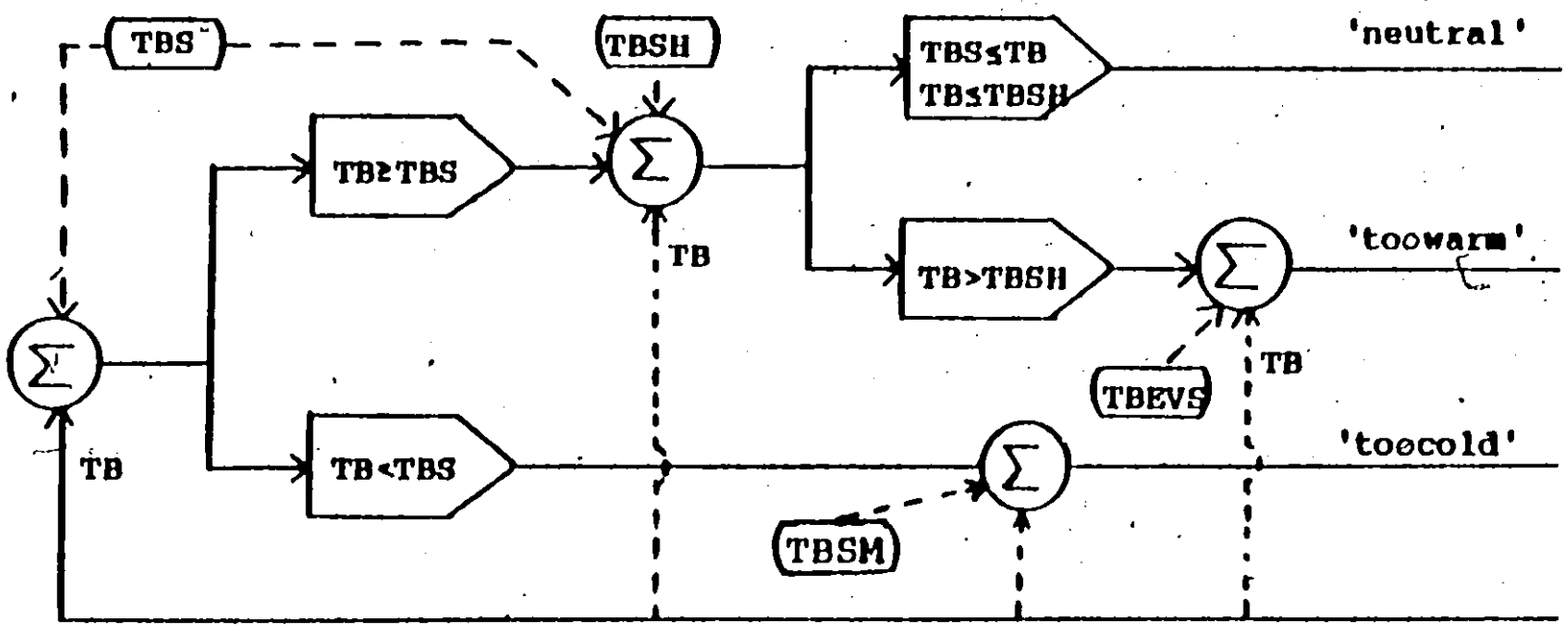
FIGURE 1 Flow diagram of controller ('thermostat') function in the thermoregulation model.

- comparator that compares by adding input values.

- 'gate' that allows only values beyond specified limits to pass for further processing.

- reference or 'quasi reference' temperature values used to trigger or grade responses.

Fig 1


TBS
TBSH
TBS≤TB
TB≤TBSH
'neutral'
TB≥TBS
TB
TB>TBSH
'toowarm'
TB
TBEVS
TB
TB<TBS
'toecold'
TBSM

2). the body trunk, where the fur and fat deposits act as a double wall of insulation. The insulative value of the inner layer, i.e., fat, is regulated in a manner mimicking the effects of changing blood circulation;

3) evaporation, triggered at an upper reference temperature (TBEVS) is expressed as a simple fraction of the total metabolism.

The 'thermostat' setting, set point (TBS), was adjusted to the mean deep body temperature documented in this study prior to oiling (36.5°C or 0.4 degrees lower than the original setting determined from previous investigations (Best, 1976; Øritsland, 1970, 1969)). The other reference temperatures of the model are kept at the same distance from TBS as in the standard model setting.

During walking an obligatory increase in metabolism, the metabolic factor of walking (F), is generated. The degree of change is proportional to body size and walking speed as determined from locomotory studies of polar bears (Hurst et al., 1981; Øritsland et al., 1981).

Thermal Properties of Body Structures: Experimental results are respected at all times in formulating heat flow equations. Literature concerning other mammals is used when information derived specifically from polar bears is lacking.

It is recognized that there are distinctive differences in the insulative value of fur on the basis of season (Jacobsen, 1980; Hart, 1956) and body region (Jacobsen, 1980; Dawson and Brown, 1970). Heat transfer values for the body trunk used in the present model are those taken from fall

pelage (Section 3.3.1). They are intermediate experimental values of 1.8 $W/m^2 \cdot °C$ (Øritsland, 1976; Hart, 1956; Scholander et al., 1950b). There is also a consideration of the effect of wind and solar radiation on fur insulation. The appendage heat transfer coefficient has not been specifically measured in polar bears. It is estimated at 3 $W/m^2 \cdot °C$, approximately double that of the body trunk. When shifting from rest to walking, an obligatory increment (EXR) of the appendage heat transfer coefficient is made. This is done to simulate the increased heat loss credited to the wind created by leg movement. Values used to simulate oiling are specified with results.

The total body surface area of mammals may be calculated from Meeh's formula (Hemmingsen, 1960). The Meeh constant ranges from 0.08 for seals (Iversen and Krog, 1973) to 0.12 for rats (Richardon, 1954). The surface area of polar bears is proportional to $mass^{0.67}$ and follows the surface law of Kleiber (1975). Meeh constants of 0.09 and 0.11 were measured for the skin and fur surface of polar bears respectively (Best, 1976). The relative thermal surface of different body areas is derived from direct measurements (Best, 1976) and thermography (Øritsland and Lavigne, 1976).

Sub skin fat layers can contribute substantially to the effective insulation of an animal. Changing blood circulation can alter the effectiveness of the double wall of insulation formed by the fur and fat (Luecke et al., 1975). Sub skin fat layers in the polar bear are unevenly distributed and are as much as 11 cm thick (Øritsland, 1970). The conductivity of fat, measured in other animals (Molyneux and Bryden, 1975) but not in polar bears, is assumed to be 0.205 $W/m^2 \cdot °C \cdot m$ (Carlson and Hsieh, 1970).

Evaporative heat and water loss have not been measured quantitatively in polar bears, but have been reported for other animals (Wunder, 1979; Folk, 1974). Best (1976) noted the onset of panting at a threshold core temperature and Øritland (1974) speculated, on the basis of thermography, that the polar bear has special adaptions for recondensation of water in respiratory air. The capacity for respiratory heat loss is assumed to be comparable to that of other non-sweating, panting animals such as the caribou and dog (Folk, 1974). It is set to a fraction of 0.2 of the total metabolism.

A series of sub-routines allows adjustments of such parameters as body size, insulation, and weather conditions prior to implementing a simulation. These subroutines are presented in Table I.

CRITICAL AIR TEMPERATURE

The concept of lower critical air temperature refers to the ambient temperature at which an animal achieves maximum thermal insulation and maintains body temperature without increasing heat production above basal level. Critical Temperature is experimentally determined by conducting a series of oxygen consumption determinations until a linear relationship between the increasing metabolism and decreasing air temperature may be graphed. It has received considerable attention as a general indicator of a specie's climate tolerance (Baust and Brown, 1980; Blix and Lentfer, 1979; Hart, 1962; Scholander et al., 1950c). The present model includes a specific subroutine, CRITA, which estimates the lower critical temperature (LCT) of an animal.

Table 1

PROGRAMME LISTINGS OF POLAR BEAR THERMOREGULATION MODEL

	PHYSIOLOGICAL CHANGES	SUBROUTINE
INSULATION	Fur insulation, body and/or legs (A,B,C)	INSU
	Solar utilization coefficient--- (SU)	INSU
	Fat thickness ---------- (TYK)	POLAR
	Evaporative heat loss fraction-- (EP)	NERV
AREA	Body weight ---------- (W)	BODYAR
	Body surface area---------- (ME)	BODYAR
	Appendage fraction---------- (MEF)	BODYAR
NERVOUS CONTROL	Reference temperature ---------- (TBS)	NERV
	Start evaporation temperature--- (TBEVS)	NERV
	Maximum heat loss temperature--- (TBSH)	NERV
	Maximum metabolism temperature-- (TBSM)	NERV
	WEATHER CHANGES	**SUBROUTINE**
ABIOTIC CONDITIONS	Air temperature ---------- (TA)	WEATHER
	Solar radiation---------- (SR)	WEATHER
	Wind speed ---------- (V)	WEATHER

The relationship between thermal conductance (h_c) of the fur and LCT is graphically presented in the following figures (Figs. 2, 3). Values of h_c derived from the in vitro pelt study were used to predict the potential changes in LCT following oiling. The amount of sub-skin fat deposits also influences the effective maximum thermal insulation, as is reflected in the difference in LCT according to fat depth (TYK). The latter could be an important consideration in the event of increased peripheral blood flow as a consequence of an oil-induced skin reaction.

CLIMATE SPACE

The term climate space was suggested by Porter and Gates (1969) to describe the values of air temperature, wind speed and solar radiation limiting the long term heat balance and thus distribution of animals. It represents a more realistic attempt than lower critical temperature in relating metabolic rate to climate.

The following figures (Figs. 4, 5, 6) again were derived respecting heat flow values determined from wind tunnel measurements of polar bear pelts (Section 3.3). Heat flow equations are of the form:

$$h_c = h + bV$$

where h = calm air conductance in $W \cdot m^{-2} \cdot {}^{\circ}C^{-1}$, b = the wind coefficient and V = wind speed in $m \cdot s^{-1}$. SU is the solar utilization coefficient or fraction of incoming solar radiation altering the heat flow through the fur.

FIGURE 2. Lower critical temperature derived from the thermoregulation model subroutine 'CRITA'. Metabolic values are expressed as a factor of the predicted basal metabolism. The critical air temperature is determined by extrapolating the linear part of the metabolism values to intersection with the air temperature at basal level.

FIGURE 3 Lower critical temperature expressed as a function of fur conductance (heat transfer coefficient). Subcutaneous fat deposits and body weights were varied. The values at 1.8 $W \cdot m^{-2} \cdot {}^{\circ}C^{-1}$ are considered normal, pre-oil predictions.

Fig 2

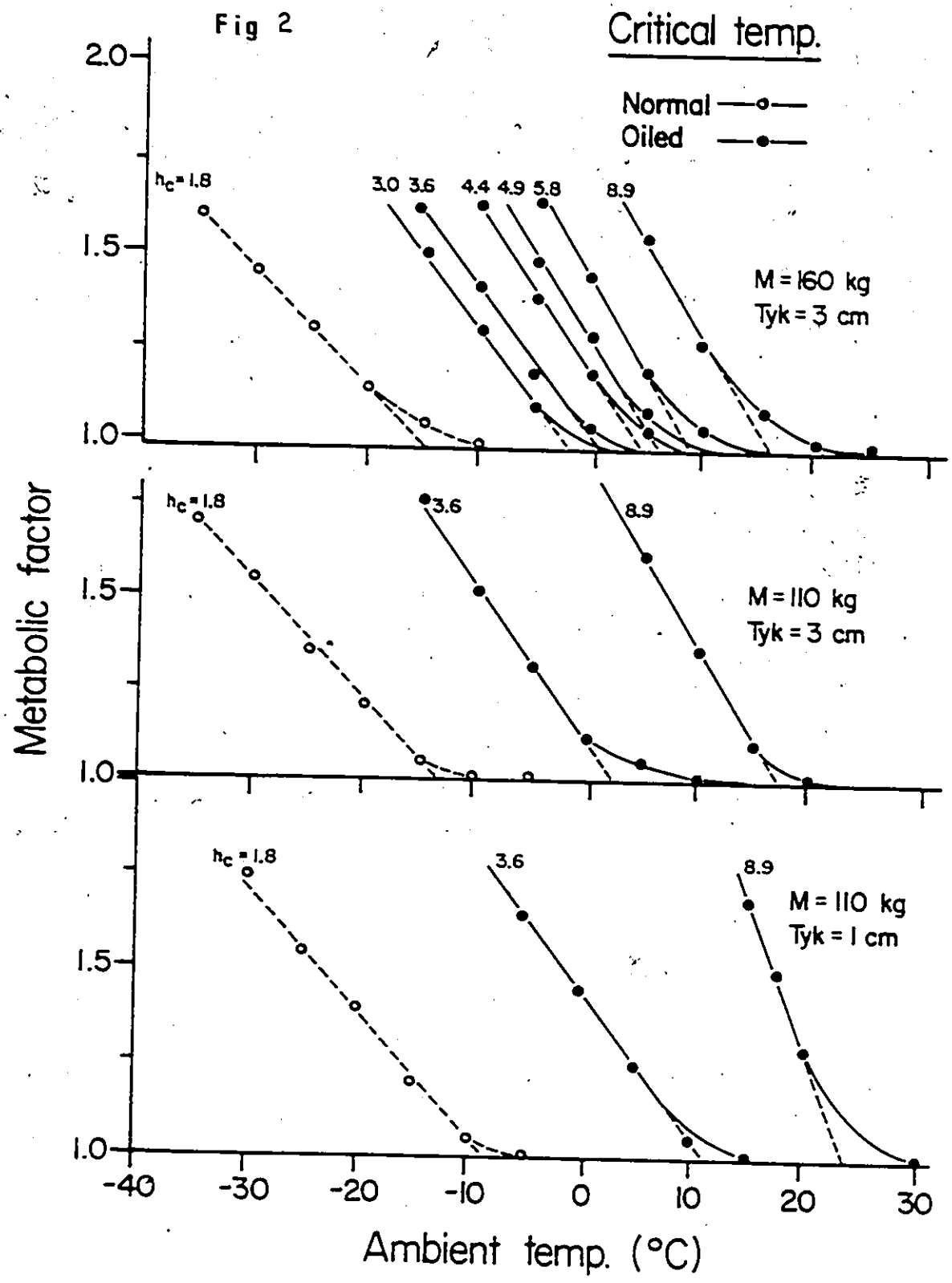

Critical temp.
Normal
Oiled
h_c = 1.8
3.0 3.6 4.4 4.9 5.8 8.9
M = 160 kg
Tyk = 3 cm
h_c = 1.8
3.6
8.9
M = 110 kg
Tyk = 3 cm
h_c = 1.8
3.6
8.9
M = 110 kg
Tyk = 1 cm
Metabolic factor
2.0
1.5
1.0
1.5
1.0
1.5
1.0
-40
-30
-20
-10
0
10
20
30
Ambient temp. (°C)

Fig 3

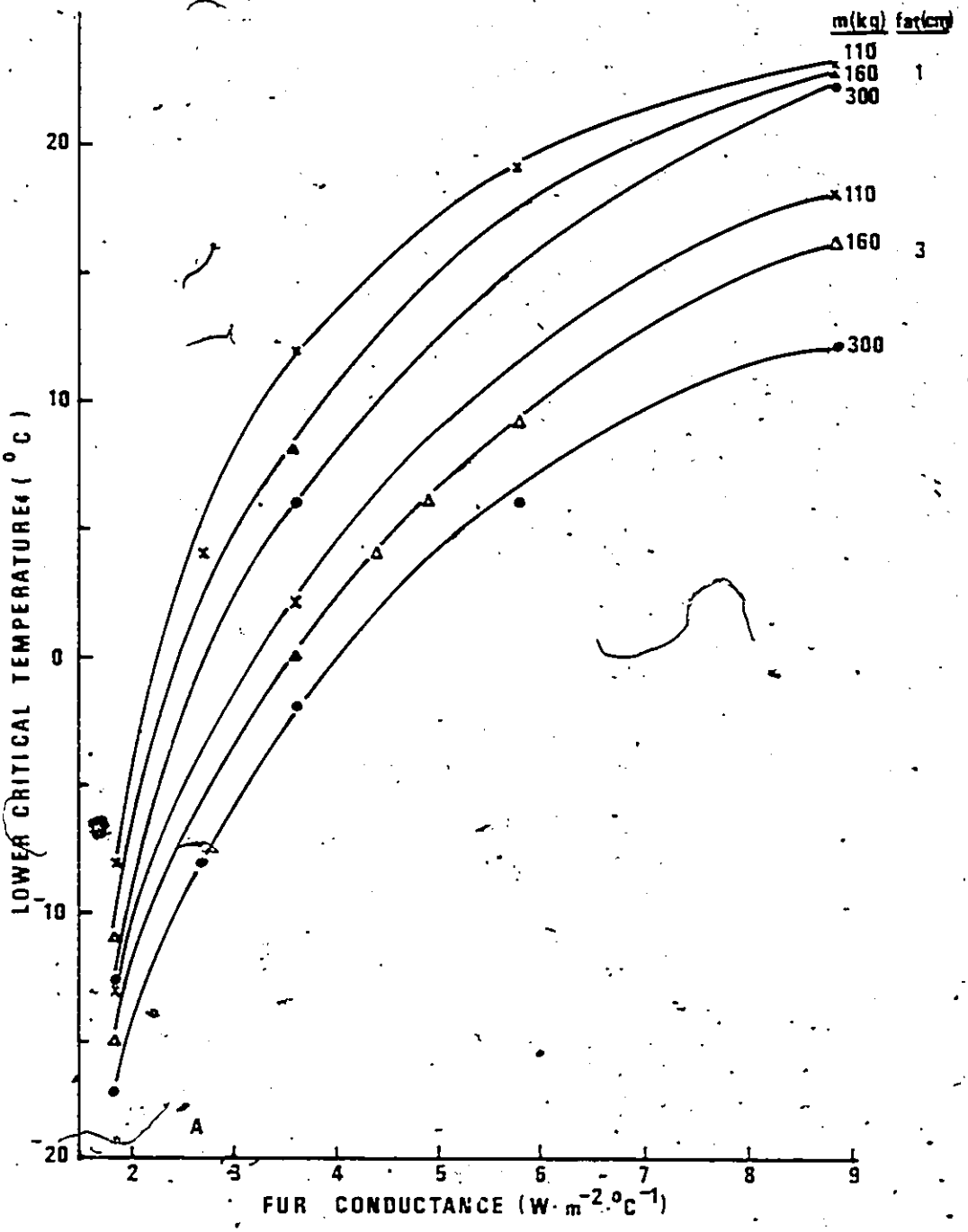

m(kg)
fat(cm)
110
160
300
1
110
160
300
3
20
10
0
-10
-20
A
2
3
4
5
6
7
8
9
LOWER CRITICAL TEMPERATURE (°C)
FUR CONDUCTANCE (W·m⁻²·°C⁻¹)

FIGURE 4 Climate space diagrams of normal and oiled polar bears. It was assumed that oil changes the heat conductance through fur. Limits of tolerance are calculated for a resting animal under the assumption that only a doubling of basal metabolism can be tolerated.

FIGURE 5 Climate space diagrams for a normal and an oiled polar bear. It is assumed that an oil-induced skin reaction causes vasodilation and negates the insulatory value of sub-skin fat deposits.

FIGURE 6 Resting matabolism of normal and oiled polar bears. Metabolic simulations (histograms) are compared to experimental resting metabolism (arrows) of the 3 polar bears at ambient temperatures of -16 to 3°C. Heat transfer or conductance through the fur is designated by h_c. Skin irritation assumes no sub-skin fat insulation.

Fig 4

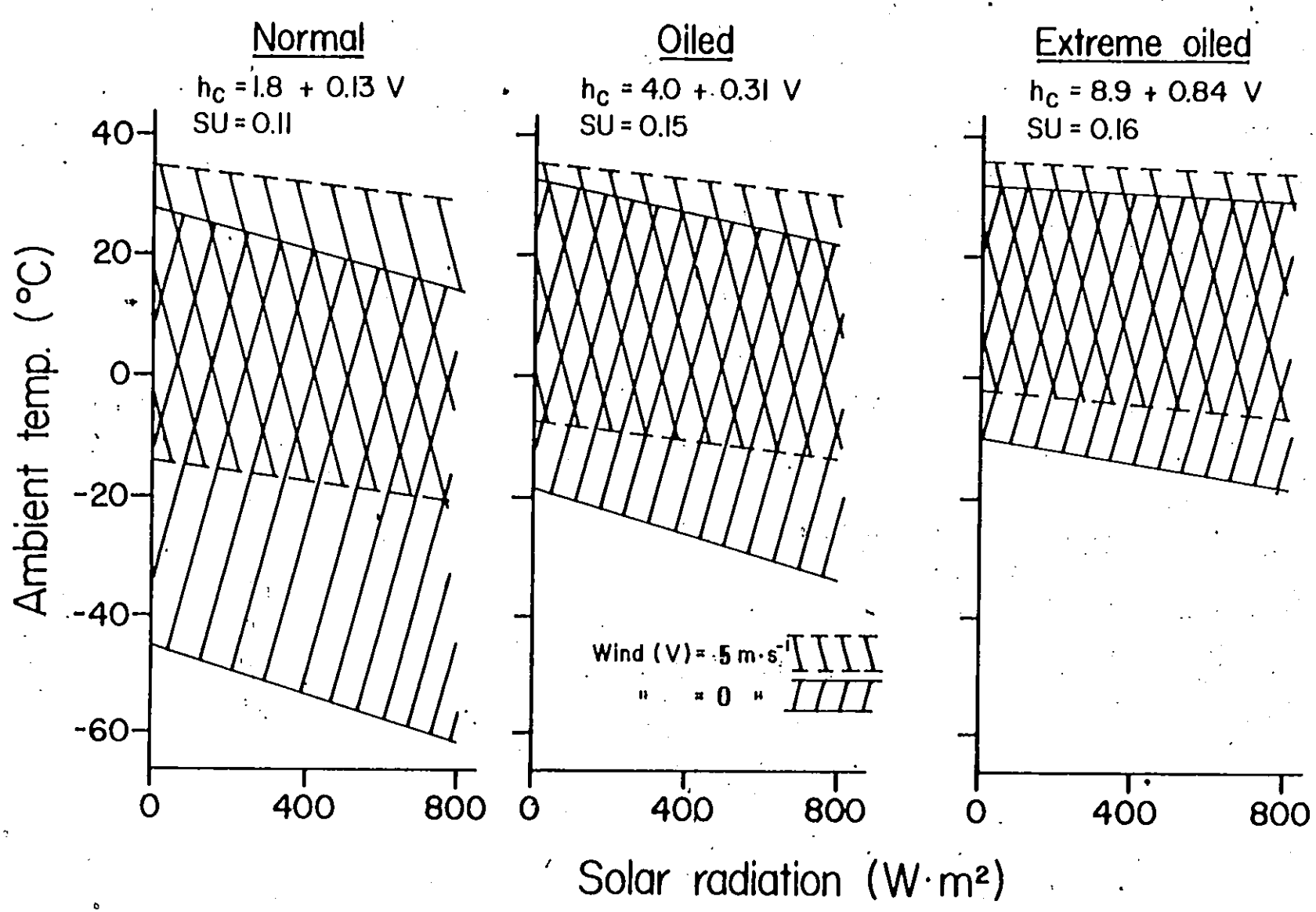

Normal
h_c = 1.8 + 0.13 V
SU = 0.11
Oiled
h_c = 4.0 + 0.31 V
SU = 0.15
Extreme oiled
h_c = 8.9 + 0.84 V
SU = 0.16
Ambient temp. (°C)
40
20
0
-20
-40
-60
0
400
800
Wind (V) = 5 m·s⁻¹
" = 0 "
Solar radiation (W·m²)

Fig 5

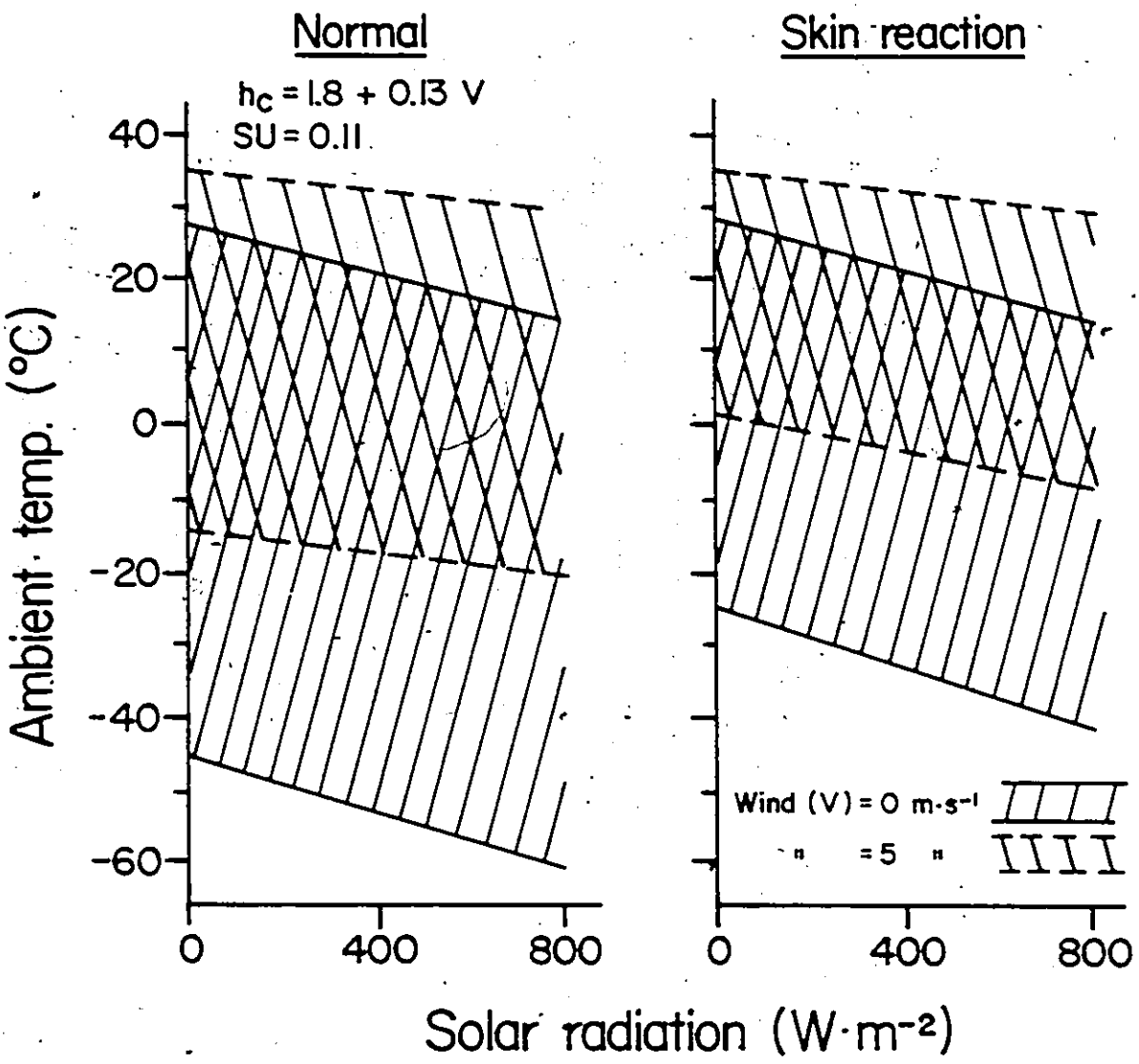
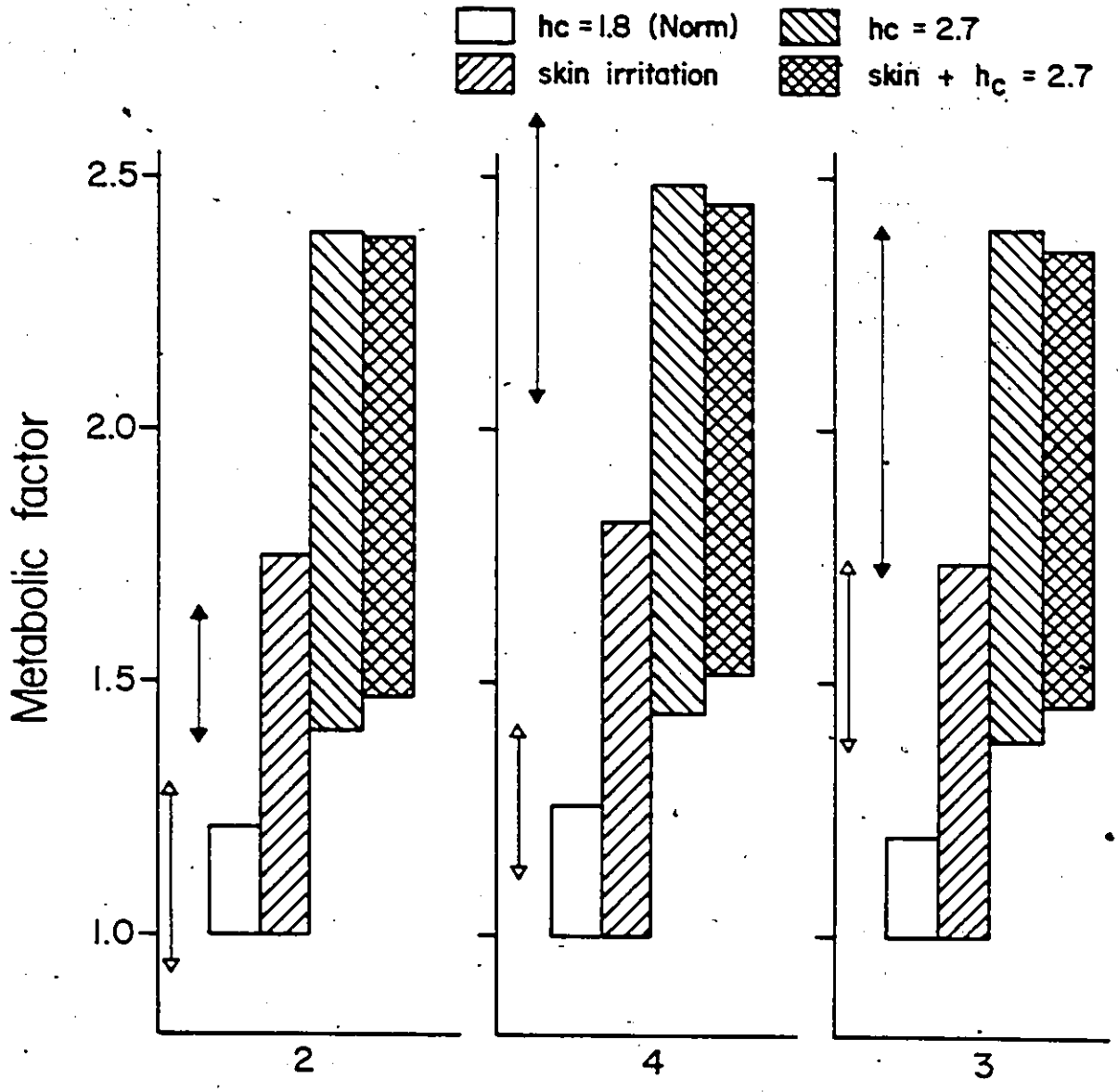

Normal
Skin reaction
h_C = 1.8 + 0.13 V
SU = 0.11
40
20
0
-20
-40
-60
Ambient temp. (°C)
0
400
800
Wind (V) = 0 m·s⁻¹
" = 5 "
Solar radiation (W·m⁻²)

Fig 6


hc = 1.8 (Norm)
skin irritation
hc = 2.7
skin + hc = 2.7
Metabolic factor
2.5
2.0
1.5
1.0
2
4
3

WATER IMMERSION

Water, due to its high conductivity, has a cooling potential about 25 times that of air of the same temperature (Weast, 1971). Semi-aquatic mammals must, therefore, either prevent or compensate for high rates of heat loss, or tolerate a degree of hypothermia (Fanning and Dawson, 1980). The thermal conductance of polar bear pelts in water can increase by a factor of 20-25 over that in air and will increase even more in agitated water (Frisch et al., 1974; Scholander et al., 1950). Oil contaminated polar bear fur has not been examined in water. Oil has caused extreme changes in the insulatory capacity, in water, of the fur of muskrats (McEwan et al., 1974), fur seals and sea otters (Kooyman et al., 1977; Costa and Kooyman, 1980).

In animals without fur, subcutaneous fat deposits can play a major role as an insulative barrier to heat loss. At the age of 1 week some phocid seals, for example, demonstrate excellent thermoregulatory capacities as evidenced by a stable body temperature during immersion in ice water (Elsener et al., 1977; Davydov and Makarova, 1964). Øritsland (1970) suggested that sub-cutaneous fat deposits could play an important role in polar bear thermoregulation. Results from this study (Section 2.4.4) showed a surprizingly high rate of heat loss in polar bears in water. The rate of drop in T_b averaged almost $4°C \cdot h^{-1}$; approximately equal to that of naked man (Hayward et al., 1975a,b). Unfortunately, due to the lack of specific control values, it was imposible to determine the contribution of oil to the magnitude of heat loss. The following simulations were completed to estimate the potential rate of heat loss assuming normal and oiled conditions

of the fur.

As in a terrestrial environment, there are a limited number of effector responses to thermal challenge. These responses include:

1) Vasomotor adjustments which regulate the rate of heat exchange between the core and peripheral tissues and subsequently between the body and the environment. Cutaneous blood vessels in the human hand, for example, constrict very effectively and the ratio of maximum to minimum blood flow may be as high as 60:1 (Forester et al., 1946). Such regional heterothermia can be particularly important to marine or amphibious mammals (Steen and Steen, 1965; Hart, 1963).
2) Thermogenesis through shivering and other metabolic processes. The scope of metabolism independent of activity can be quite substantial. Sheep, for example, can increase their metabolic heat production 7-fold through shivering (Bennett, 1973). Heat produced by swimmming can be lost through a dramatic increase in convective heat transfer to the circulating water (Frisch et al., 1974; Hayward et al., 1975b).

In the following computer simulations (Figs. 7, 8, 9) three variables were altered independently to test the effects on the rate of heat loss and/or the change in deep body temperature. The variables are:

1) Fur insulative values. Normal model calm air conductance values of the body trunk (A) and legs (AA) were multiplied by 25 to simulate the increased conductive value of water. Both values were doubled again to 88 and 172 $W \cdot m^{-2} \cdot {}^{\circ}C^{-1}$ respectively to simulate the potential effect of oil.

FIGURE 7 The change in deep body temperature (T_b) of polar bears in 0°C water. Fat thickness (TYK) and fur conductance values (A,AA) were maintained constant while the metabolic rate (MFMAX) was altered. Simulated values (solid lines) are compared with experimental data (dotted lines). Bears are considered normal, i.e., normal non-oiled fur conductance values are used in all simulations.

FIGURE 8 The change in T_b of polar bears in 0°C water. The fur conductance and the metabolic rate were maintained constant while the subcutaneous fat thickness (TYK) was altered. Cooling following oiling was simulated by a doubling of fur conductance values.

FIGURE 9 Body cooling of polar bears in 0°C water. The predicted rate of cooling is expressed as a function of sub-cutaneous fat thickness (TYK) at 3 different metabolic rates (MFMAX). Cooling rate following oiling was simulated by a doubling of fur conductance values. Experimentally determined rates are presented for bears 2 and 3.

Fig 7

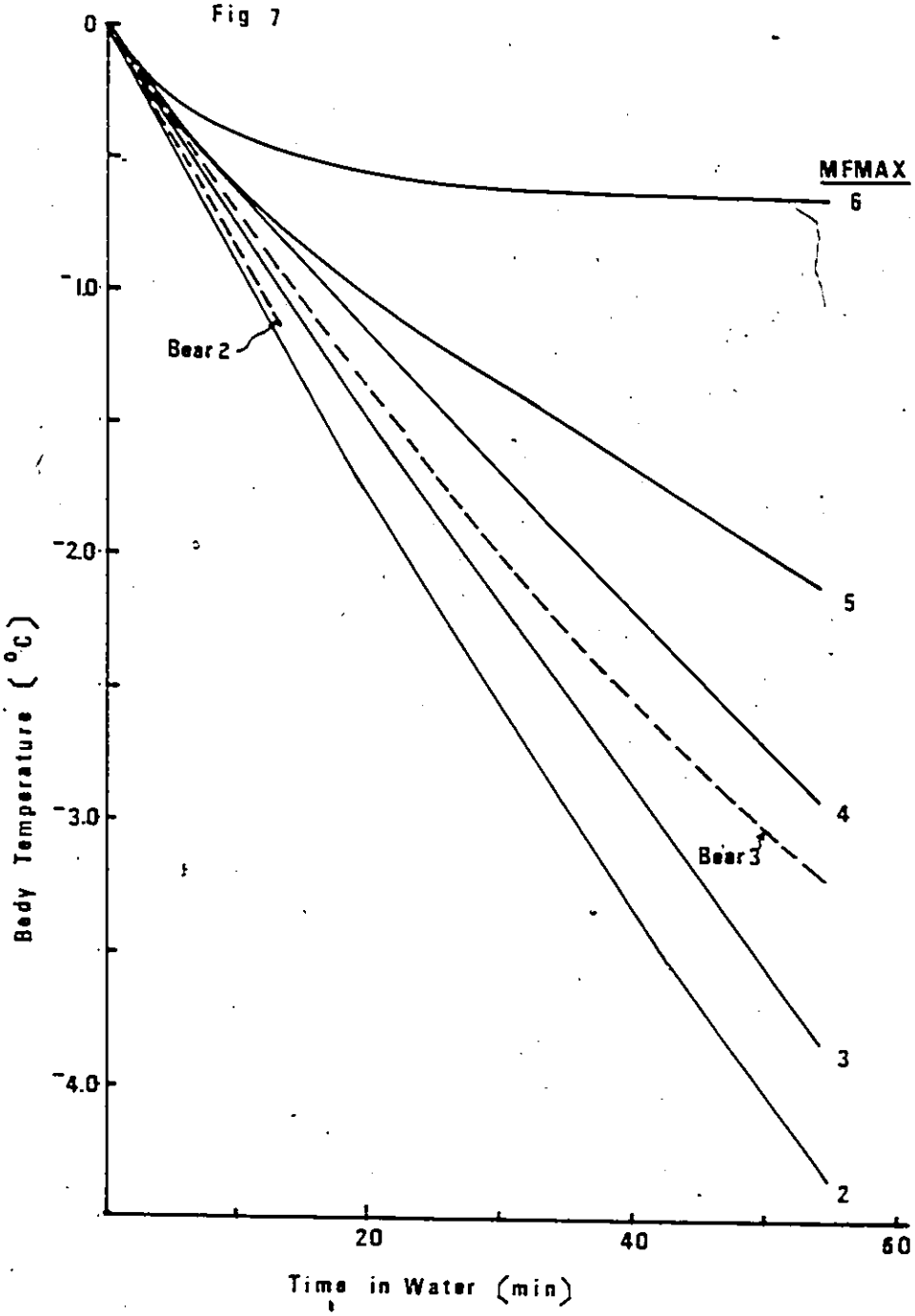

0
-1.0
-2.0
-3.0
-4.0
Body Temperature (°C)
MFMAX
6
5
4
3
2
Bear 2
Bear 3
20
40
60
Time in Water (min)

Fig. 8

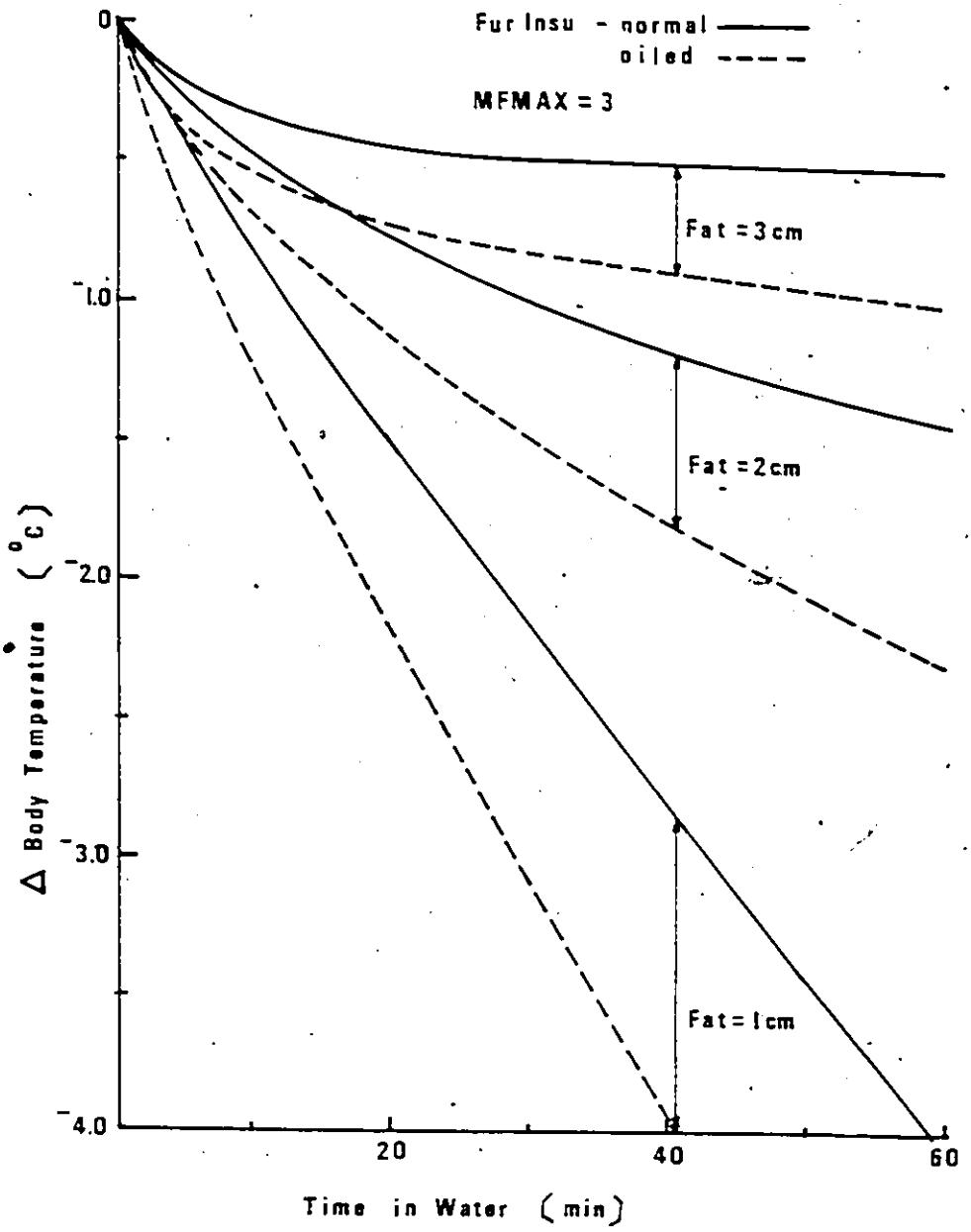
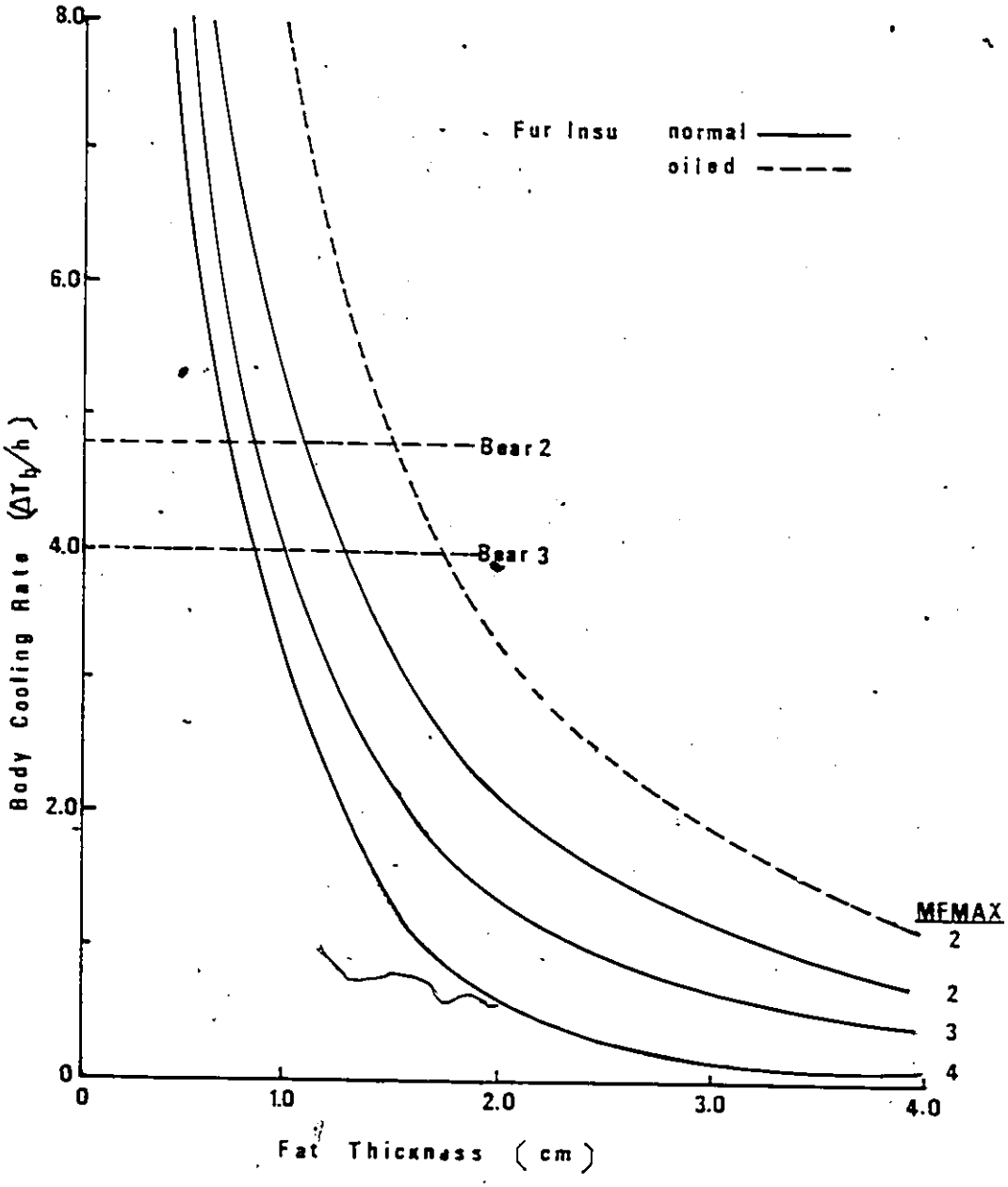

Fur Insu - normal
oiled
MFMAX = 3
Fat = 3 cm
Fat = 2 cm
Fat = 1 cm
0
-1.0
-2.0
-3.0
-4.0
Δ Body Temperature (°C)
20
40
60
Time in Water (min)

Fig 9


8.0
6.0
4.0
2.0
0
Fur Insu
normal
oiled
Bear 2
Bear 3
Body Cooling Rate (ΔTb/h)
MFMAX
2
2
3
4
0
1.0
2.0
3.0
4.0
Fat Thickness (cm)

2) Fat thickness (TYK) values of 1, 2 and 3 cm were used. The fat thickness is judged as a relative indicator of the energetic fitness of the animal at a particular season and age.

3) Maximum metabolic factor (MFMAX) was varied to simulate an oil, or swimming-induced increase in metabolic heat production.

II. ENERGY PROGRAM

INTRODUCTION

The rationale for the program 'ENERGY' follows the preliminary thesis of Best (1977) and extends the concept to the energetic consequences of oil fouling. Best demonstrated that a polar bears' 'average' kill of a 1.9 year old ringed seal would provide approximately 5[illegible]600 kcal of metabolizable energy. By using estimates of the daily energy budget of a free ranging bear (DEB) (Section 4.6), we can predict the sustenance time derived from one prey item.

The high cost of walking particularly in young animals (Section 2.3.3) radically influences the DEB of sub-adult animals. Oil-induced metabolic increments would also necessitate a very high hunting efficiency in order to sustain body weight. A further consideration is that young, inexperienced polar bears are generally poor hunters (Stirling and Latour, 1978) and are most vulnerable to severe environmental conditions (Kingsley, 1979; Siniff et al., 1978). Sub-adult polar bears would probably be most affected by an oil spill encounter. Pregnant or lactating females, by virtue of their normally increased energetic demands, could also be particularly susceptible to oil contact.

PROGRAM DESCRIPTION

The program 'ENERGY' was written to simplify calculations of the total energetic cost of daily activity or DEB. It allows for changes in body size and walking speed in determining the proportional cost of each activity, i.e., sitting, walking. The values are expressed in kcal·day^{-1} and as a fraction of the total DEB. The cost for each activity is also expressed as a fraction of basal metabolism. Finally, the routine estimates the number of days that an 'average' seal would sustain a free-ranging polar bear.

There are two methods of simulating the energetic consequences of oil exposure:

1) To apply metabolic increment values derived from the oil, polar bear study (Section 2,3). For example, this would involve a mean increase in resting values to 1.5 times predicted values, and an increase of 1.24 over predicted walking costs (Fig. 11).

2) The second method involves the use of predicted metabolic values derived from the thermoregulation model to simulate the thermogenic increase in metabolism necesary to sustain T_b. For example, extrapolation of MF values from the CRITA subroutine were used to estimate the factor increase necessary to compensate for an oil-induced reduction in fur insulation (Fig. 10).

FIGURE 10 Daily energy budgets of normal and oiled polar bears at different ambient temperatures. The metabolic cost of maintaining a stable T_b are presented in terms of kcal·day^{-1} and the sustainance time per 'average seal' kill. Metabolic values were determined from the subroutine 'CRITA'. Partitioning of costs per activity were derived from the program 'ENERGY'.

FIGURE 11 Sustainance time per seal expressed as a function of body mass. Oiled values were derived assuming metabolic increments, determined experimentally, of 1.24 times normal for walking and 1.5 times normal for all other activities.

Fig 10

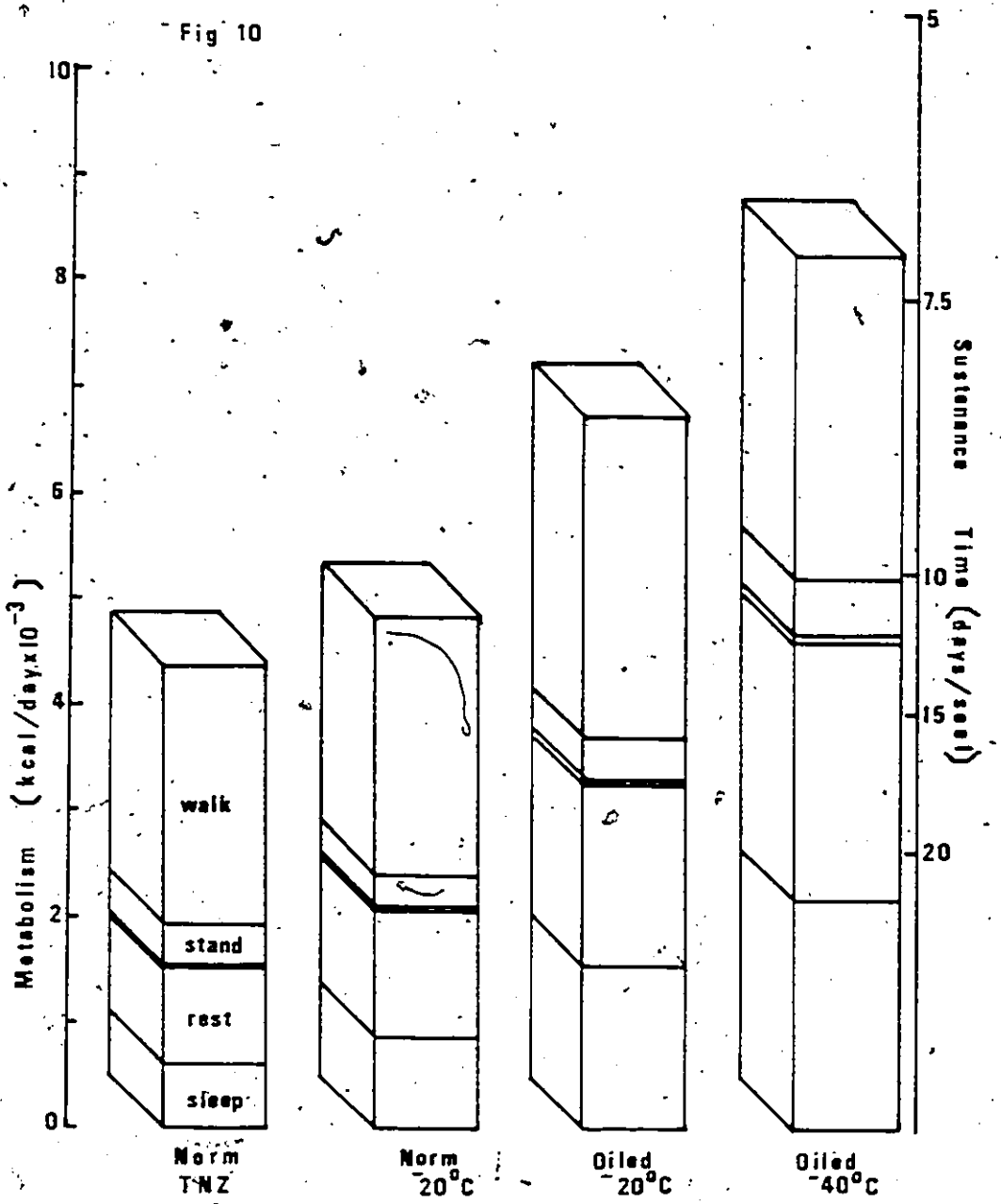
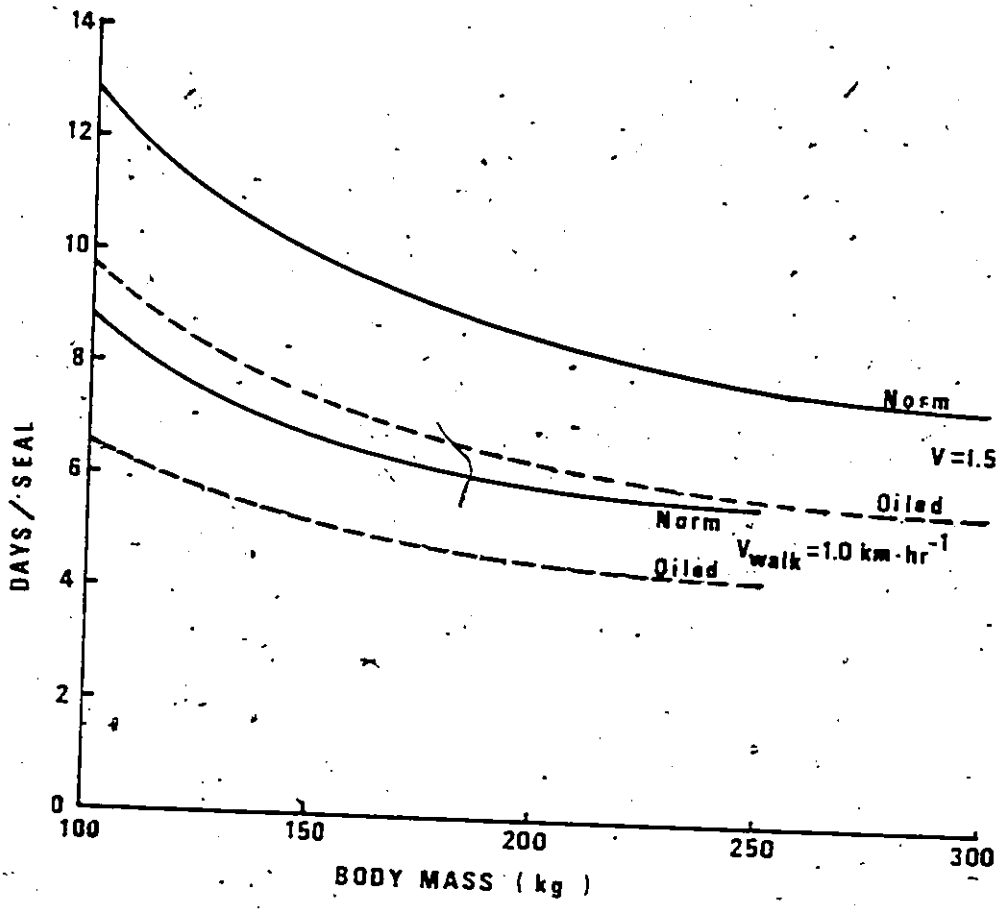

Metabolism (kcal/day x10⁻³)
10
8
6
4
2
0
walk
stand
rest
sleep
Norm TNZ
Norm -20°C
Oiled -20°C
Oiled -40°C
5
7.5
10
15
20
Sustenance Time (days/seal)

Fig 11


14
12
10
8
6
4
2
0
DAYS / SEAL
100
150
200
250
300
BODY MASS (kg)
Norm
V=1.5
Oiled
Norm
Oiled
V_{walk}=1.0 km·hr^{-1}

III. STARVATION–GROWTH MODEL

INTRODUCTION

Starvation or restricted food intake could follow unusually severe environmental conditions (Kingsley, 1979; Siniff et al., 1978), or a marine perturbation such as an oil spill. The survival times of polar bears restricted to using body energy reserves only is estimated using an energy balance model of arctic mammals developed in the language of APL by Øritsland (1976). The original model allows for investigation of food intake and the incorporation of energy into lean body mass and fat reserves. For the purpose of this study, however, I have restricted use of the model to starvation under conditions of 0 food intake. This could be critical if an oil exposed individual became anorexic (Øritsland et al., 1981) or incapable of effective hunting.

MODEL DESCRIPTION

Priority is given to maintenance of the lean body mass while energy flows are balanced against fat mass. Basal metabolism is set to decrease linearly with body weight to a value of 0.6 times normal corresponding to 0.7 times standard body weight (Kleiber, 1975). Maintenance energy requirements are considered as the sum of 3 levels of activity: basal, lying and walking.

Simulations are performed over 1 day time steps and terminated (animal dead) if body weight and basal metabolism reach the limiting value of 0.6 times standard.

The caloric value of fat (FEQ) is set to 9.5 kcal/g while the caloric value of the lean body mass (EQ) is set to 2 kcal/g. The energy content of the fat is thus determined by multiplication of the caloric value times the weight of the animal and fraction of body constituted by fat. The energy content of the lean body mass is determined in a similar manner. The present model is designed especially to investigate the results of considering the body as two energy compartments. It gives top priority to stabilization of the lean body mass, i.e., the maintenance energy is taken primarily from the body fat.

Model predictions were shown to correspond well to observed starvation in the dog (Kleiber, 1975), man (Keys et al., 1950; Kleiber 1975), and Svalbard reindeer (Øritsland, 1976).

The reader is urged to see the orginal model description (Øritsland, 1976) for a more complete, and just treatment of the energy balance model.

MODEL ATERATIONS

The original model was changed (GR: line 12) to consider 5 levels of activity as compared to 3. The energetic cost of each level of activity was assigned a value (Hurst, 1981; Best, 1976) and multiplied by the time, per day, spent at each activity. The daily activity budget is taken from observations of free ranging polar bears as observed by Stirling (1974).

	Factor of BMR		Fraction of day on activity	
sleeping	AF1	1.0	T1	0.297
resting	AF2	1.1	T2	0.328
sitting	AF3	1.5	T3	0.008
standing	AF4	1.7	T4	0.075
walking	AF5	*	T5	0.296

* the energetic cost of walking is a function of the size of the animal and the walking speed (Section 2.3.2). Before initiating the energy balance programme (GR) the animal is standardized by the program ST. At this time the weight and walking speed is given, thus determining AF5.

Reduction in activity during prolonged starvation is common. In the ecological perspective, however, reduced activity also implies a reduction of food intake and thus an increased probability of death. For the purpose of these simulations the activity was maintained at what was considered 'normal' values.

To simulate oil exposure, the activity coefficients (AF1 etc.) were multiplied by an amount deemed sufficient to compensate for oil induced increments in metabolism. The methods were similar to those described for the program 'ENERGY'; using both experimentally derived values and those predicted by the thermoregulation model subroutine 'CRITA' (Figs. 12, 13, 14).

FIGURE 12 Survival times of normal non-oiled polars predicted by the starvation model (GR). The initial body weight and percent of body fat was varied and the survival time estimated in days.

FIGURE 13 Survival times of normal (solid lines) and oiled (dotted lines) polar bears expressed as a function of the amount of fat reserves. Oil values were derived assuming metabolic increments, determined experimentally, of 1.24 times normal for walking and 1.5 times normal for other activities.

FIGURE 14 Survival times of normal and oiled polar bears expressed as a function of the initial body weight. The percent fat was varied, and oiled metabolic values were derived as in Fig. 13.

Fig 12

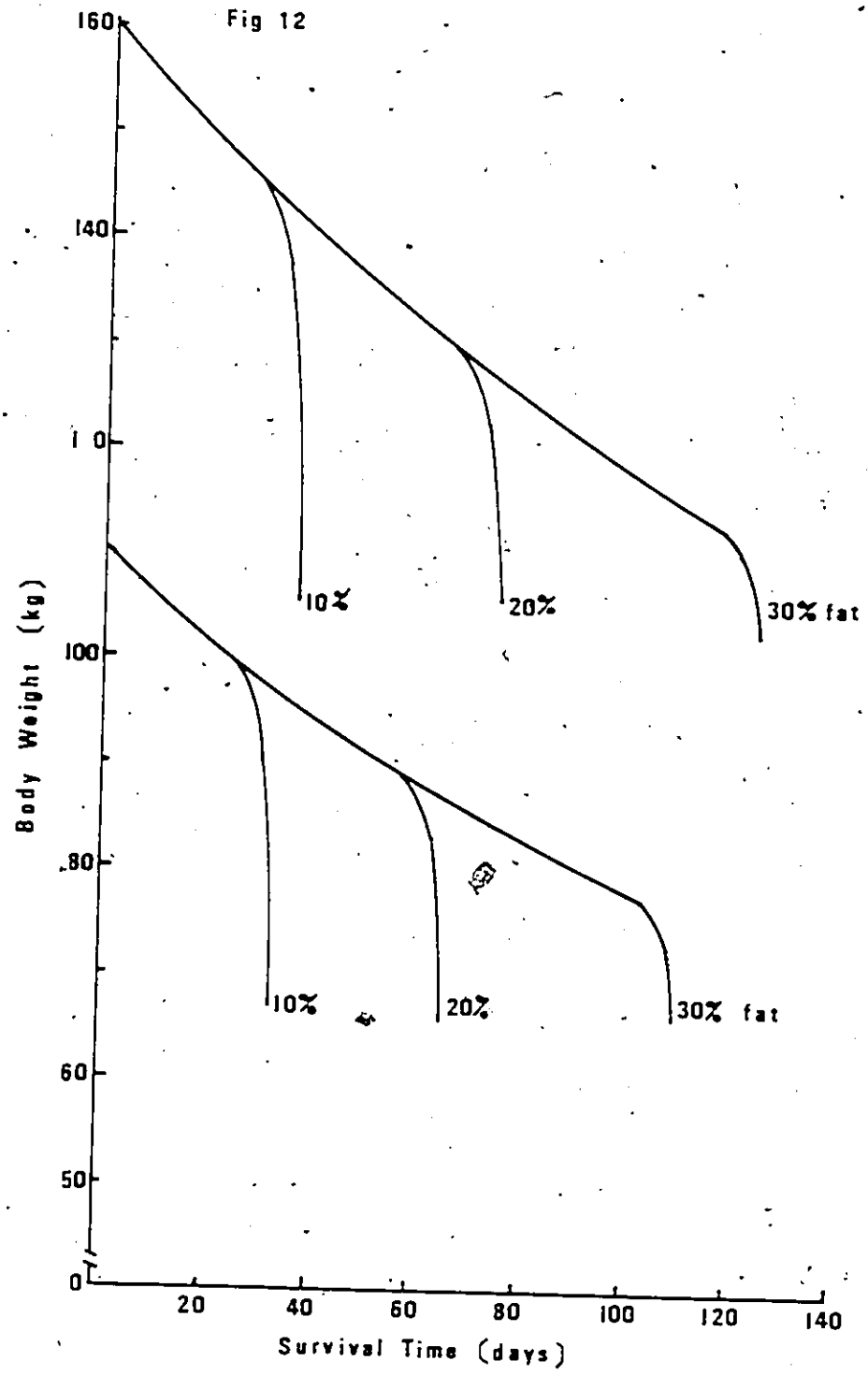

160
140
120
100
80
60
50
0
Body Weight (kg)
10%
20%
30% fat
10%
20%
30% fat
20
40
60
80
100
120
140
Survival Time (days)

Fig 13

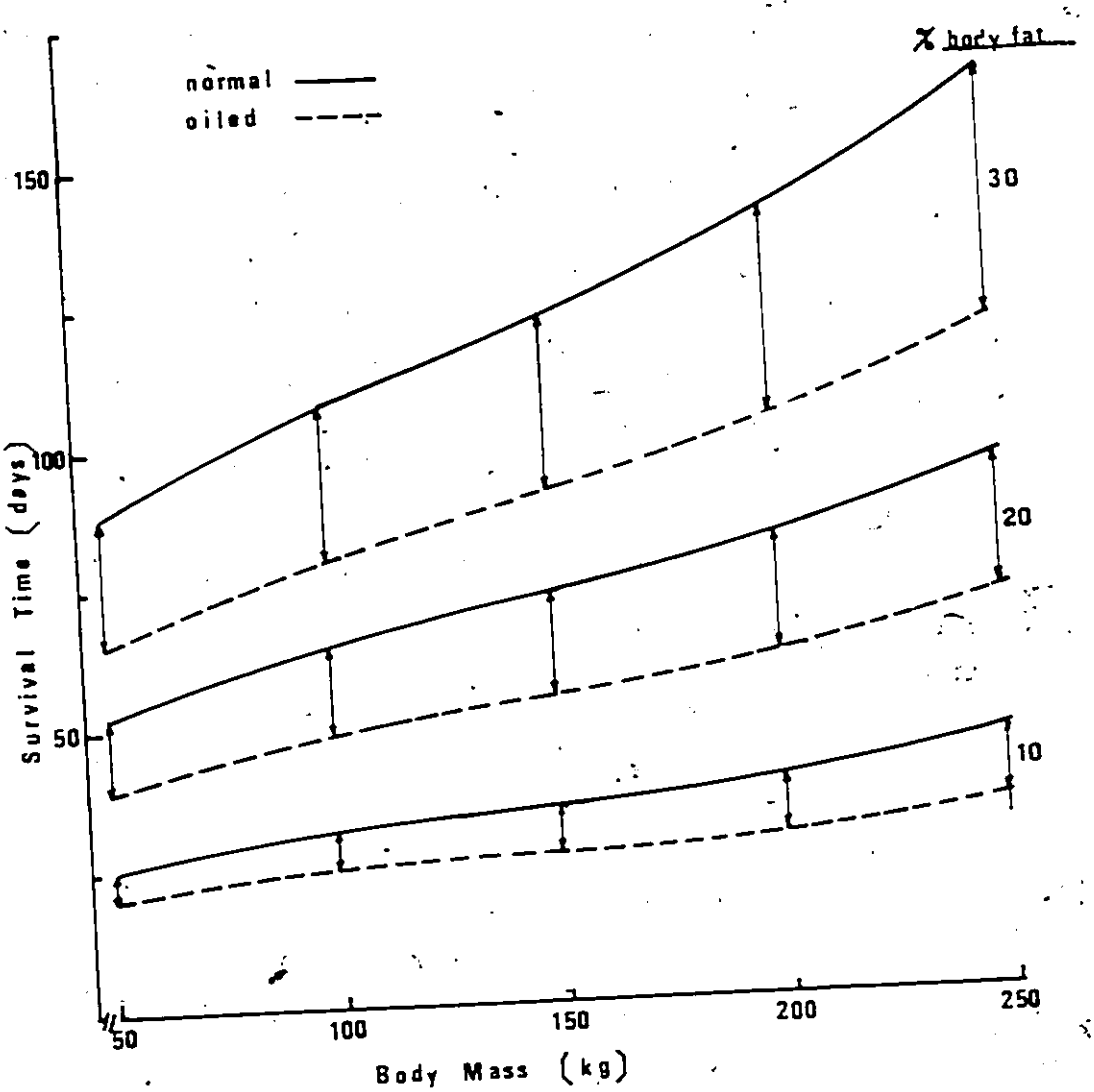
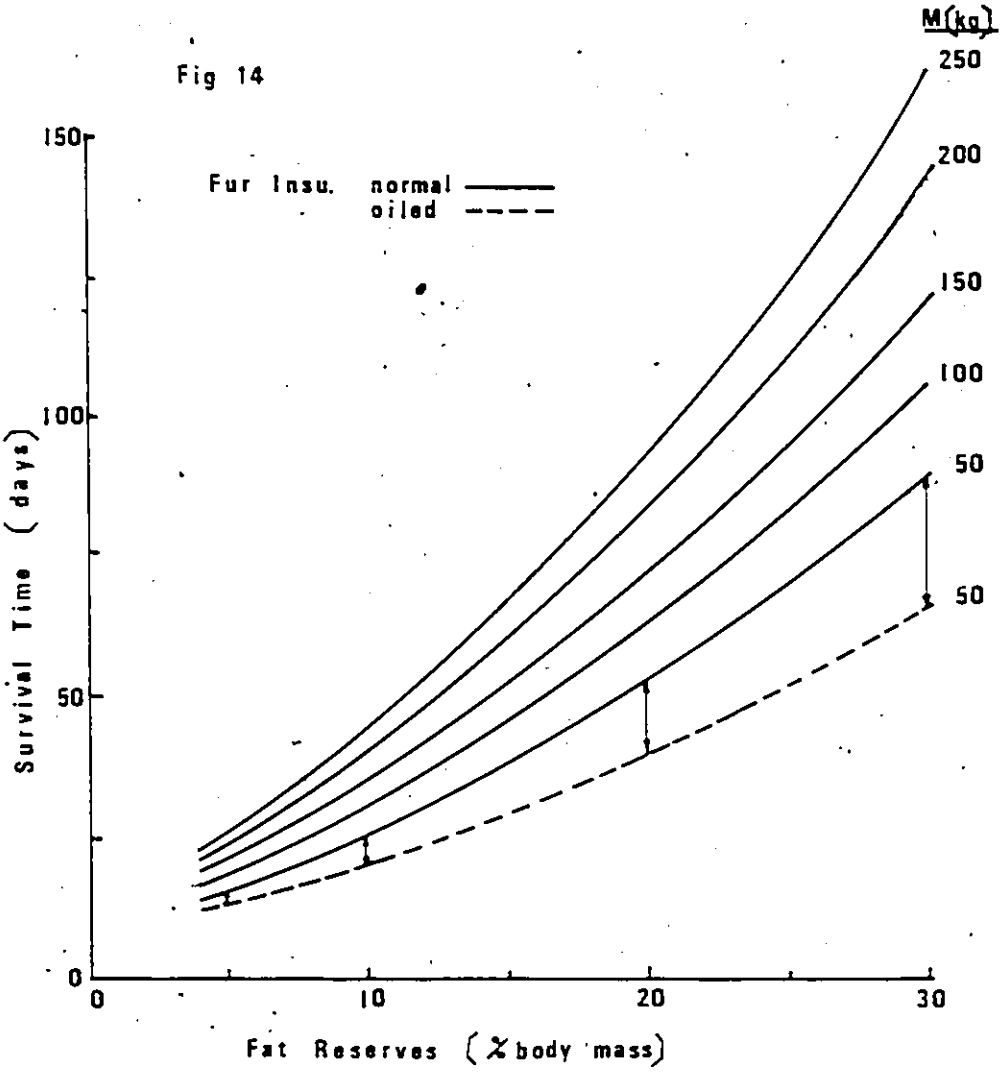

% body fat
normal
oiled
150
100
50
Survival Time (days)
30
20
10
50
100
150
200
250
Body Mass (kg)

Fig 14


M(kg)
250
200
150
100
50
50
Fur Insu. normal
oiled
Survival Time (days)
150
100
50
0
0
10
20
30
Fat Reserves (% body mass)

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* Refer also to references following the thesis text.

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Thermoregulation Model

```
      )FNS
BODYAR
CRITA
GAA
INSU
MODHOW
NERV
POLAR
SEE
SETP
TEST
WEATHER

      ▽POLAR[□]▽
 ▽  POLAR;A;I;AS;Y
[1] T←POLAR←⍳0
[2] 'THIS IS A HEAT BALANCE MODEL'
[3] →(AEV=0)/AL
[4] 'EVAPORATIVE HEAT LOSS IS COUPLED, CHECK "NERVE"'
[5] 'FOR MORE INFO WITHIN THES PROGRAM,("POLAR")'
[6] 'ENTER 1. NO INFO WANTED ENTER 0'
[7] AL:A←□
[8] →(A=1)/DS
[9] 'BODY WEIGHT IS:';W;' KG.'
[10] 'FAT THICKNESS: ';TYK;' M'
[11] 'DEEP BODY TEMP IS: ';TB;' C'
[12] 'ANSWER WITH CORRECT VALUE WHEN BOX APPERS'
[13] ' '
[14] ' '
[15] 'FAT THICKNESS?'
[16] TYK←□
[17] 'DEEP BODY TEMP?'
[18] TB←□
[19] 'RESTING (1 FOR YES 0 FOR NO)?'
[20] Y←□
[21] →(Y=1)/BF
[22] AAA←AAA+EXR
[23] 'GIVE WALKING SPEED (KM/HR)'
[24] VLK←□
[25] GAA
[26] →(F≥1.7)/BI
[27] F←1.7
[28] →BI
[29] BF:F←1
[30] AAA←AAA
[31] BI:I←1
[32] TSN←TS
[33] TBN←TB
[34] MFN←MF←1
[35] MADD←MFMAX-1
[36] ⍝CONTROLLER ACTIVATION:
[37] CH:DTB←TB-TBS
[38] →((TB<TBS)∧TB>TBSH)∘.((TBS≥TB)∧(TB≥TBSH)))/(L1,L2,L3)
```

```
[39] ⍞'TOO COLD'
[40] L1:TF←TA[I]+0.5
[41] EV←0
[42] →((TF≤¯2),(TF>¯2))/(F1,N1)
[43] F1:TF←¯2
[44] N1:BL←TYK
[45] MF←1+MADB×(TBS-TB)÷(TBS-TBSM)
[46] →(MF>MFMAX)/A1
[47] →STR
[48] A1:MF←MFMAX
[49] →STR
[50] ⍞'TOO WARM'
[51] L2:BL←0.001
[52] TF←TB-0.5
[53] MF←1
[54] EVF←TB-TBEVS
[55] →((EVF>0),(EVF>1))/(E1,E2)
[56] →STR
[57] E1:EV←EVF×M×EP
[58] →STR
[59] E2:EV←M×EP
[60] →STR
[61] ⍞'TB WITHIN BOUNDS'
[62] L3:TF←(¯2+TB)×DTB÷(TBSH-TBS)
[63] EV←0
[64] →((TF>TB),(TF≤TB))/(F2,N2)
[65] F2:TF←TB
[66] N2:BL←0.001+TYK×DTB÷(TBSH-TBS)
[67] →(TF<¯2)/TJ
[68] →TT
[69] TJ:TF←¯2
[70] TT:MF←MF
[71] STR:HCI←KF←BL
[72] HLB1←HCI×(AA+BB×V[I]*CC)×(TB-TA[I])
[73] HLB1←HLB1÷(HCI+(AA+BB×V[I]*CC))
[74] HLB←HLB1-SU×SR[I]×SFB
[75] M←3.4×(W*0.75)×MF×F
[76] HLS←(AAA+BBA×(V[I]*CCA))×(TF-TA[I])×AS
[77] TS←(HLB÷(AA+BB×V[I]*CC))+TA[I]
[78] TSN←TSN,TS
[79] EB←3100×W×TB
[80] EB←EB+(M×DT[I])-((HLB×AB)+HLS+EV)×DT[I]
[81] TB←EB÷(3100×W)
[82] TBN←TBN,TB
[83] MFN←MFN,MF
[84] I←I+1
[85] →(I>6)/U
[86] →(I<PDT)/CH
[87] 'TB:';TBN
[88] →STO
[89] STO:'CONTINUE?(1 FOR YES, 0 FOR NO)'
[90] AS←□
[91] →(AS=0)/0
[92] I←1
[93] →CH
[94] DS:MODHOW
[95] U:TEST
[96] →((TST=20)∨(TST<0.005))/TP
[97] →CH
[98] TR:'USE  SEE  FOR DISPLAY OF RESULTS'
```

```
      ▽BODYAR[□]▽
 ▽ BODYAR
[1] 'SET BODY WEIGHT'
[2] W←□
[3] ' '
[4] 'THE MEEH CONST. IS NOW:';MEB+MEA
[4.1] 'SET VALUE OF YOUR ANIMAL'
[5] ME←□
[6] 'SET APPENDAGE FRACTION OF TOTAL AREA (0<MEF<1)'
[7] MEF←□
[9] MEA←ME×MEF
[10] MEB←ME-MEA
[10.1] AS←MEA×W*(2÷3)
[11] AB←MEB×W*(2÷3)
[12] 'THE TOTAL BODY AREA IN SQ. M. IS:';AB+AS
[13] 'THE AREA OF APPENDAGES AND TRUNK RESPECTIVELY ARE:';AS,AB
[14] 'FINI'
 ▽

      ▽INSU[□]▽
 ▽ INSU
[1] 'THE FUR HEAT TRANSFER COEFF IS AN EQUATION:'
[2] 'COEF.=A+B×(WIND SPEED)*C'
[3] 'PRESENT VALUES ARE :A=';AA;'B=';BB;'C=';CC
[4] 'ENTER CORRECT VALUES'
[5] 'A?'
[6] AA←□
[7] 'B?'
[8] BB←□
[9] 'C?'
[10] CC←□
[11] ' '
[12] 'SOLAR UTILISATION IS: ';SU;'W/SQ.M'
[13] 'ENTER CORRECT VALUE'
[14] SU←□
[15] 'THE HEAT TRANSF. COEFF. FOR THE APPENDAGES HAVE'
[16] 'THE SAME FORM AND IS NOW:A=';AAA
[17] 'B=';BBA;'C=';CCA;'ENTER CORECT VALUES'
[18] 'A?'
[19] AAA←□
[20] 'B?'
[21] BBA←□
[22] 'C?'
[23] CCA←□
[24] ' '
[25] 'OK_INSU IS FINI'
 ▽

      ▽WEATHER[□]▽
 ▽ WEATHER
[1] 'AIR TEMP. IS:  ';TA[1];' C'
[2] 'ENTER THE SHIFT YOU WANT'
[3] TA←TA+□
[4] ' '
[5] 'WIND SPEED IS:  ';V[1];'  M/S'
[6] 'ENTER THE SHIFT YOU WANT'
[7] V←V+□
[9] 'GLOBAL RADIATION IS:  ';SR[1];' W/SQ.M'
[10] 'ENTER THE SHIFT '
[11] SR←SR+□
[12] 'OK NEW WEATHER IS SET'
 ▽
```

```
      ▽CRITA[□]▽
 ▽  CRITA;R;TAS;TAC;TSTEP
[1]  'THIS IS A SEARCH FOR CRITICAL AIR TEMP'
[2]  'GIVE START AND END VALUES FOR THE SEARCH'
[3]  'START(HIGH)VALUE FOR SEARCH?'
[4]  TAS←□
[5]  'END(LOW) VALUE FOR SEARCH?'
[6]  TAL←□
[7]  'GIVE STEP SIZE(DEG.C)FOR SEARCH'
[8]  TSTEP←□
[9]  V←V×0
[10] SR←SR×0
[11] TA←TA×0
[12] TA←TA+TAS
[13] POLAR
[14] MCR←MFN[⍳MFN]
[15] TAN←TA[2]
[16] CH:TA←TA-TSTEP
[17] POLAR
[18] MCR←MCR,MFN[⍳MFN]
[19] TAN←TAN,TA[2]
[20] →(TA[2]>TAL)/CH
[21] ' '
[22] ' '
[23] 'METABOLISM IS'
[24] MCR
[25] 'FOR AIR TEMPERARURES'
[26] TAN
 ▽
```

```
      ▽NERV[□]▽
 ▽  NERV
[1]  'DEEP BODY SET POINT TEMP IS: ';TBS;' C'
[2]  'ENTER THE SET POINT WANTED: '
[3]  TBS←□
[4]  'LIMIT TRIGGERING FULL HEAT LOSS AND MIN: HEAT PROD.IS:'
[5]  TBSH;' C'
[6]  'SET YOUR NEW LIMIT'
[7]  TBSH←□
[8]  'LIMIT FOR MAX PROD. AND MIN. HEAT LOSS IS:'
[9]  TBSM;' C,SET NEW LIMIT'
[10] TBSM←□
[11] 'SIMULATE WITH EVAP. HEAT LOSS COUPLED?:1FOR YES,0 FOR NO'
[12] AEV←□
[13] →(AEV=1)/E
[14] EP←0
[15] →N
[15.1] ' '
[16] ' '
[17] E:'TB TRIGGERING EVAP ONSET IS NOW: ';TBEVS
[18] 'SET YOUR VALUE'
[19] TBEVS←□
[20] 'EVAP. HEAT LOSS FRACTION (EP) IS NOW:'; EP
[21] 'SET YOUR VALUE'
[22] EP←□
[23] N:'NEURAL CONTROL SETTING FINISHED'
 ▽
```

```
      ▽SETP[0]▽
 ▽    SETP
[1] 'ENTER SET POINT SHIFT'
[2] S←□
[3] TBS←TBS+S
[4] TBSH←TBSH+S
[5] TBSM←TBSM+S
[6] TBEVS←TBEVS+S
[7] 'TBS';TBS;'TBSH';TBSH;'TBSM';TBSM;'TBEVS';TBEVS
 ▽
```

```
      ▽GAA[0]▽
 ▽    GAA
[1] EF←1241×(W*0.75)
[2] EF←EF+(507+1.625×W)×VLK×W
[3] EF←EF÷1000
[4] EF←EF×4.7
[5] EF←EF×1.162
[6] F←EF÷(3.4×(W*0.75))
 ▽
```

```
      ▽TEST[0]▽
 ▽    TEST
[1] →((TB<35)∨(TB≥39.5))/OU
[2] TST←+/(((⍴TBN)-5)↓TBN)
[3] TST←TST÷5
[4] TST←|(TST-TB)
[5] →(0.005>TST)/STOP
[6] →SL
[7] OU:'SIMSTOP. TB IS OUT OF BOUNDS.';TST←20
[8] →SL
[9] STOP:'TB STABLE AT:';TB
[10] 'THE NUMBER OF ELEMENTS IN THE RESULT VECTOR IS:' ; ⍴TBN
[11] SL:
 ▽
```

```
      ▽SEE[0]▽
 ▽    SEE;A;D
[1] 'THE MOST INTERESTING RESULTS ARE:'
[2] 'TBN=DEEP BODY TEMPS:'
[3] 'TSN=SKIN TEMPERATURES'
[4] 'MFN=METABOLIC FACTORS'
[4.1] 'BL=FUNCTIONAL BLUBBER THICKNWSS'
[5] 'ALL OTHER VARIABLES ARE ALSO AVAILABLE:'
[7] 'REF. PROGRAM DESCRIPTION.'
[8] ' '
[9] 'NOW ENTER VARIABLE NAME:'
[10] A←□
[11] ' '
[12] ' '
[13] A
 ▽
```

Energy

```
      ▽ENERGY[0]▽
 ▽  ENERGY
[1] 'GIVE WEIGHT'
[2] M←□
[3] 'GIVE WALKING SPEED'
[4] V←□
[5] BM←70×(M*.75)
[6] A←.297×BM
[7] B←.328×1.1×BM
[8] C←.008×1.5×BM
[9] D←.075×1.7×BM
[10] E←A+B+C+D
[11] S←(.505-(.00157×M))×V
[12] W←S+(1.056×M*-.25)
[13] WA←W×V
[14] WAL←WA×4.8
[15] WALK←WAL×M×24×.296
[16] F←(E÷M)+WAL
[17] TO←E+WALK
[18] 'COST IN KCAL/DAY AND FRACTION OF TOTAL'
[19] 'SLEEP    ';A;'    AND    ';A÷TO
[19.1] 'REST     ';B;'    AND    ';B÷TO
[20] 'SIT      ';C;'    AND    ';C÷TO
[21] 'STAND    ';D;'    AND    ';D÷TO
[22] 'SUBT     ';E;'    AND    ';E÷TO
[23] 'WALK     ';WALK;'    AND    ';WALK÷TO
[24] 'TOTAL    ';TO;'    AND    ';TO÷TO
[25] '  '
[26] 'FRACTION OF BASAL METABOLISM'
[27] 'SUBT    ';E÷BM
[28] 'WALK    ';WALK÷BM
[29] 'TOTAL   ';TO÷BM
[30] '  '
[31] 'DAYS PER SEAL';52600÷TO
 ▽
```

```
      ▽DYR[□]▽
 ▽  DYR
[1] 'STANDARD WEIGHT IS:       ';WS
[2] 'PERCENT FAT IS:           ';FPR
[3] 'GIVE STANDARD WEIGHT'
[4] WS←□
[5] 'DO YOU WANT TO CHANGE FAT PRCTN?'
[6] S←□
[7] →(S=1)/LA
[8] FA←FPR×WS
[9] FAES←FA×9500
[10] LB←LBPR×WS
[11] LES←EQ×LB
[12] →17
[13] LA:'GIVE NEW FAT PRCNT,(0<FPR≤1)'
[14] FPR←□
[15] LBPR←1-FPR
[16] →8
[17] 'BODY COMPOSITION:'
[18] 'STANDARD WEIGHT(WS).     :';WS
[19] 'PERCENT FAT              :';FPR
[20] 'FAT MASS                 :';FA
[21] 'LEAN BODY MASS           :';LB
 ▽

      ▽ST[□]▽
 ▽  ST
[1] 'STANDARD WEIGHT IS:       ';WS
[2] 'PERCENT FAT IS:           ';FPR
[3] 'WALKING SPEED IS:         ';V
[4] 'GIVE STANDARD WEIGHT'
[5] WS←□
[6] 'GIVE WALKING SPEED'
[7] V←□
[7.1] →((WS<100),(WS>250))/(LC,LD)
[7.2] →LE
[7.3] LC:TW←.348
[7.4] →8
[7.5] LD:TW←.1125
[7.6] →8
[7.7] LE:TW←.505-(.00157×WS)
[8] WA←(1.056×WS*-.25)+(TW×V)
[9] AF5←(WA×V×4.8×WS×24)÷(70×(WS*0.75))
[10] 'DO YOU WANT TO CHANGE FAT PERCNT?'
[11] S←□
[12] →(S=1)/LA
[13] FA←FPR×WS
[14] FAES←FA×9500
[15] LB←LBPR×WS
[16] LES←EQ×LB
[17] →21.1
[18] LA:'GIVE NEW FAT PRCNT,(0<FPR≤1)'
[19] FPR←□
[20] LBPR←1-FPR
[21] →13
[21.1] AF1←1
[21.2] AF2←1.1
[21.3] AF3←1.5
[21.4] AF4←1.7
```

```
[22] 'ACTIVITY COEFFICIENTS:'
[23] 'SLEEP, AF1    :';   AF1
[24] 'REST,  AF2    :';   AF2
[25] 'SIT,   AF3    :';   AF3
[26] 'STAND, AF4    :';   AF4
[27] 'WALK,  AF5    :';   AF5
[27.1] '    '
[28] 'BODY COMPOSITION:'
[29] 'STANDARD WEIGHT (WS)      :';WS
[30] 'PERCENT FAT               :';FPR
[31] 'FAT MASS                  :';FA
[32] 'LEAN BODY MASS            :';LB
 ▽

      ▽GR[□]▽
 ▽  GR
[1] I←⍳1
[2] W←FA+LB
[3] WN←W
[4] L6:NE←NFL×T[I]
[5] MBF←¯0.33+(1.33×W)÷WS
[6] →((MBF<0.6),(MBF>1),((0.6≤MBF)∧(1≥MBF)))/(L1,L2,BME)
[7] L1:MBF←0.6
[8] →BME
[9] L2:MBF←1
[10] →BME
[11] BME:MB←70×(W*0.75)×MBF
[12] MA←(MB×AF1×T1×T[I])+(MB×AF2×T2×T[I])+(MB×AF3×T3×T[I])+
[12.1] MAW←(MB×AF5×T5×T[I])
[12.2] MA←MA+MAW                    →(MB×AF4×T4×T[I])
[13] B←NE-MA
[14] LE←B+LB×EQ
[15] LEB←LE-LES
[16] →(LEB>0)/L3
[17] FAE←(FA×9500)+LEB
[18] →(FAE≥0)/L4
[19] LE←(LB×EQ)+FAE
[20] LB←LE÷EQ
[21] FA←0
[22] →V
[23] L4:LB←LES÷EQ
[24] FA←FAE÷9500
[25] →V
[26] L3:FA←FA+LEB÷9500
[27] →(FA≥(FAES÷9500))/L8
[28] LB←LES÷EQ
[29] V:W←LB+FA
[30] WN←WN,W
[31] I←I+1
[32] →(I>⍴T)/L7
[33] →((MBF≥0.6)∧(W≥(0.6×WS)))/L5
[34] →L6
[35] L7:'SIMULATION FINISHED. GROWTH IS:'
[36] ⎕WN
[37] →0
[38] L5:'ANIMAL STARVED TO DEATH, WEIGHT LOSS IS:'
[39] ⎕WN
[40] 'SURVIVAL    = ';((⍴WN)-1);' DAYS'
[41] 'WEIGHT AT DEATH IS  ';WN[(⍴WN)-1];' KG'
[42] →0
[43] L8:'ANIMAL IMPOSSIBLY FAT, SIMUL. STOPPED:'
[44] ⎕WN
 ▽
```