# HAULING OUT BEHAVIOUR OF HARBOUR SEALS (*Phoca vitulina richardsi*), WITH PARTICULAR ATTENTION TO THERMAL CONSTRAINTS

by

Peter Watts

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# ABSTRACT:

# HAULING OUT BEHAVIOUR OF HARBOUR SEALS (*Phoca vitulina richardsi*), WITH PARTICULAR ATTENTION TO THERMAL CONSTRAINTS

Peter Watts, Ph.D.
University of British Columbia, 1991

Supervisor:
Prof. Carl J. Walters

Harbour seals throughout their range are known to "haul out" onto land according to a daily cycle, which has never been fully investigated. This cycle may represent a tradeoff between the need to forage and the need to avoid aquatic predators; if so, seals should forage when prey availability is greatest and remain hauled at other times. A model based upon these premises accounted for approximately two thirds of the variation in observed hauling behaviour at a harbour seal colony in the Strait of Georgia, once other environmental effects had been filtered from the data. Some such effects could not be corrected for; since air temperature and solar radiation follow the same general pattern as that predicted by the hauling model, the possibility that hauling occurs in response to thermal conditions could not be excluded. This issue was addressed by correlating hauling activity at three seal colonies with "flux" $F_s$, an index of heat exchange between a seal and its environment. Once time of day and tidal effects were accounted for, there was no evidence of a positive correlation between hauling and $F_s$. However, under warm summer conditions there was a steep negative relationship. This is consistent with the possibility that hauled harbour seals are vulnerable to hyperthermia due to their adaptation to an aquatic lifestyle; the same blubber layer which keeps them warm when immersed may make it difficult for them to lose excess heat when on land. This was confirmed by a series of controlled experiments. Captive seals overheated when exposed to a radiant thermal environment similar to that in which wild animals stopped hauling. These data allowed me to derive an equation which described the rate of change in a seal's core temperature as a function of both present core temperature and $F_s$. I incorporated this function into a simulation model which described hauling behaviour in terms of a foraging/predator-avoidance tradeoff. The model performed well when used to predict the haul out durations of a sample of wild radio-tagged harbour seals in a known thermal environment. However, it is apparent that the processes which constrain hauling in this species are somewhat better understood than those which presumably cause it. An understanding of the foraging efficiency of harbour seals throughout the day, and of the predation risks they face, is probably fundamental to an understanding of hauling; yet these issues remain virtually unexplored.

In memory of Mike Bigg.

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Heartfelt thanks to you all, and goodbye.

# 1. GENERAL INTRODUCTION

## 1.1 HAULING OUT IN HARBOUR SEALS

All pinnipeds forage in the water, and give birth on land or ice. The shore-bound reproductive phase of their lives can last for months (for example, socially organised species like elephant seals *Mirounga sp.*) or for as little as four days in the case of the hooded seal *Cystophora cristata* (Bowen *et al.* 1985). Many species are almost entirely pelagic, coming ashore only to reproduce; northern fur seals *(Callorhinus ursinus)* and harp seals (*Phoca groenlandica*) are two examples. Other species (e.g. California sea lions *Zalophus californianus*, and gray seals *Halichoerus grypus*) "haul out" onto solid substrates much more frequently, for reasons which often seem unrelated to reproduction. The harbour seal, *Phoca vitulina*, is one such species.

Harbour seals are common phocids, widely distributed along the coasts of both the North Atlantic and North Pacific Oceans. They live mainly in coastal and estuarine waters, although they are sometimes found in rivers a considerable distance from the coast (Roffe and Mate 1984). Five subspecies are currently recognised: *P. vitulina vitulina*, from the eastern Atlantic; *P. vitulina concolor*, from the western Atlantic; *P. vitulina richardsi*, the Pacific harbour seal; the insular seal *P. vitulina stejnegeri*, from the Asian coast of the North Pacific; and *P. largha*, the larga seal, an ice-breeding subspecies found in the Bering and Chukchi Seas, as well as along the Asian North Pacific coast. King (1982) gives a concise overview of the natural history of each subspecies.

Throughout their range, harbour seals routinely haul out for hours at a time, often daily. Hauling out generally follows a diel cycle (see below), with numbers on land peaking near mid-day and declining at night[1].

The reasons for this commonly observed behaviour have not been closely investigated. This is perhaps surprising, given the large number of published studies on hauled harbour seals. Numerous studies simply summarise trends in data, with little or no attention to underlying causes. Many papers describe a colony of harbour seals in terms of observed daily or seasonal hauling patterns, with occasional reference to an environmental correlate or two (e.g., Allen *et al.* 1984, Pauli and Terhune 1987, Schneider and Payne 1983, Sullivan 1980). It is usually reported that hauling is maximal during the summer months and minimal during the winter (e.g., Boulva and McLaren 1979, Loughlin 1978, Sullivan 1980, Thompson 1989); but with the exception of peaks due to pupping and moulting (Boulva and McLaren 1979, Sullivan 1980) the issue of whether these seasonal differences reflect a change in numbers or behaviour is dealt with in passing (Boulva and McLaren 1979), or not at all. Mid-day peaks in the diel hauling cycle are widely reported with little or no discussion of their potential

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[1] There are exceptions to this trend, however (e.g., Paulbitsky 1975, Renouf *et al.* 1981).

significance (e.g., Stewart 1984, Stewart and Yochem 1985). Even telemetry studies, which obtain data from dozens of seals for months at a time (Pitcher and McCallister 1981, Stewart and Yochem 1985, Thompson 1989) spend most of their length on recitation of feeding movements or apparent hauling preferences. Any discussion of the possible reasons for these patterns is often anecdotal.

A smaller segment of the literature focuses specifically upon the social significance of hauling in groups, rather than the more basic issue of why seals haul out in the first place. This work usually explores specific hypotheses regarding the underlying causes of grouped hauling; advocates of various positions have met with variable success. For example, it has been suggested that grouped hauling reduces the individual effort necessary to scan for predators (da Silva and Terhune 1988); however, that study appears to suffer from a serious confound which render its conclusions doubtful[2]. An alternative viewpoint is that grouping is in some way related to mate selection (Renouf and Lawson 1986), but this would not explain why harbour seals often haul out in groups year-round when the mating season lasts two months at most. Even so, studies which attempt to test hypotheses usually generate more insight than those which simply report data, and several quite rigorous efforts have resulted; Härkönen (1987) and Krieber and Barrette (1984) are two noteworthy examples.

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[2] Harbour seals haul initially in small groups which grow in numbers throughout the day; seals in smaller groups have therefore been hauled for less time than those in larger groups. This alone may be enough to explain the correlation between group size and scanning rate, since a seal that has been resting for hours may have "settled down", and be less active than one which has just emerged from the water.

But on the basic issue of why seals haul out in the first place, the literature has little comment. Schneider and Payne (1983) suggest that hauling out to rest saves metabolic energy, but provide no evidence to this effect; while Boulva and McLaren (1979) make essentially the same anecdotal argument, only at greater length (see Chapter 2). Passing comments that seals haul out to "rest" or "bask" are not uncommon in the literature, and are almost never supported (harbour seals can and frequently do rest while immersed).

Ironically, perhaps the most rigorous evidence of an underlying cause for hauling comes not from the field but from the laboratory: epidermal cells of harbour seals do not metabolise properly below 17°C, which implies that seals must haul out (at least intermittently) to allow their skin to grow. Additionally, phocid seals may be incapable of fast-wave sleep when submerged (Ridgway *et al.* 1975); perhaps harbour seals have to haul out in order to dream (although sleep while submerged is commonly observed). However, neither of these explanations is entirely satisfactory, since other phocids (such as the harp seal) spend most of each year at sea, to no apparent ill effect.

It is therefore quite a simple matter to summarise the present state of insight into hauling out behaviour of harbour seals:

1. Harbour seals generally haul out following a diel cycle.
2. This is widely assumed to occur for some simple reason such as "basking in the sun" or "resting".

3. Point (2) notwithstanding, the reasons for diel hauling have never been deeply explored.

## 1.2 MODELS OF CONSTRAINT

Life is not an easy target for reductionist analysis. This is particularly true in the field of ecology, where the arena of study includes whole populations of organisms, in constant interaction with their environment and each other. Such systems are far too complex to be well understood through direct observation.

A traditional response has been to deal not with the system itself, but a simplified mathematical analog thereof: a model. Since models are particularly popular with population and ecosystem biologists (Fowler and Smith 1981, Swartzmann and Kaluzny 1987, and Walters 1986 are three recent examples), individual organisms have generally become lost in the simplification process. The population is defined, not as a collection of individuals, but as a single component whose volume changes according to "transition rules" representing such processes as birth, predation, and competition. Each component is essentially a black box; it interacts with other components according to specific rules, but its inner workings (the processes leading to those rules) remain undefined. Walters (1986) definition of models as "caricatures of reality" is as apt as any.

When dealing with behavioural aspects of biology, models operating on the level of whole populations are clearly inappropriate. The past two decades have seen the advent of an entirely new class of model, which deal with the interaction of individuals with their environment. At this more intimate scale, global components such as birth rate, predation rate, and competitive effects change so slowly that they are largely irrelevant. Instead, such factors as heat exchange or prey selection are important; core temperature or gut fullness replace population size as the state variable.

These behavioural models fall into the realm of "biophysical ecology", a recent marriage of ecology with classical thermodynamic physics. Biophysical ecologists treat the organism as the black box, whose surfaces exchange energy with the physical environment. To date, most such models have dealt with thermal balance of animals; this is calculated using a series of equations describing radiative, conductive, convective, and evaporative exchange between the animal and its environment. (A metabolic heat component is generally included when dealing with endotherms.) It is therefore possible to calculate an organism's thermal state in any environment; by comparing such estimates with the conditions necessary for thermoneutrality, behavioural and distributional predictions are possible. These range from relatively simple statements of the range of conditions an animal can tolerate ("climate space diagrams") to predictions of foraging budgets and diel variations in habitat preference (Gates 1980).

The biophysical approach to behaviour has yielded valuable insights into the behaviour of a diverse range of taxa including small mammals (Bakko *et al.* 1988, Morehardt and Gates 1974), birds (Porter and Gates 1969), and reptiles (Roughgarden *et al.* 1981, Scott *et al.* 1982). There are, however, limitations upon how far one can take this approach. Essentially, it deals in terms of constraint; biophysical models describe the thermal limits within which an animal can operate. Within these limits--where thermal constraints are relatively unimportant--it is impossible to make meaningful predictions using the biophysical approach. The situation is analogous to that of an animal grazing in a pasture bounded by an invisible fence. Biophysical models are very effective at describing the location of the fence, and can safely predict that the animal will not venture beyond it; but they are powerless to predict the animal's behaviour within the pasture. Recent advances in the sophistication of these models (Porter 1989) have successfully defined the pasture in a greater number of environmental dimensions (and even show potential for studies at the population level) but are ultimately still limited to describing constraints imposed by the physical (nonliving) environment.

Biophysical models, then, work most effectively for species which are strongly constrained by their thermal environment. The dependence of body temperature on external conditions is much greater for ectotherms than for endotherms of the same size, for example; one would therefore expect a biophysical model to be a better predictor of ectotherm behaviour. Likewise, a small animal is much more susceptible to thermal stress than a large animal because of its greater surface area to volume ratio. Shrews would therefore be more apt subjects for biophysical modelling than whales.

For these reasons, it is not surprising that most biophysical models to date have dealt with small-bodied animals, particularly ectotherms (see above). There is no reason why they cannot also be applied to large-bodied endotherms, and this has in fact been done with some success (Schmitz 1990). However, the relative thermal independence of large animals implies that proportionately more of their behaviour is due to other factors, requiring different modeling techniques (the dynamic programming models of Mangel and Clark (1988) have proven to be good candidates in this regard.) Thermodynamic constraints are generally of reduced importance to large endotherms.

Pinnipeds--or any amphibious mammal, for that matter--might be expected to break this rule. Truly amphibious mammals must somehow reconcile the conflicting demands of two completely different thermal environments, and an adaptation beneficial in one medium may well be counterproductive in another.

Water conducts heat 25 times more efficiently than does air. Because of this, aquatic endotherms are in little danger of overheating; they can effectively dissipate heat even when water temperature is only slightly less than that of the body core (Whittow 1987). In fact, the main thermal concern of an immersed endotherm is to minimise heat loss. To this end, aquatic mammals have evolved a number of heat-retention strategies including peripheral vasoconstriction, countercurrent heat-exchange retia in the appendages, dense waterproof fur which traps air next to the skin during immersion (e.g., the sea otters *Enhydra lutris*), and a massive layer of insulative blubber which can account for almost half of the total body mass (all phocids).

Passive heat dissipation occurs much more slowly on land than in the water, meaning that overheating is of greater concern in a terrestrial setting. This poses particularly severe problems to any animal equipped with the heat-retaining adaptations mentioned above. The same insulation which prevents hypothermia in an immersed endotherm increases the danger of overheating once it leaves the water. This is a greater problem for animals that use blubber as their primary insulator, since the insulating effects of fur can be mitigated to some extent by air circulation between the hairs (Gates 1980). Alternatively, animals with blubber can increase evaporative heat loss through panting (eg, the northern fur seal *Callorhinus ursinus*) or profuse salivation (eg, the California seal lion, *Zalophus californianus*) when in danger of hyperthermia.

Phocid seals lack either option. Not only do they possess a thick layer of blubber, but they lack functional sweat glands or any other specialised strategy for enhancing evaporative heat loss. The only effective thermoregulatory strategy that remains is behavioural; when a phocid on land ("hauled out") begins to overheat, its only real option is to return to the water. This should tie phocid behaviour to the physical environment much more closely than would normally be the case for a large-bodied endotherm. In fact, hauling behaviour among phocids may be a predictable function of the physical environment.

## 1.3 THESIS OVERVIEW

The research reported in the following pages was undertaken on the premise that all living organisms are essentially puppets of their environment, and that an amphibious life style may make the strings somewhat more apparent than would otherwise be the case for a large mammal. Harbour seals are fitting subjects for such studies, both because of their wide climatic range and because they are relatively unspecialised (and may thus be thought of as "typical" phocids).

The body of the thesis consists of four major parts. Chapter 2 presents a simple theoretical model which describes diel hauling behaviour as a basic tradeoff between the need to eat and some cost (possibly the risk of predation) associated with remaining immersed. Insomuch as it is fitted to naturalistic (hence uncontrolled) observations, the model cannot be confirmed; however, its predictions are consistent with observed patterns, and provide a logical framework upon which to hang more direct environmental effects.

Chapter 3 explores evidence from field studies suggesting that hauling behaviour is constrained by the thermal environment, and that these constraints are consistent with the premise that harbour seals are vulnerable to hyperthermia when on land.

Chapter 4 relates a series of experiments on captive harbour seals, which establish that overheating does in fact occur under thermal conditions commonly encountered by seals hauling in the wild. Further, this chapter derives an empirical model of the hyperthermic reponse, which predicts change in core temperature as a function of both environmental heat state and present core temperature.

Chapter 5 combines the insights gleaned from Chapters 2-4 in a simulation model which predicts how long harbour seals are likely to remain hauled under given environmental conditions. These predictions are compared to hauling data obtained from a radio-tagged sample of wild harbour seals.

Several aspects of the work reported in Chapters 2-5 are based upon assumptions which, although biologically sensible, are necessarily speculative. In Chapter 6, I briefly discuss possible reasons for this "insight gap", and prospects for bridging it in the future.

Finally, a note on format. Each chapter was designed to be more or less self-contained. Although all chapters report upon different aspects of the same basic research, the reader should be able to read any chapter independently of the others. This means that there is some necessary redundancy in the various introductions. I hope that anyone reading this volume cover to cover will forgive the repetition.

# 2. DIEL HAULING BEHAVIOUR IN HARBOUR SEALS (*Phoca vitulina*): CAUSES AND CONSTRAINTS.

## 2.1 ABSTRACT

Like many other pinnipeds, harbour seals regularly haul out onto land throughout their range. This behaviour follows a regular diel cycle. Several possible explanations for hauling out have been put forth, usually based on natural history observations; behavioural thermoregulation is a popular contender. However, the issue has not received close attention, possibly because hauling behaviour is affected by a large number of environmental factors; it is difficult to separate those which drive hauling, from those which merely constrain or disrupt it in some way. Over two years at a harbour seal colony in the Strait of Georgia, I recorded hauling activity around the clock concurrent with a variety of environmental variables. Regression analysis was used to ascertain which conditions were correlated with reduced hauling activity; by excluding observations made under such conditions, I obtained a data set which was relatively free of confounding noise, and therefore more representative of the diel hauling cycle. This data set was used to fit a simple model ($r_{adj}^2$=0.651) which was based on the premises that harbour seals 1) maximise foraging efficiency by feeding at night, and 2) remain hauled whenever they are not foraging. The latter assumption implies a significant cost associated with immersion; this may be due to the predation

risk faced by immersed animals. The model predicts a pronounced asymmetry in the diel hauling cycle, with maximal hauling occurring in late afternoon; this pattern was strongly evident in the filtered data set. Since the model predicts hauling behaviour reasonably well using a simple foraging/immersion-minimizing paradigm, the proposed thermoregulatory explanation may be unnecessary (although such thermoregulatory problems may influence hauling to some extent). Quantitative estimates of predation risk and prey availability are needed for more rigorous analysis. Although many complex factors affect the latter parameter, it may be possible to infer prey availability from the rate at which harbour seals return to the haul-out site after foraging.

## 2.2 INTRODUCTION

All pinnipeds haul out. In many species this appears to be simply a reproductive constraint; twenty million years (King 1982) of pinniped evolution have not produced an animal reproductively independent of land or ice. For this reason, even the most pelagic pinnipeds (the northern fur seal, *Callorhinus ursinus*, and the harp seal, *Phoca groenlandica* are two examples) must haul out during at least some part of the year.

However, there are also a number of pinniped species that haul out throughout the year, for reasons apparently unrelated to reproduction. Harbour seals (*Phoca vitulina*) are probably the best known example. Exactly why these animals haul out year-round has rarely been addressed. Although a number of studies have explored the question of why harbour seals haul out in groups (Godsell 1988, Renouf and Lawson 1986, da Silva and Terhune 1987), the more fundamental question of why they haul out in the first place has not been closely examined.

One explanation which appears to have wide acceptance is that hauling out is an act of behavioural thermoregulation (King 1982). Seals are thought to haul out on warm days to bask in the sun, and to avoid hauling in cold weather (Boulva and McLaren 1979). This premise has intuitive appeal, and there is evidence that phocid seals must warm their surfaces periodically to allow their skin to metabolise (Feltz and Fay 1966). However, the suggestion that cold seals haul out to sun themselves may owe more to anthropomorphism than to any rigorous analysis of pinniped energetics. Even postabsorptive, resting harbour seals remain thermoneutral in seawater as cold as -1.8°C (Ashwell-Erickson and Elsner 1980), and it is not uncommon for harbour seals to frequent waters which are days distant in swimming time from the nearest possible haul-out site (M. Bigg[3] pers. comm.) In fact, exposure to sunlight can cause hauled phocids to overheat (Chapters 3 and 4, Finley 1979, Whittow 1978).

It is also unlikely that harbour seals stay immersed to avoid cold weather. The thermal conductivity of water is twenty-five times that of air; it is difficult to imagine weather conditions so cold that homeothermy would be less expensive for an immersed seal than for a hauled one. Although thermoregulation may be one component of hauling behaviour (Krieber and Barrette 1984), it is unlikely to be the driving one.

Several other reasons for phocid hauling have been suggested, ranging from sleep (Schneider *et al.* 1980) and grooming (Sullivan 1979) to Vitamin D synthesis (McLaren 1958); these have generally been based on natural history observations of how seals behave when hauled out. Unfortunately, the fact that hauled seals engage in a given behaviour does not establish that behaviour as the reason for hauling. Seals certainly sleep when they are hauled out, for example; but they also sleep while immersed.

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[3] Dept. of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C.

Hauling out may in fact occur for very simple reasons; it may be unnecessary to invoke a variety of complex explanations. Pinnipeds must enter the water to forage, and are so well adapted to an aquatic lifestyle that some species only haul out for reproductive purposes. In the case of the harbour seal, it could be argued that hauling would not occur at all unless there were some significant cost associated with remaining in the water. If this is the case, then harbour seals should immerse only to feed and to mate (mating is aquatic in this species), and remain hauled at all other times.

Whatever the underlying reason(s) for hauling, it is (they are) influenced to a great extent by a variety of confounding environmental factors. Tidal height generally constrains the space available for hauling (Krieber and Barrette 1984, Pauli and Terhune 1987, Schneider and Payne 1983, Sullivan 1980). Hauling is reduced under strong winds (Schneider and Payne 1983) and in the presence of precipitation (Krieber and Barrette 1984). On the other hand, it can be positively correlated to air temperature (Boulva and McLaren 1979, Krieber and Barrette 1984.) When one deals with data sets obtained by observing wild populations, there is always a danger that functional relationships could be drowned in extraneous noise.

This paper presents a simple theoretical model based on the premise that hauling in harbour seals is basically a trade-off between the need to forage and some cost associated with remaining immersed. I argue that although a thermoregulatory component can not be ruled out, the greatest part of this cost is likely to be the danger of predation. The model is then compared to observations made on a colony of harbour seals in the coastal waters of British Columbia. To reduce variation caused by other variables, the model is fitted to a data set in which the effects of potentially confounding environmental factors have been minimised.

## 2.3 MATERIALS AND METHODS

### 2.3.1 Model Background

Harbour seals have access to two habitats: a terrestrial haul-out free from aquatic predators, but devoid of prey, and a productive but dangerous aquatic environment. Each seal must balance its expected foraging success (which can be maximised by remaining perpetually immersed) against the danger of being eaten (which can be minimised by remaining perpetually hauled out). It is possible that the daily hauling cycle of harbour seals is a basic manifestation of that balance.

The effects of aquatic predation on the dynamics of harbour seal populations remain almost completely unexplored (although some work has been done on possible behavioural responses to the danger of land-based predators (da Silva and Terhune 1988)). Throughout the waters of British Columbia, seal populations have been increasing exponentially since the early seventies (Olesiuk *et al.* 1990); until recently, predation was assumed to have a negligible effect on their numbers (M. Bigg, pers. comm.). However, some basic calculations make it quickly evident that this is not the case.

Along the Canadian Pacific coast, the most conspicuous aquatic predators of harbour seal are transient killer whales (or, simply "transients") (*Orcinus orca*) (Bigg *et al.* 1987). Based upon observations from around the southern end of Vancouver Island, an average transient eats approximately 1.5 harbour seals/day (R. Baird[4], unpublished data). About 110 of these animals have been recorded in B.C. waters (Bigg *et al.* 1987), although it is unlikely that all of these would be present at the same time.

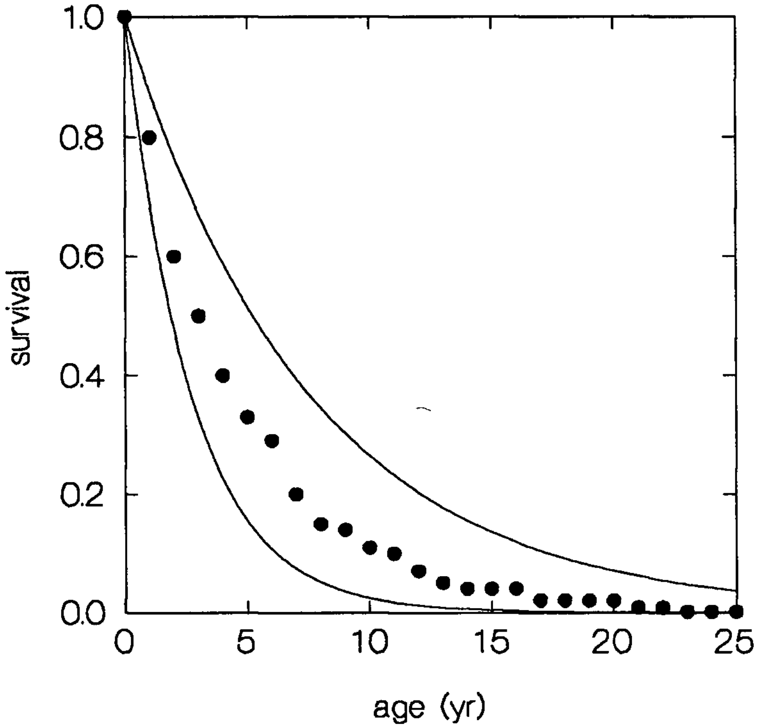

**Figure 2.1** Predicted harbour seal survival to different ages, assuming a mean transient killer whale population of 20 (upper curve) and 50 (lower curve). Data (filled circles) adapted from Bigg 1969a.

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[4] Dept. of Biological Sciences, Simon Fraser University, Burnaby, B.C.

The B.C. harbour seal population is thought to be about 90,000 animals (Olesiuk *et al.* 1990). Assuming that the number of transient killer whales in the same area ranges from 20-50 at any given time, and that predation pressure on the seal population is evenly distributed, the probability that a given harbour seal will be eaten ranges from 0.00034 to 0.00085 each day. At first glance these appear to be very good odds for the seal. However, they act cumulatively over time, 365 days a year, and lead to a predicted 0.5-0.85 probability of being eaten by a killer whale before reaching five years of age (Fig. 2.1). (The potential lifespan of a harbour seal is up to 30 years (Bigg 1969a).) Note that this only represents mortality due to killer whales; predation by sharks (often considered the major cause of pinniped mortality--Ainley *et al.*, 1985, 1981, Boulva and McClaren 1979, Le Boeuf *et al.* 1982, Scheffer and Slipp 1944) would pose an additional threat.

These are, admittedly, very crude calculations, and can not be expected to yield precise estimates. However, Figure 2.1 does coincide nicely with the age structure for this species reported by Bigg (1969). This suggests that aquatic predators have a major impact on the survival of harbour seals, and are likely to exert strong selection pressure against unnecessary immersion.

Of course, harbour seals must enter the water at some point to forage. It would therefore make sense to do so when chances of foraging success are greatest, and to remain hauled at all other times. On this basis, seals should forage nocturnally. Food availability is greatest at night due to the nocturnal migration of prey species into surface waters (Helfman 1986). In the coastal waters of British Columbia, over half of the harbour seal diet consists of herring (*Clupea harrengus*) and assorted gadids (Olesiuk *et al.* 1990a); most of these species are vertical migrators (Beamish 1966, Blaxter 1985, Harden Jones 1968). Harbour seals may be capable of dives up to 200m in depth (Kooyman *et al.* 1972), so their prey is probably within physical reach even during the day. However, daytime dives to such depths would be far more expensive energetically than those required to forage after nightfall.

In addition, deep daytime dives may put foraging seals at a visual disadvantage. It takes about thirty minutes for the eyes of harp seals (*Phoca groenlandica*) to become fully dark-adapted (Lavigne *et al.* 1977), and it is reasonable to assume that similar constraints exist for *P. vitulina*. Radiotagged harbour seals in Puget Sound (see Chapter 5) generally stayed under water for less than five minutes at a time (Watts, unpublished data); a deep-diving animal might not have time to completely adapt to the relative darkness before returning to the brightly-lit surface. This would further reduce foraging efficiency during the day.

Although these facts would suggest that harbour seals should forage throughout the night, foraging may be particularly successful during twilight. Schooling fish such as herring generally rise to the surface as a group, disperse throughout most of the night, and regroup just before their dawn retreat into deeper water (Blaxter 1985). This concentration into relatively tight schools during twilight may make them particularly vulnerable to foraging harbour seals. Furthermore, diffuse twilight from the surface enhances the visual contrast of any object seen from below, while reducing that of an object seen from above (Lythgoe 1979). Pinnipeds can take advantage of this by swimming beneath potential prey and striking upwards (Hobson 1966). Whether this confers a significant advantage to crepuscular foraging for harbour seals is uncertain, however; on a moonlit night they can theoretically see moving objects at nearly 500m depth (Wartzok 1981). Enhanced visual contrast at twilight may not be much additional benefit to an animal with such acute night vision, and may even be a disadvantage (potential prey would be more easily able to detect the approach of overhead predators, for instance).

### 2.3.2 Model Derivation

The dynamics of hauling may be regarded as a problem in "patch selection", in which the terrestrial and aquatic environments represent patches with different chances of foraging success and predation. Simulation models using dynamic programming techniques have successfully predicted patch use patterns across a wide variety of taxa (Mangel and Clark 1988). This approach is not viable in the present context, due to the lack of quantitative data on predation danger and (more importantly) prey availability at different times. It is therefore necessary to base a somewhat less detailed model upon the following two assumptions:

a) there is a significant cost associated with immersion (possibly due to the presence of aquatic predators), so that the less time a harbour seal spends in the water, the better; and

b) harbour seals can maximise their foraging efficiency by hunting at night, when vertically migrating prey are both closer to the surface and easier to see. They will feed during the night and remain hauled out at all other times.

The quantity of interest is hauling activity at any "photoperiodic time" t ($H_t$). $H_t$ can be expressed simply as the number of animals hauled out, or as some measure of the proportion of the daily maximum number hauled out.

Implicit in the assumptions above is that hauling activity is largely driven by daily cycles in ambient light intensity. Since such cycles vary seasonally, data collected at the same time on different days represent different points in the photoperiod. Time of day must therefore be expressed on a temporal scale for which day length is standardised (photoperiodic time).

Such a scale can be derived by describing a day not in terms of hours, but in terms of solar elevation. Thus, the day begins as the sun rises past an elevation angle[5] of -18° (the onset of astronomical twilight), and ends as it sinks beneath the same angle; the length of this period is arbitrarily set to 1. Therefore, t at solar noon is always 0.5. When $t>1$, it is after nightfall but before midnight; when $t<0$, it is after midnight but prior to the onset of morning twilight.

---

[5] Solar elevation can be calculated as a trigonometric function of latitude, Julian day, and time of day (Campbell 1977, p55).

Of course, day length is not constant throughout the year, and twilight does not always occur at the same time. During the summer solstice at 49° latitude, solar elevation is only below -18° for about an hour each night; while during the winter, night can last for up to 12 hours. Thus, although day length and twilight always remain fixed on the standard scale, the amount by which t exceeds 1 or falls below 0 changes throughout the year. t ranges as widely as -0.5 to 1.5 during the winter months; during the summer this range can be as low as -0.15 to 1.15.

Prior to sunrise, most harbour seals should be hunting at sea. However, as dawn approaches (and foraging efficiency declines) they should return as quickly as possible to the safety of the haulout. The rate of their return depends upon the extent to which they dispersed while feeding the previous night; a colony whose individuals dispersed to forage will take longer to reassemble on land than one whose members hunted closer to home. (In fact, given the increased predation risk involved in straying from the haulout site, seals may only travel further afield when prey is scarce in the immediate vicinity. It may therefore be possible to make basic inferences about food availability by analyzing the rate at which seals return to their haul-out sites: see below.) A convenient function to model this early increase in hauling is a sigmoid curve (Fig. 2.2a) of the form

$$E_t = c + \frac{mt^a}{1_a^a + t^a}\ ,\ 0 \leq t \leq 1 \qquad (2.1)$$

where $E_t$ is the hauling activity at photoperiodic time t;

c is the number of seals already hauled out just prior to sunrise (expected to be low);

m is the total increase in hauling activity (the amplitude of the sigmoid curve);

$i_a$ is photoperiodic time when $E_t$=0.5m (the inflection point of the curve); and

a represents the rate of arrival at the haul-out site (the steepness of the slope around $i_a$).

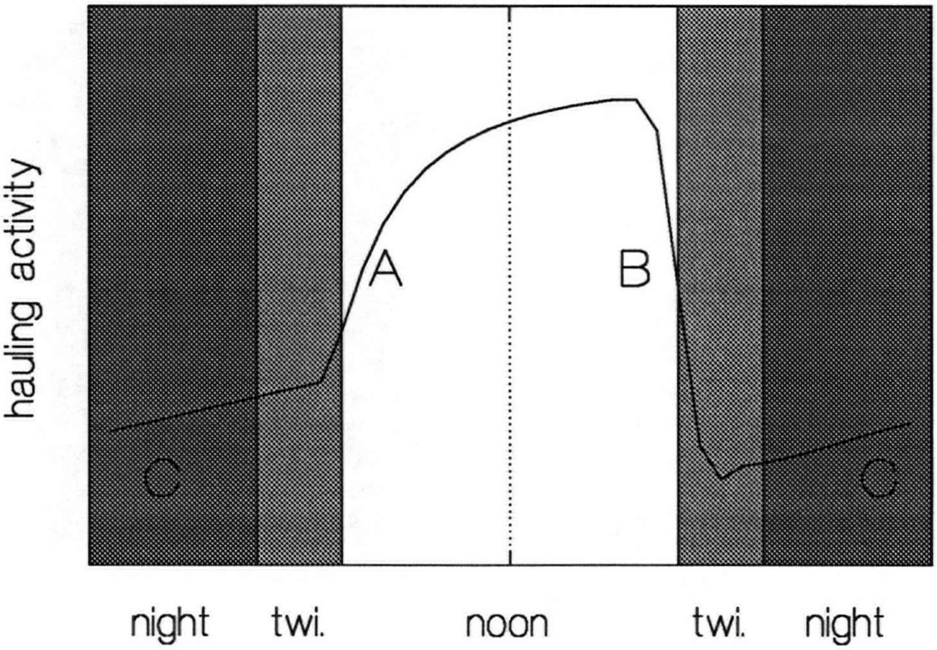

**Figure 2.2** A generalised diel hauling cycle. See text for details of annotation.

The maximum number of seals, once hauled out, should remain fairly constant until the approach of sunset. Now the number of hauled out seals should drop precipitously as most of the colony immerses to take advantage of twilight feeding conditions (Fig. 2.2b). There will be some variance associated with this immersion; ambient light levels around sunset vary seasonally, and even daily (depending upon cloud cover). It is also possible that individual seals have slightly differing perceptions of the onset of "twilight". Assuming that this variance about t=1 is roughly normal, the foraging exodus can be described as another sigmoid function, the amplitude of which is determined by $E_t$:

$$I_t = \frac{E_t t^d}{i_d^d + t^d}\ ,\ 0 \leq t \leq 1 \tag{2.2}$$

where $I_t$ is the reduction in hauling activity at photoperiodic time t;

$i_d$ is the photoperiodic time when the number of hauled out seals has been reduced by half; and

d represents the rate of departure from the haul-out site.

Hauling activity $H_t$ from t=0 to t=1 is simply the rising hauling activity defined by Eq. 2.1, minus the proportion of that value expected to reimmerse at photoperiodic time t (Eq. 2.2):

$$H_t = E_t - I_t,\ 0 \leq t \leq 1 \tag{2.3}$$

If seals simply re-enter the water a set time after hauling out (for example, after becoming hungry or after resting for some accustomed period), the rate of their departure should be roughly equal to that of their arrival ($a \approx d$), and the curve described by Eq. 2.3 will be more or less symmetrical. If, however, the population enters the water at sunset to feed, then the rate of departure rate will be greater than that of arrival ($d > a$), and Eq. 2.3 should describe an asymmetrical curve (Fig. 2.2).

Seals probably prefer to feed every night. Food passes through the phocine digestive tract in as little as 5 hours (Helm 1984), which implies that seals should be hungry after a single day's fast. In fact, harbour seals rarely remain hauled for more than 14 hours at a time (Stewart and Yochem 1985), and radiotagged animals from Puget Sound generally left their haulout for at least some part of every night (unpublished data; see Chapter 5). It is therefore unlikely that a great deal of hauling activity occurs between dusk and dawn.

However, it is likely that some proportion of the population feeds to satiation before dawn. Such animals should then haul out early, to minimise risk from predators. One might therefore expect to see a slow increase in hauling throughout the night (Fig. 2.2c), leading to some initial hauling value c at $t=0$ (Eq. 2.1).

In general terms, then, the model predicts a gradual increase in hauling activity throughout the early part of the day (due to the dispersion of animals during the night), followed by an abrupt drop in hauling near sundown (due to a mass foraging exodus). Seals should avoid entering the water except to feed, and even then should do so only at the most profitable times.

### 2.3.3 Field methodology

Hauling data were collected from a colony of about 200 harbour seals at Snake Island in the Strait of Georgia (Fig. 3.1a), from summer 1986 to spring 1988. Sampling occurred in periods of 4-9 days at approximately monthly intervals throughout the year. The number of hauled out seals was counted at half-hour intervals throughout the day, concurrent with a variety of environmental variables (Table 2.1). During the night, the same observations were made hourly (when I had field assistance) or every 2.5-3 hours (when I was alone). Night counts were made using a "Startron" passive vision starlight amplification system.

**Table 2.1** Environmental variables measured concurrently with census counts.

| Variable | Units |
|---|---|
| Julian Day | |
| Time of Day | h |
| Tidal height | m |
| Wind speed | $ms^{-1}$ |
| Air temperature | °C |
| Solar radiation[1] | $Wm^{-2}$ |
| Precipitation | mm/h |
| Time since last disturbance | h |

The raw data were processed on-site by a battery-operated lap-top computer (NEC PC-8201A), which applied a cosine function to slack-tide predictions from government tide tables (Canadian Hydrographic Service 1986, 1987, 1988) to calculate tidal height at time of counting.

Solar radiation was only measured during 1987-88, using a "Weather Measure" R401 mechanical pyronometer.

Wind speed was measured using a "Wind Wizard" hand-held anemometer held 2m above ground level.

Lunar phase was calculated using a cosine function with a period equal to one lunar month (29.531 days); it varied in value from 1 (full moon) to -1 (new moon).

The site was defined as "disturbed" if some identifiable stimulus (usually boat traffic) caused at least 5% of the hauled out contingent to re-enter the water. Since disturbed seals generally re-hauled within an hour of the stimulus, any readings taken within an hour of a disturbance were excluded from analysis.

### 2.3.4 Analysis

Since the maximum number of hauled out seals varied from day to day, and comparison of the data between days is essential to analysis, hauling activity was standardised by expressing each count as the proportion of the maximum number of seals hauled out both seasonally and daily. Thus, a count of 25 seals taken on a winter day when a total of 50 hauled out would yield a daily proportion of .5; if a maximum of 75 seals hauled out during the whole winter, the seasonal proportion would be 0.33.

These proportions were then expressed as arcsine square-root transforms, to satisfy analytical assumptions of normality and homogeneity of variance (Zar 1984). The transform of the seasonal proportion is hereafter referred to as "seasonal haul"; that of the daily proportion, "daily haul".

Seasonal haul was used to assess the effects of various environmental factors on hauling activity[6]. Following preliminary scatterplot analysis, each variable (except lunar phase) was regressed (stepwise linear) against seasonal haul; if a variable proved significant ($P<.05$), census counts associated with potentially constraining values of that variable were excluded from further analysis if possible.

Since scatterplot analysis of lunar phase showed what appeared to be a significant but nonlinear relationship, this variable was not subjected to linear regression. Instead, it was separated into a series of discrete categories of equal width (0.2); the seasonal haul out data associated with each of these categories was analyzed using a Kruskal-Wallis one-way ANOVA, and census counts associated with potentially constraining categories of lunar phase were excluded from further analysis.

In principal, then, the remaining data are relatively free of short-term variation due to the measured environmental factors, and hence more closely reflect underlying hauling behaviour.

Using the selected data subset, daily haul was fitted to the model described by Equations 2.1-2.3. The model was also fitted to four random samples of the original

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[6] Daily haul is inappropriate because of its insensitivity to variation between days. A daily maximum haul of 1 seal on a windy day, once standardised, takes the same value as a daily maximum haul of 150 seals on a calm day; daily haul can therefore not be used to detect environmental effects unless a wide range of conditions occurs within a single day.

data set, each of approximately the same size as the filtered subset; this permitted some measure of the improvement to the fit resulting from the selection procedure described above.

## 2.4 RESULTS AND DISCUSSION

### 2.4.1 Field data

A scatterplot of daily haul vs. photoperiodic time, uncorrected for environmental effects, confirms a pronounced midday peak in hauling activity, and a great deal of variation in the data (Fig. 2.3).

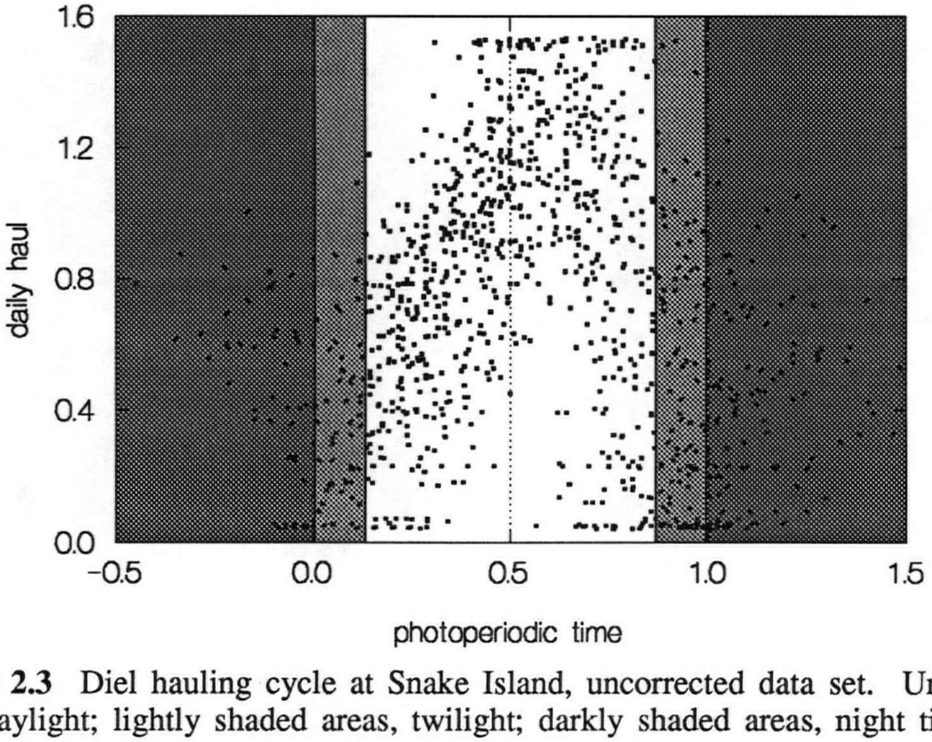

**Figure 2.3** Diel hauling cycle at Snake Island, uncorrected data set. Unshaded area, daylight; lightly shaded areas, twilight; darkly shaded areas, night time.

**Table 2.2** Summary statistics of stepwise regression of environmental variables onto seasonal haul.

| Variable | Coefficient | Std. Error | Tolerance | P | Cumulative $r^2$ |
|---|---|---|---|---|---|
| 1. Constant | 0.760 | 0.049 | | <0.001 | |
| 2. Insolation | 0.001 | $5.\cdot10^{-5}$ | 0.609 | <0.001 | 0.350 |
| 3. Tidal height | -0.122 | 0.010 | 0.809 | <0.001 | 0.442 |
| 4. Wind | -0.018 | 0.004 | 0.834 | <0.001 | 0.471 |
| 5. Air °C | 0.007 | 0.002 | 0.679 | 0.002 | 0.478 |
| 6. Precipitation | -0.001 | $1.\cdot10^{-5}$ | 0.965 | 0.147 | 0.479 |

N = 804 Total $r^2$ = .479 Std. error of estimate = 0.258

*Correlation matrix of regression coefficients*

| | 1. | 2. | 3. | 4. | 5. | 6. |
|---|---|---|---|---|---|---|
| 1. | 1.000 | | | | | |
| 2. | -0.061 | 1.000 | | | | |
| 3. | -0.800 | 0.295 | 1.000 | | | |
| 4. | -0.356 | -0.330 | 0.055 | 1.000 | | |
| 5. | -0.609 | -0.476 | 0.110 | 0.309 | 1.000 | |
| 6. | -0.084 | 0.052 | 0.054 | -0.119 | 0.079 | 1.000 |

Environmental variables found to be significantly correlated with seasonal haul included tidal height, wind speed, solar radiation, and air temperature (Tables 2.2). Lunar phase was also found to be significant (see below). The negative relationship between hauling and precipitation (Fig. 2.9) was not significant. The tolerance associated with each of these variables is high, indicating that there is no significant multicollinearity among the independent variables (Table 2.2). The following subsections deal with each variable in turn.

### Tidal height.

Not surprisingly, there is a strong negative relationship between tidal height and hauling activity (Fig. 2.4). Somewhat more unexpected is the apparent fact that extremely low tides (<0.5m) can constrain hauling activity as much as higher ones. This may be due to the physiography of Snake Island itself. At very low tides, the water surrounding the haulout site is too shallow for quick maneuvering; this effectively denies hauled out seals an escape route in the event of land-based disturbance. Large numbers of seals did not haul out under these conditions, remaining instead in shallow water, close to shore.

From tidal heights of 1m to 5m, there is a steady and continuous decline in mean seasonal haul. To select a subset of these data in which tidal effects are reduced, it is necessary to compromise. A large number of observations were collected within the relatively narrow range of tidal heights from 3-4m, but these tidal heights largely

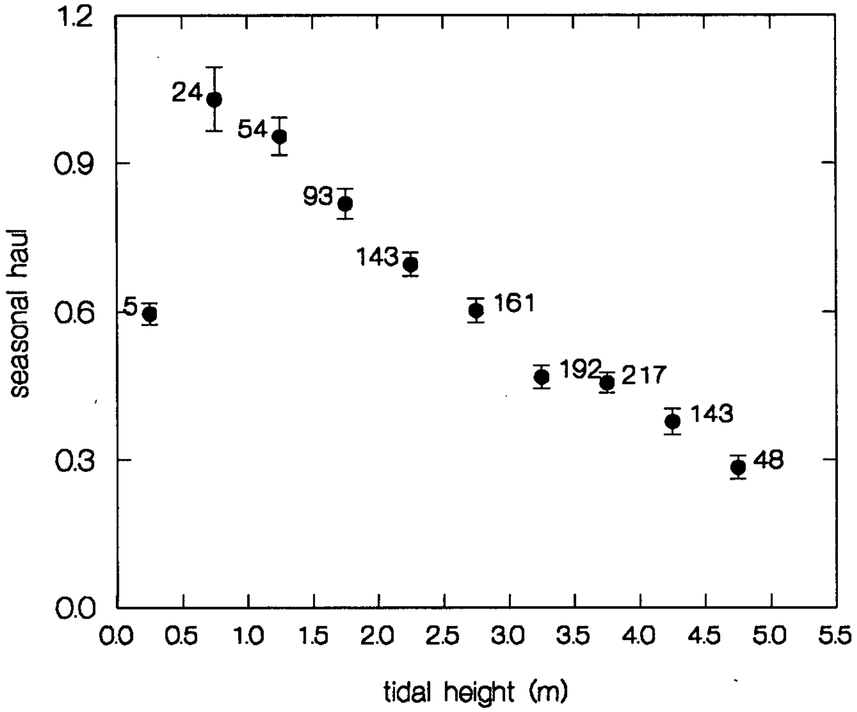

**Figure 2.4** Mean seasonal haul at different tidal heights. Standard error and n shown for each mean.

restrict hauling out. This is not such a problem at lower tides, but a wider range of tidal heights would be required to get the same sample size. I decided to exclude all data taken at tidal heights of less than 0.5m or greater than 2.25m; this should reduce the tidal effect on hauling while maintaining a reasonable sample size (*n*=241).

### Wind speed.

The negative relationship between hauling and wind speed is highly significant, but has a low regression coefficient (Table 2.2). Light and moderate winds do not appear to exert significant effects (Fig. 2.5). Accordingly, only observations made when wind

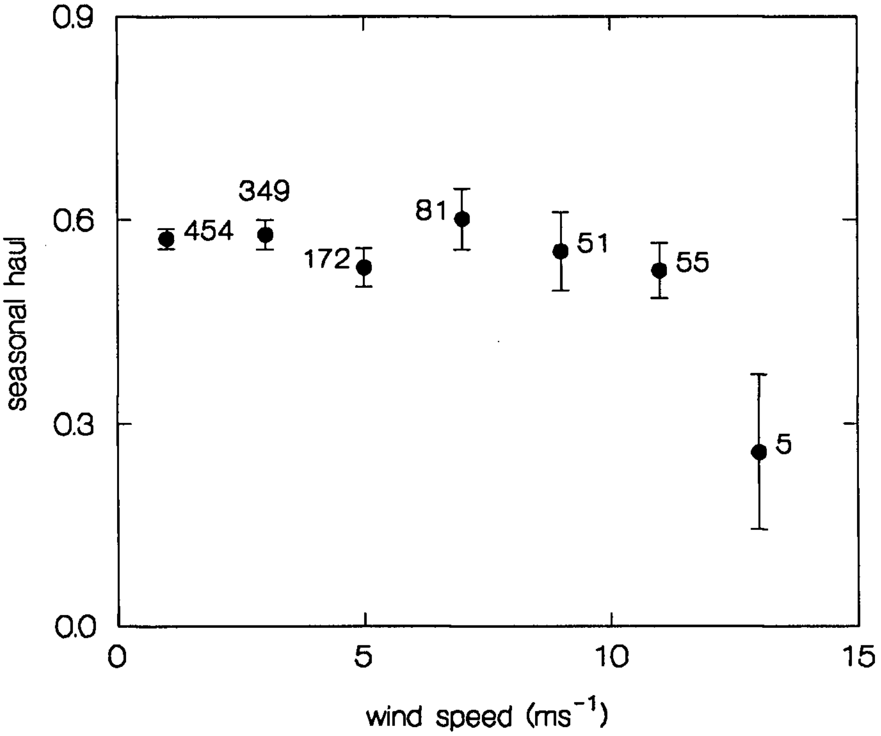

**Figure 2.5** Mean seasonal haul at different wind speed categories. Standard error and n shown for each mean.

speed exceeded 10ms$^{-1}$ were excluded when fitting the model.

### Solar radiation and air temperature.

Both solar radiation (Fig. 2.6) and air temperature (Fig. 2.7) are strongly correlated with seasonal haul. This is not surprising; both variables are minimal during the night and maximal around mid-day, and hauling follows roughly the same pattern. This does not imply a causal relationship, however; the model predicts an approximately mid-day peak in hauling for reasons which have nothing to do with the thermal environment.

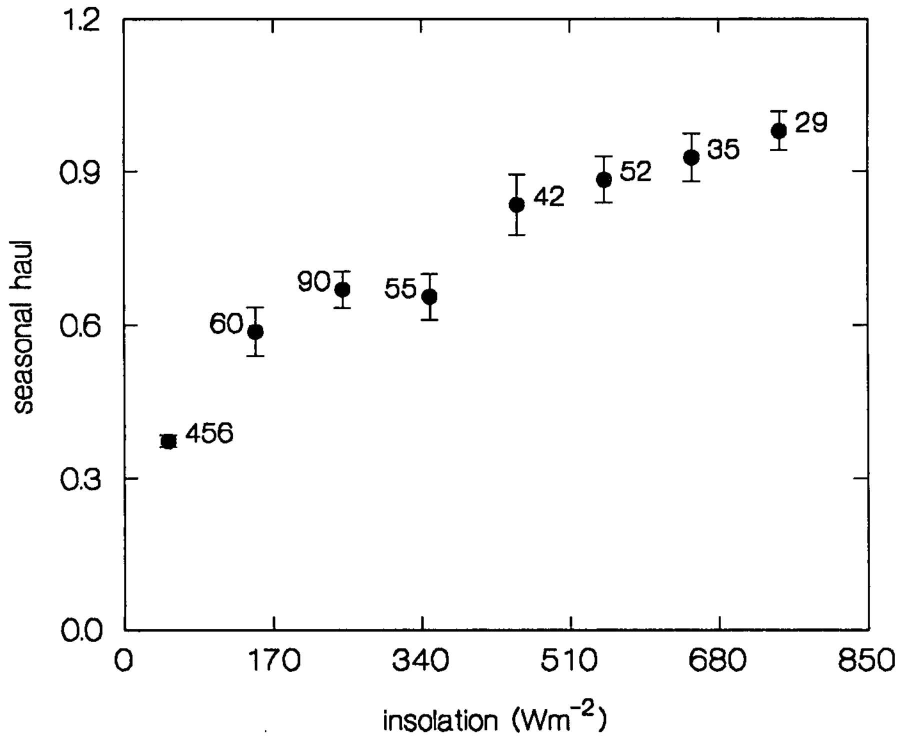

**Figure 2.6** Mean seasonal haul at different levels of insolation. Standard error and n shown for each mean.

To examine whether there is a functional relationship between hauling out and these factors, it would be necessary to select only data in which other potentially relevant variables do not change. If, for example, a significant relationship between hauling and solar radiation persisted during a time in which food availability and tidal height did not change, these variables would be unconfounded (Chapter 3). In this case, it was impossible to do so and still retain data from all times of day. For the purposes of this study, therefore, it was necessary to ignore the correlations between solar radiation, air temperature, and hauling activity.

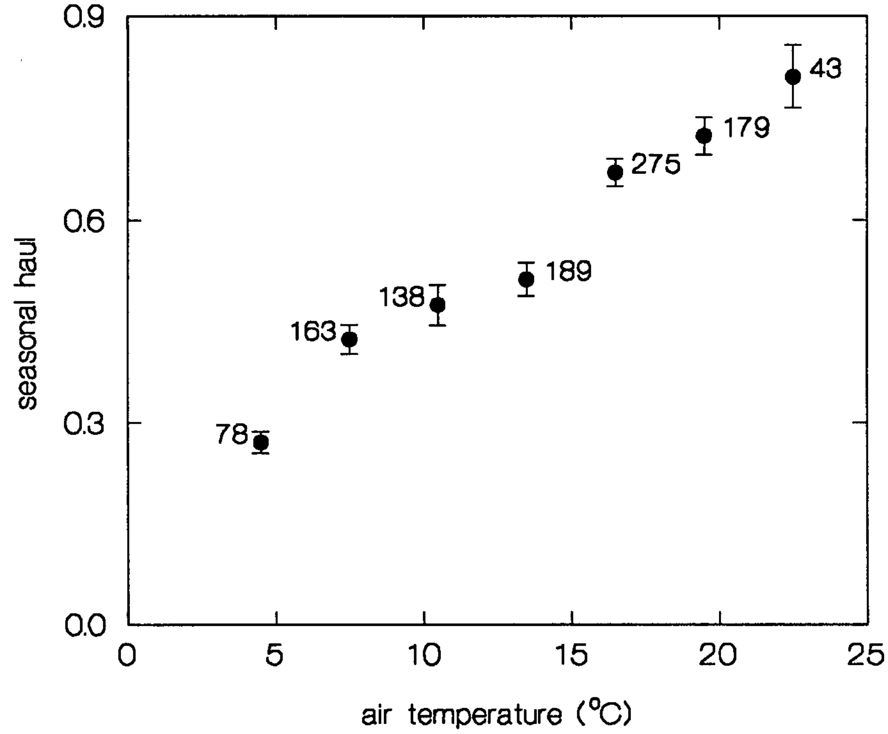

**Figure 2.7** Mean seasonal haul at different categories of air temperature. Standard error and n shown for each mean.

## Lunar phase.

While studying haul-out activity of the Galápagos fur seal (*Arctocephalus galápagoensis*), Trillmich and Mohren (1981) discovered that nocturnal hauling is higher during the full moon than at other times. They hypothesised that bright moonlight might 1) make immersed fur seals more visible to sharks, a natural predator, or 2) force vertically migrating prey deeper into the water column, making them less available to foraging seals. In either case, the result would be a reduction in the

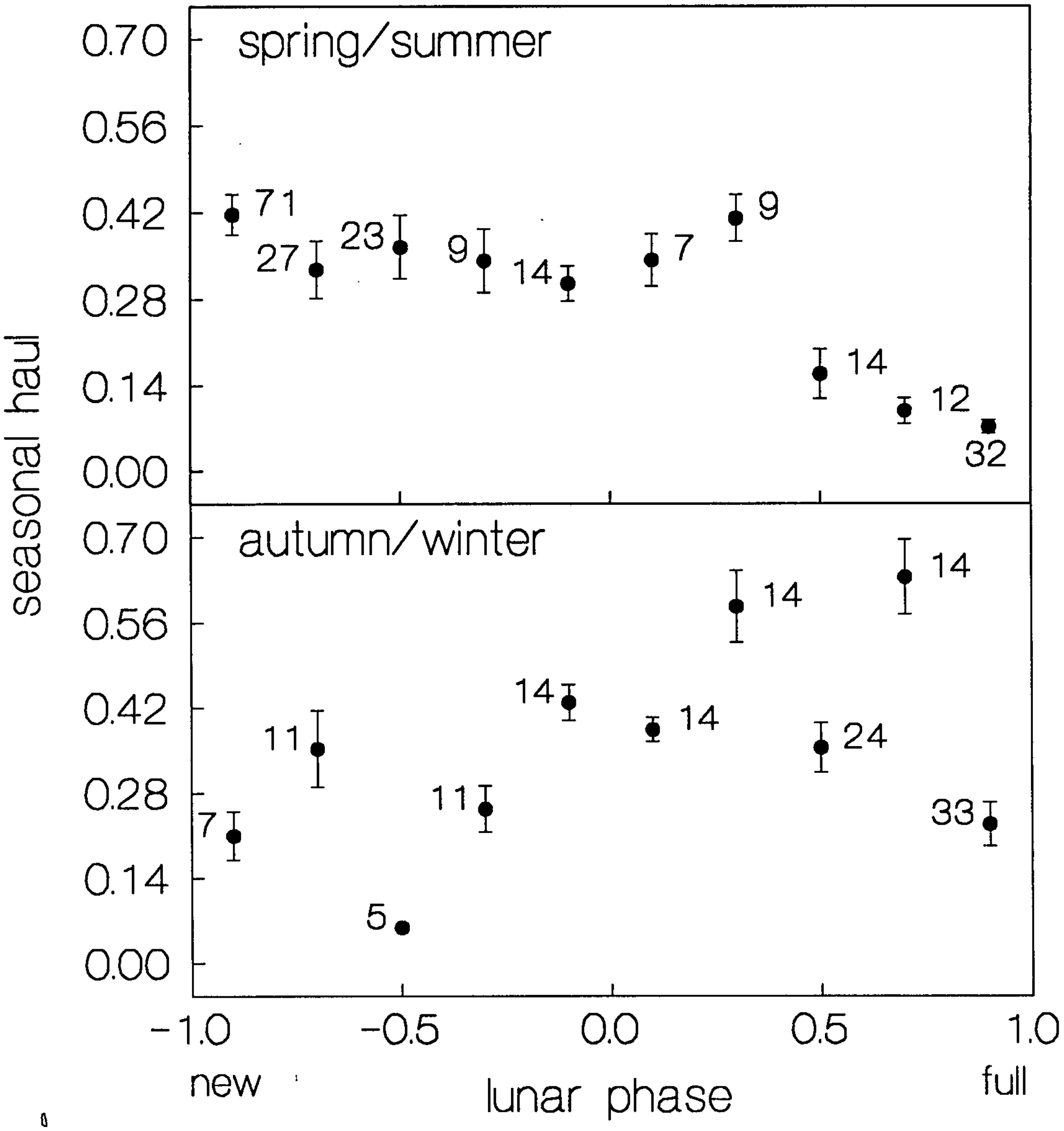

**Figure 2.8** Mean seasonal haul at different lunar phases during spring/summer and autumn/winter night-time periods. Standard error and n shown for each mean.

number of seagoing animals on bright moonlit nights.[7]

Roughly the reverse pattern holds for harbour seals at Snake Island. There is a significant and pronounced decline in the number of animals hauled out at night when the moon is near full, at least during spring and summer (Fig. 2.8) (Kruskal-Wallis statistic=74.795, $P<0.001$ with 9 d.f., $N=218$). Although there are also significant differences between groups during the autumn and winter months (Kruskal-Wallis statistic=63.094, $N=147$), there was no obvious overall trend associated with lunar phase (Fig. 2.8). If Fig. 2.8 does represent a photic effect, this seasonal difference is likely due to the cloudier skies which prevail during autumn and winter; lunar brightness is of little relevance if the light is obscured by clouds.

The reduced hauling (and presumably increased foraging) activity during the full moon suggests that other factors more than offset the deeper distribution of prey and any increased risk of predation. (There is no information to indicate whether killer whales also forage nocturnally.) Increased visibility of prey to the seals is one obvious possibility.

In any event, it is obvious from Fig 2.9 that nocturnal hauling activity is depressed when lunar phase exceeds 0.4, during spring and summer. All night-time readings made under such conditions were therefore excluded when fitting the model.

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[7] Another possibility, not mentioned by Trillmich and Mohren (1981), is that increased moonlight might increase the foraging efficiency of the fur seals, allowing them to satiate and return to the haul-out sooner than on darker nights.

## Precipitation.

Precipitation was not found to have a significant influence on seasonal haul. This may be due largely to the near absence of readings made while it was raining (Fig. 2.9). However, since there does appear to be a dramatic decline in seasonal haul whenever precipitation **does** occur, I decided to err conservatively. Readings taken in the rain were excluded when fitting the model.

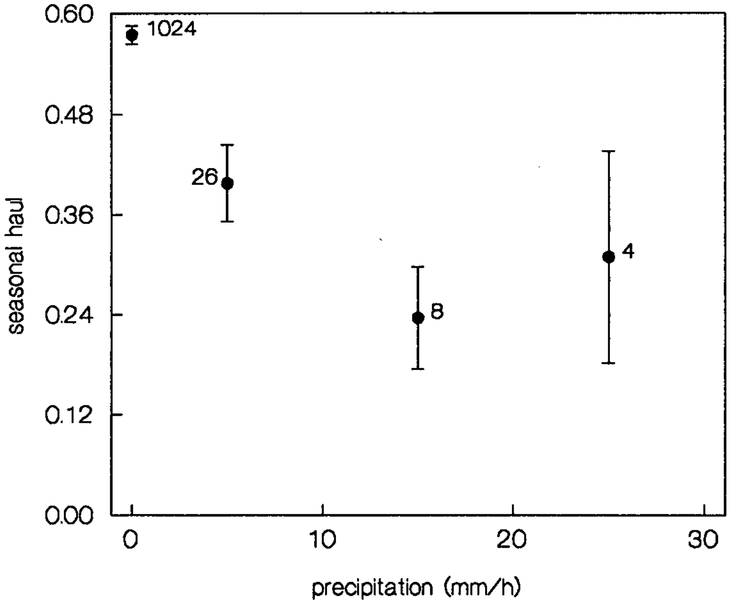

**Figure 2.9** Mean seasonal haul at different levels of precipitation. Standard error and n shown for each mean.

## Other constraints.

The discussion so far has centred upon external constraints on normal hauling behaviour. There are, however, at least two endogenous events which have been observed to increase hauling activity: moulting and pupping (Boulva and McLaren 1979, Sullivan 1980).

The pupping season in the Strait of Georgia extends from mid-June to mid-September (Bigg 1969b); during this period mothers spend a disproportionate amount of their time hauled out, attending their pups. The annual moult, which occurs mainly during October, affects seals of both sexes; basal metabolism declines by 15-20% (Ashwell-Erickson *et al.* 1986), and the skin must be kept warm for extended periods to facilitate regrowth of the pelage (harbour seal skin cells cannot metabolise properly at temperatures below 17°C (Feltz and Fay 1966)). Harbour seals therefore haul out in great numbers, for long periods of time, when moulting; at Snake Island, annual maximum hauls were invariably observed during October.

Data collected during either the pupping or moulting periods were therefore excluded when fitting the model.

### 2.4.2 Model evaluation.

The Snake Island database consists of over a thousand records. Ninety five survived the elimination process. The selected data fit the model far better than any of the randomly selected samples (of equivalent size) taken from the original database (Fig. 2.10, Table 2.3).

**Table 2.3** Summary statistics of environmentally filtered and randomly selected data sets fitted to general model of diel hauling (Eq. 2.3).

| Parameters | Randomly Selected Data Sets | | | | Filtered Data Set |
|---|---|---|---|---|---|
| | 1* | 2 | 3 | 4 | |
| c | 0.462 | 0.531 | 0.358 | 0.303 | 0.598 |
| m | 2.031 | 3.201 | 3.563 | 28.890 | 1.610 |
| a | 2.944 | 6.081 | 3.228 | 1.806 | 1.484 |
| $i_a$ | 0.534 | 0.455 | 0.445 | 3.019 | 0.717 |
| d | 4.101 | 2.796 | 1.823 | 4.744 | 14.047 |
| $i_d$ | 0.673 | 0.474 | 0.406 | 0.657 | 0.833 |
| *Statistics* | | | | | |
| N | 92 | 84 | 90 | 83 | 95 |
| Std. error of estimate | 0.481 | 0.350 | 0.445 | 0.410 | 0.199 |
| $r_{adj}^2$ | 0.287 | 0.410 | 0.235 | 0.376 | 0.651 |
| F | 61.767 | 91.027 | 56.653 | 60.753 | 380.651 |
| P | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

*Subset for which data are plotted in Fig. 2.10a

There is, as predicted, an unmistakable asymmetry in the mid-day hauling peak evident from the selected data; this is not nearly as evident in the randomly selected subsamples. Once the effects of other variables are reduced, hauling activity is maximal during the afternoon and declines dramatically at the onset of twilight.

Mid-day peaks in hauling activity are commonly reported in the harbour seal literature (Allen *et al.* 1984, Boulva and McLaren 1979, Pauli and Terhune 1987, Stewart 1984). Few of these studies have dealt rigorously with a wide variety of environmental factors (although the effects of tidal height have generally been acknowledged). There are nonetheless some indications that the peak actually tends to occur during the afternoon rather than mid-day (Allen *et al.* 1984, Pauli and Terhune, Stewart 1984), although none of these authors have remarked on the possible significance of this tendency.

Ringed seals (*Phoca hispida*) in the arctic also show a mid-day peak in their summer hauling behaviour, but one which is symmetrical about solar noon and of relatively low amplitude (Finley 1979). This is interesting in light of the extremely long summer photoperiod at that latitude. Night did not fall during the period that Finley collected his data (June). His results are to be expected if hauling in phocid seals is driven by diel variation in prey availability, which is in turn driven by changes in light level; reduced variation in ambient light should result in a reduced advantage to night-time foraging.

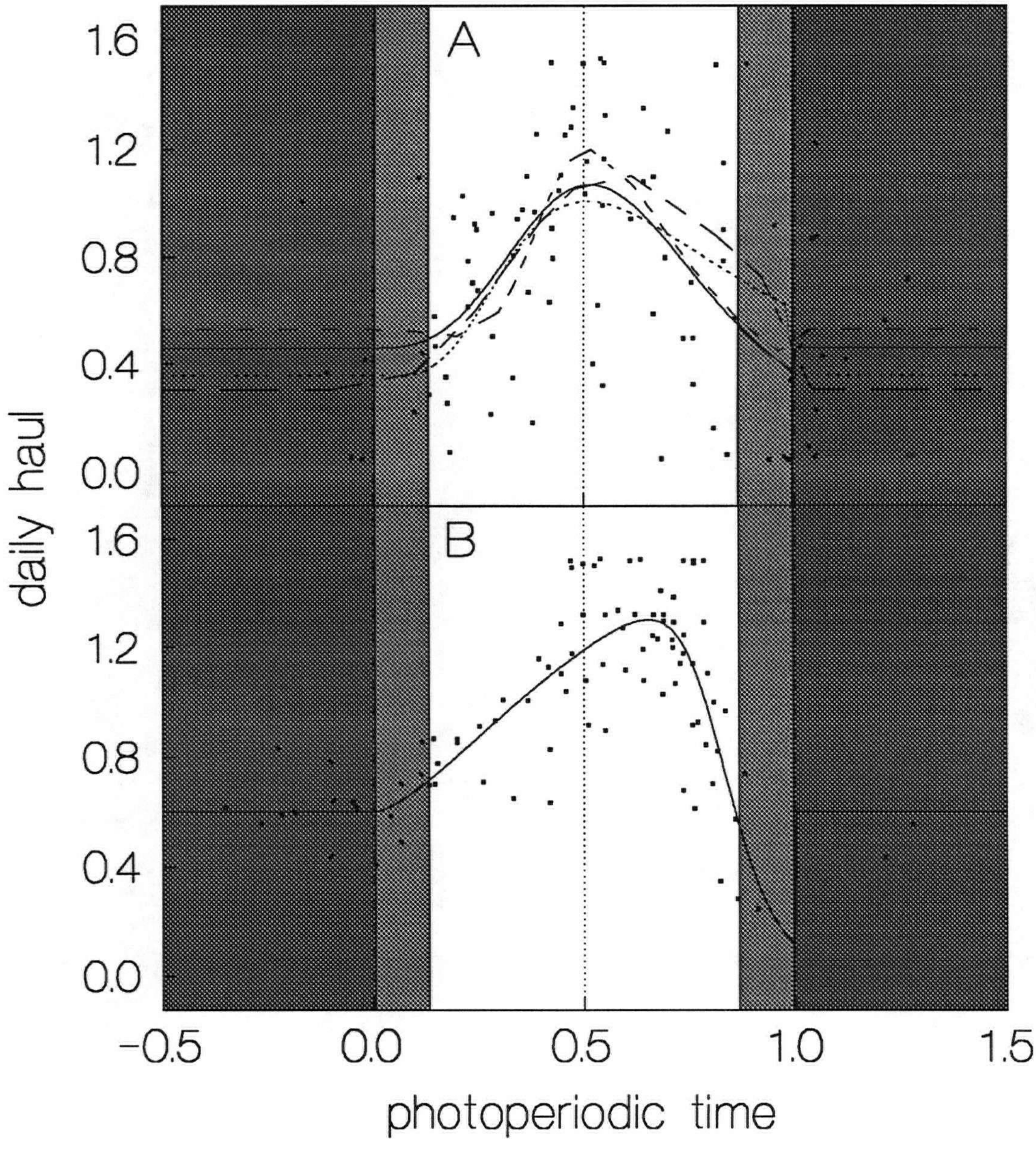

**Figure 2.10** A model of diel hauling in harbour seals, fitted to (A) 4 random subsets of hauling data (data shown fit solid curve), and (B) a subset selected to minimize environmental variability.

Relatively few night-time readings met the environmental selection criteria, and most of these were taken between midnight and dawn (Fig. 2.10). These can not be analysed in terms of photoperiodic time because of the inconsistent scaling of t when it exceeds 1 or drops below 0 (2.2.2). However, night-time measurements can be scaled against an arbitrary "night" of length 1, for which 0=sunset, 1=sunrise, and midnight=0.5. (This is exactly the same approach used to derive t within its range of 0 to 1, but scaled to hours of darkness rather than light.) Based on the available (transformed) night-time data, nocturnal hauling activity (when solar elevation<-18°) is best described as a constant (Table 2.4).

There is, however, some indication that hauling activity does increase throughout the night. The fitted model predicts that hauling activity during dusk appears to be somewhat lower than that during dawn; there are more seals hauled out at the start of the day than are left at the end of it. This leads to a somewhat jarring discontinuity in the fitted curve at t=1, which (despite the nocturnal constant) implies an increase in hauling throughout the night. This is consistent with the premise that some seals find enough prey to satiate themselves early during the night, returning to the haul-out site while it is still dark.

### 2.4.3 A relative index of prey availability?

The need for quantitative measures of predation and foraging success probabilities has already been mentioned. The latter quantity is particularly difficult to estimate.

**Table 2.4** Summary statistics of a linear regression of daily haul against standardised "nocturnal time" (x), for solar elevation<-18°.

| | Coefficient | Std. error | t | P(2-tailed) |
|---|---|---|---|---|
| constant | 0.629 | 0.052 | 12.186 | <0.000 |
| x | -0.111 | 0.163 | -0.680 | 0.509 |

N=14 $r_{adj}^2$=0.037 Std. error of estimate=0.115 F=0.643 P=0.509

Harbour seals are opportunistic foragers (Olesiuk *et al.* 1990), consuming lamprey (Roffe and Mate 1984) crustaceans and cephalopods (Spalding 1964), and a wide variety of pelagic and demersal teleosts (Boulva and McLaren 1979, Brown and Mate 1982, Spalding 1964). Prey availability is therefore a complex function of preference across a range of items, abundance of various species at different depths and times of day, (including such things as variations in schooling behaviour), and migrational and seasonal factors affecting both the seals and their food. Although it is a simple matter to argue that foraging at night is more efficient than foraging during the day, it is impossible to quantify this advantage with the available data.

It may, however, be possible to derive a relative index of prey availability by studying the rate at which harbour seals accumulate at their haul-out site following a period of foraging. If one accepts that harbour seal behaviour is strongly influenced by the danger of predation, and that haul-out sites act as refugia from predators, then it is safe to conclude that

1) seals will forage no further from the haul-out site than necessary, and

2) they will return directly to the haul-out site once satiated.

If this is the case, seals in areas of low food availability will have to forage further afield than those in areas with abundant prey, and it will take them longer to get back. The rate at which seals haul out in the morning should reflect this; in terms of Equation 2.2, the inflection point $i_h$ should be inversely related to food availability.

**Table 2.5** Linear regressions of daily haul (y) onto tidal height (x) at three sites in the Pacific northwest, during spring and summer.

| Site | Relationship | N | $r_{adj}^2$ | Std. error | F | P |
|---|---|---|---|---|---|---|
| Snake Island | y=1.616-0.325x | 676 | 0.519 | 0.307 | 729 | <0.001 |
| Pam Rocks | y=1.419-0.287x | 405 | 0.532 | 0.309 | 459 | <0.001 |
| Gertrude Island | y=0.882-0.074x | 174 | 0.034 | 0.494 | 7 | 0.008 |

This in itself is no great gain, since in order to test such a relationship one must still somehow independently assess prey availability. However, harbour seals off the coast of Sweden generally forage in waters less than 30m deep (Härkönen 1988); if this is also true of seals resident in the Pacific northwest, then prey availability is at least partly related to the prevalence of shallow water in the vicinity of the haulout site.

In addition to Snake Island, two other sites in the Pacific northwest were the subject of related studies on hauling in harbour seals (Fig. 3.1) (Chapters 3 and 5). Although neither of these sites was sampled around the clock, sufficient data were collected during twilight and daylight to warrant comparison with Snake Island during the spring and summer months. Of these two additional sites, tidal height constrains hauling activity at Pam Rocks to approximately the same degree as it does at Snake Island (Table 2.5). Furthermore, both sites share the same sort of rocky topography, and have comparable weather conditions (Fig. 3.7).

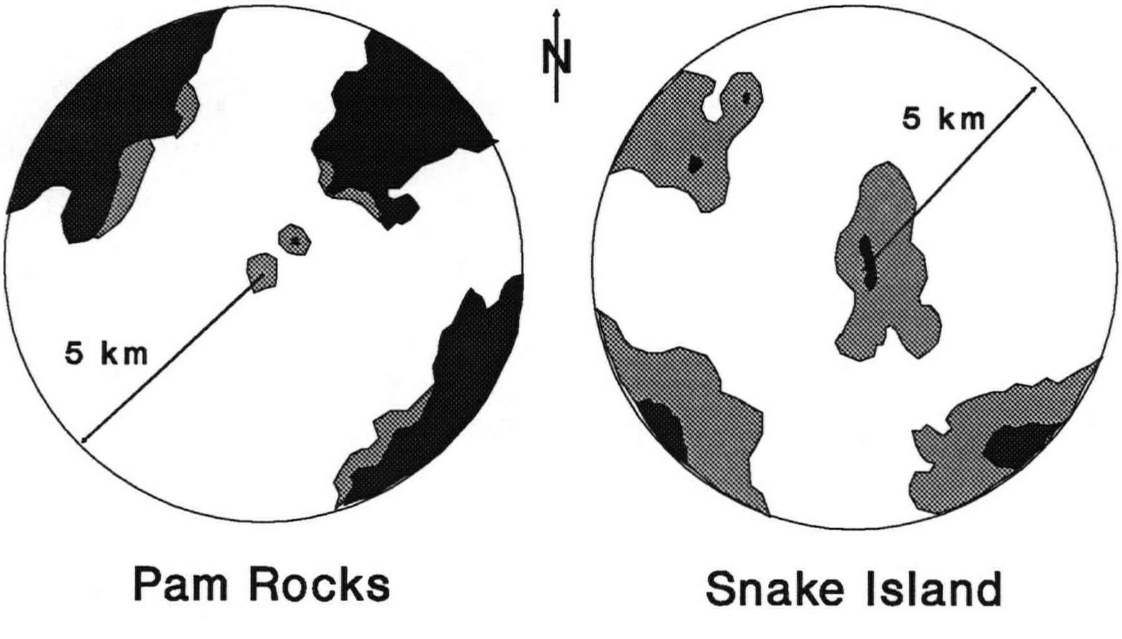

**Figure 2.11** Topography within 5km of Pam Rocks and Snake Island, showing land (solid areas) and seabed less than 30m deep (shaded areas).

There is however one important difference between the two sites; at Snake Island, approximately 18% of the area within a 5km radius is less than 30m deep, while for the area surrounding Pam Rocks the figure is only 4% (Fig. 2.11). In light of this disparity, a comparison of the morning hauling activity profiles of the two sites reveals an interesting contrast (Fig. 2.12). Compared to Snake Island, Pam Rocks shows a marked delay in the onset of hauling, and a steeper rate of increase once it occurs. One interpretation of this is that greater number of seals stayed closer to home at Snake Island than at Pam Rocks; this implies that prey availability is greater near Snake Island, which is consistent with the submarine physiography of the two areas. Although this relationship remains speculative, it is intriguing and should be explored across a wider variety of haul-out types.

## 2.5 CONCLUSIONS

Once the effects of various environmental variables have been reduced, the daily hauling pattern of the Snake Island harbour seal colony can be described by a simple model based on two universal rules; minimize cost of immersion, and do not starve. Seals can meet these demands by avoiding the water when foraging efficiency is low (i.e., during daylight). This is what the data from Snake Island show.

The data also show that the rate of evening departure from Snake Island is much greater than the rate of morning emergence. If each seal simply hauled out until it felt

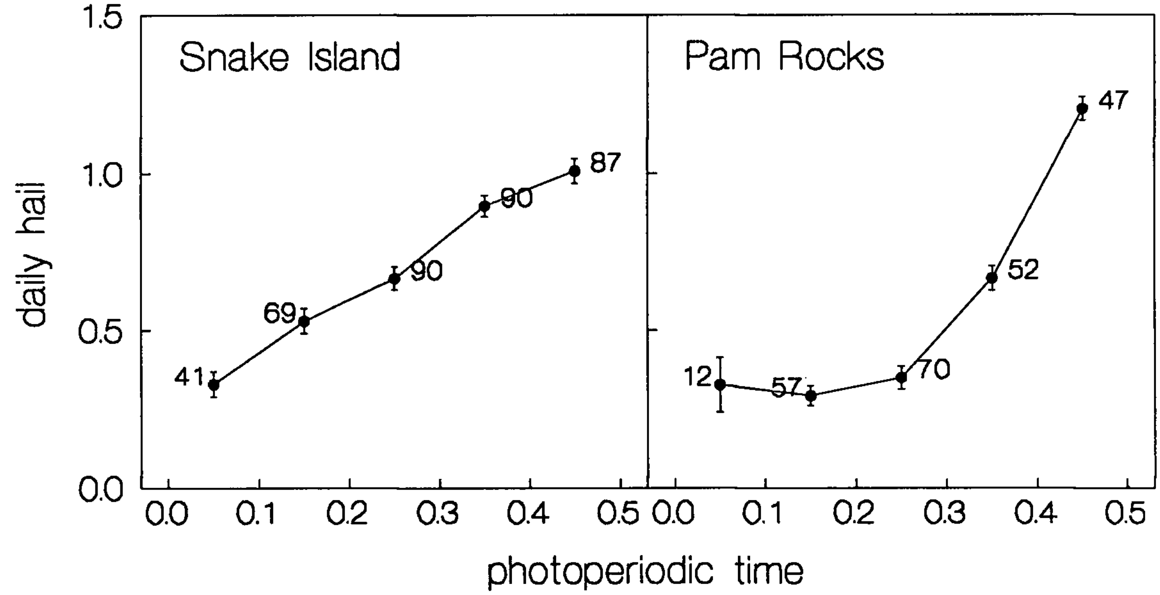

**Figure 2.12** Mean daily haul throughout the morning at Snake Island and Pam Rocks. Standard error and N shown for each mean.

rested or hungry, this would not happen; departure and arrival rates would be approximately equal. However, a rapid departure rate would be expected if seals wait for the best foraging conditions before they immerse, since the optimum foraging window begins at about the same time for all seals.

A major limitation of this model is that its predictions are made in terms of a general "immersion cost", the nature of which remains unconfirmed. Predation certainly seems to be the likeliest candidate (2.3.1), and is certainly more parsimonious than the thermoregulation hypothesis. However, the predictions of the model are consistent with any significant cost associated with immersion; therefore, other possibilities can not be entirely ruled out.

The driving forces implicit in this model are expressed so simplistically as to seem almost trivial. Reliable estimates of the probabilities associated with predation and foraging success would certainly permit more rigorous and detailed analysis of these forces, but the utter simplicity of the present model also has a certain strength. Since the general hauling cycle can be described in such simple terms (at least at Snake Island), there is little need to invoke more complex rationales. In particular the role of behavioural thermoregulation may have been accorded too much prominence.

However, this is not to deny that thermoregulation has any role in hauling whatsoever. Even when using a data set selected to minimise environmental effects, there is considerable observed variation in the overall hauling pattern (Fig. 2.10b). Some of this is doubtless due to the relatively wide range of "acceptable" tidal heights necessary for a reasonable sample size (Fig. 2.4). However, a possible relationship between hauling and the thermal environment (Figs. 2.7, 2.8) could not be controlled for because of the common correlation these variables have with time of day. Such a relationship could significantly contribute to the remaining variation in the data. The possibility of thermal influences on basic hauling patterns warrants further investigation.

# 3. THERMAL CONSTRAINTS ON HAULING OUT IN HARBOUR SEALS (*Phoca vitulina*)

## 3.1 ABSTRACT

Measurements of the thermal environment were made in conjunction with regular counts of hauled out harbour seals at three sites in the Pacific northwest. Solar radiation, wind speed, and air temperature were all significantly correlated with numbers hauled out. These were incorporated into a thermal index of heat flux (expressed in $Wm^{-2}$) between the seal and its environment. Mid-day hauling activity declined sharply with increasing levels of flux, when flux was positive (i.e., when seals theoretically gained net heat from their environment); it did not change with negative values of flux. This could be described by a nonlinear piecewise regression equation ($r_{adj}^2$=0.648). No significant differences in hauling activity were detected between sites throughout most of the year; however, during the summer, one site with significantly higher mean flux than the others also exhibited significantly lower hauling activity. In contrast with the other two sites (which exhibited a commonly-reported mid-day peak in numbers hauled), hauling at the warmer site was skewed to peak in mid-afternoon, after the hottest part of the

day had passed. These findings are consistent with the premise that under temperate summer conditions, hauling out can result in overheating. This may be an important constraint on hauling behaviour.

## 3.2 INTRODUCTION

Hauling out in harbour seals has been attributed to a variety of causes. These include sleep (Schneider *et al.* 1980), predator avoidance (Terhune 1985), mate selection (Renouf and Lawson 1986), and skin cell maintenance (Feltz and Fay 1966). Numerous field studies have reported (mainly negative) correlations between hauling and various environmental factors, including tide (Calambokidis *et al.* 1979, Krieber and Barrette 1984, Schneider and Payne 1983, Sullivan 1980), air temperature (Krieber and Barrette 1984), high wind (Schneider and Payne 1983), and precipitation (Krieber and Barrette 1984). For the most part, however, such studies simply report the existence of these correlations without much discussion of any underlying functional relationships.

There are at least two strong theoretical reasons why harbour seals should spend as much time as possible out of the water: immersion is energetically costly, and it is dangerous. The peripheral tissues of harbour seals cannot metabolise properly at temperatures below 17°C (Feltz and Fay, 1966); since the skin temperature of an immersed seal is very close to ambient (Hart and Irving 1959), periodic hauling is likely necessary for routine skin growth and maintenance. Further, a hauled out seal does not have to expend energy holding position against currents and wave action.

Of possibly greater importance is the danger of being eaten by a predator while at sea. Although this has received scant attention in the literature, calculations suggest that a typical harbour seal in British Columbia waters has an 80% chance of being eaten by a killer whale before it reaches five years of age (Chapter 2). Hauling sites provide refuge from aquatic predators.

These considerations suggest that harbour seals should spend as much time as possible hauled out, entering the water only to forage. Foraging occurs mainly at night (Chapter 2). However, there is reason to believe that seals may also immerse for thermoregulatory reasons during the day.

Amphibious mammals must reconcile the conflicting thermal demands of two completely different environments. Water conducts heat twenty-five times more effectively than does air: to minimise hypothermia when immersed, seals have evolved a blubber layer which can amount to 30% of their total mass (Ryg *et al.* 1990). However, adaptations to prevent heat loss in the water may backfire in air, where it is often more beneficial to lose heat than to conserve it. Blubber impedes heat flow across the body wall, and peripheral vasodilation is only partially effective in bypassing this insulation (McGinnis 1975, Oritsland and Ronald 1978). Heat loss must therefore occur mainly from the head and flippers (Hart and Irving 1959, McGinnis 1975), where the blubber layer is almost nonexistent.

To complicate matters further, the skin and pelage of phocid seals act as a heat trap. Depending upon the reflectivity of the pelt, solar radiation is reflected by the hairs to the skin, which is darkly pigmented and highly absorptive. The functional significance of this arrangement seems variable; on ice floes in the Gulf of St. Lawrence it enhances external heating of harp seals (Øritsland 1971, Øritsland and Ronald 1973), while for monk seals in the tropics it has been suggested that a hot (hence radiative) body surface actually shields the body core from high heat loads (Whittow *et al.* 1975). In either case, the immediate effect is a buildup of heat at the body surface which cannot be dissipated by sweating (phocid seals do not sweat--Montangna and Harrison 1957, Whittow *et al.* 1975).

An important consequence of this heat trap is that when a seal is exposed to strong sunlight, not even the flippers are effective heat dissipators. All irradiated body surfaces gain heat (McGinnis 1975); only surfaces which are shaded or in contact with the substrate can lose it. Conduction of heat to the substrate is an important aspect of thermoregulation among phocids, and some species from lower latitudes (such as the elephant seal *Mirounga angustirostris*) have developed behaviours such as "sand-flipping", which enhance conductive heat loss (White and Odell 1971). Harbour seals generally lack such strategies (but see McGinnis 1975); even on a wet sand substrate without direct sunlight, a harbour seal can lose only about a quarter of its metabolic heat production via conduction at an air temperature of 30°C (Ohata and Whittow 1974). This percentage would be somewhat lower in direct sunlight.

The only other means of heat loss available to a hauled out seal would be evaporation from the respiratory tract. In gray seals this only accounts for 6-13% of total heat production (Folkow and Blix 1987); Gates (1980) states that 20% is a reasonable figure for most mammals.

Hauled out harbour seals may therefore face a real danger of hyperthermia on warm days. Hawaiian monk seals (*Monachus schauinslandi*), the most tropical phocid species, can only remain hauled out and dry for extended periods on days which are cloudy, rainy, or have strong winds (Whittow 1978). There is also anecdotal evidence that harbour seals at the same latitude immerse to avoid hyperthermia (Whittow 1987). However, these are examples of phocids living at the most tropical extreme of their normal range; it is not known whether the danger of overheating exerts more general effects.

This paper reports on research conducted on wild harbour seals in the Strait of Georgia and Puget Sound, well within any thermal or geographic limits of the species. By measuring hauling activity under a wide variety of naturally occuring environmental conditions, I could ascertain how much of the correlation between environment and hauling could be explainable in thermoregulatory terms.

## 3.3 METHODS

### 3.3.1 Field studies

I studied three harbour seal colonies in the Pacific Northwest during 1986 to 1988 (Fig. 1). Snake Island (in the Strait of Georgia) was sampled most intensively; it is a

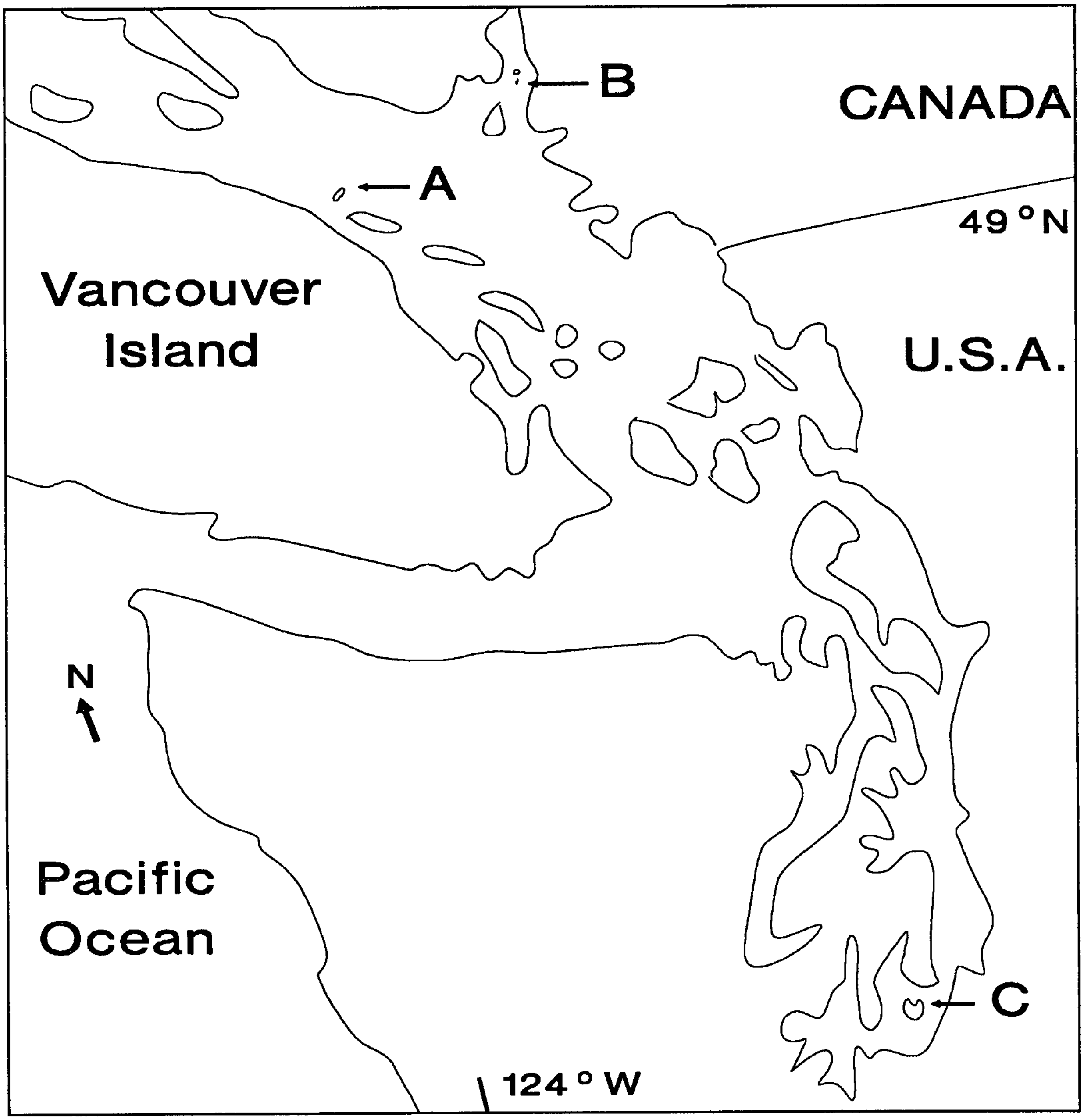

**Figure 3.1** The study area, showing locations of a) Snake Island (Strait of Georgia); b) Pam Rocks (Howe Sound); and c) Gertrude Island (Puget Sound).

rocky habitat upon which a maximum of about 200 seals hauled out. It was sampled monthly during 1986-87, with each sampling period lasting about a week (as was also the case for the other sites).

Pam Rocks (in Howe Sound) is a reef with a maximum recorded haul out of more than 300 animals. Since relatively violent weather made access to Pam Rocks difficult during the winter months, it was only sampled monthly from April - September during 1986-87.

Gertrude Island is essentially a forested gravel bar in Puget Sound; it supports the greatest number of seals (>600) of the three sites and was used mainly for associated telemetry studies on haulout behaviour from February to November of 1988 (see Chapters 4 and 5). Sampling was monthly (excluding August).

Observations at each site followed the same basic protocol. Daylight counts of hauled out seals were made at regular intervals (every half-hour at Snake Island and Pam Rocks; every hour at Gertrude Island because of the greater time required to make the counts). For the most part, seals were counted as 'hauled out' if most of their bodies were out of the water. This included seals resting in the splash zone, or completely hauled out but still wet. At Gertrude Island, however, separate counts were also made of wet and dry hauled out seals from June 1988 onwards.

A variety of environmental variables were measured concurrent with each count (Table 3.1). Raw data were processed by a battery-operated lap-top computer (NEC PC-8201A) on site, which used slack-tide predictions from government tide tables

(Canadian Hydrographic Service, 1986, 1987, 1988) to calculate tidal height at the time of counting. Solar radiation was only measured during 1987-88, using a Weather Measure R401 mechanical pyronometer. Wind speed was measured using a hand-held anemometer, held 2m above ground level. Any identifiable stimulus causing at least 5% of the hauled out contingent to re-enter the water (e.g., boat traffic, coyotes) was defined as a 'disturbance'; 'time since last disturbance' denotes the minimum number of hours the haulout site had been left undisturbed at the time of the reading.

**Table 3.1** Environmental variables measured concurrently with census counts.

| Variable | Units |
|---|---|
| Julian Day | |
| Time of day | h |
| Tidal height | m |
| Wind speed | $ms^{-1}$ |
| Wind bearing | (absolute north is 0°) |
| Air temperature | °C |
| Solar radiation[1] | $Wm^{-2}$ |
| Precipitation | $mm\ h^{-1}$ |
| Time since last disturbance | h |
| Sea surface temperature | °C |

[1] Measured 1987-88 only.

### 3.3.2 Analysis

To permit comparison among sites, each seal count was standardized by expressing it as a proportion of the maximum number of seals hauled out at that site. This was done for both daily and annual maxima. Thus, a count of 25 seals taken on a day when a maximum of 50 hauled out would be converted to a daily proportion of 0.5 for that site; if a maximum of 75 seals hauled out at that site during the whole year, the annual proportion would be 0.33.

These proportions were converted to arcsine square-roots for regression analysis, to satisfy assumptions of normality and homogeneity of variance (Zar 1984). Since seals generally returned to the haul-out site within an hour of being disturbed, readings taken an hour or less after a disturbance were excluded from consideration.

Environmental variables potentially relevant to the thermal state of hauled out seals were regressed (stepwise linear) against the transformed proportion of annual hauled out maximum (hereafter referred to as 'annual haul'), to ascertain their overall significance. Neither polynomial nor interaction terms were tried, since earlier results suggested that simple linear components were adequate to detect significant correlations (Chapter 2). Although tidal height is not thermally relevant, it limits the area available for hauling and was thus also considered.

To simplify further analysis, thermally significant variables (wind speed, solar radiation, and air temperature) were incorporated into a single variable called flux ($F_s$). Flux describes radiant and convective energy exchange between the environment and a horizontal 10cm diameter circle of live seal skin under radiant skies. Essentially, it is a simple balance of inputs and outputs:

$$F_s = \text{shortwave}_{in} + \text{longwave}_{in} - \text{longwave}_{out} - \text{windchill} \tag{3.1}$$

If flux is positive, inputs exceed losses and the patch is gaining heat energy; if negative, the patch is losing heat energy. More quantitatively,

$$F_s = a_{ssw}S + a_{slw}\varepsilon_a\sigma(T_a + 273)^4 - \varepsilon_s\sigma(T_s + 273)^4 - h_c(T_s - T_a) \tag{3.2}$$

where $a_{ssw}$ is the absorptivity of the seal's surface to shortwave radiation (a decimal fraction, assumed to be .87 (Limberger *et al.* 1986));

$a_{slw}$ is the absorptivity of the seal's surface to longwave radiation (>.97 for most animal surfaces (Monteith 1973));

S is measured solar radiation ($Wm^{-2}$);

$\varepsilon_a$ is atmospheric longwave emissivity (another decimal fraction);

$\sigma$ is the Stefan-Boltzmann constant ($5.673 \cdot 10^{-8} Wm^{-2} {}^\circ K^{-4}$);

$T_a$ is ambient air temperature (°C);

$\varepsilon_s$ is surface longwave emissivity (equal to $a_{slw}$);

$T_s$ is radiant surface temperature (°C); and

$h_c$ is the convective heat-transfer coefficient (see below).

A number of these components decompose into other formulae in turn. Atmospheric longwave emissivity is approximated by

$$\varepsilon_a = 0.72 + 0.005 \cdot T_a \tag{3.3}$$

for air temperatures above 0°C (Campbell 1977, p58). The convective heat-transfer coefficient is a function of wind speed and object size; assuming turbulent forced flow over a flat surface 0.1m in diameter,

$$h_c = \frac{5.85 \cdot v^{0.8}}{.1^{\cdot 2}} \tag{3.4}$$

where v is wind speed ($ms^{-1}$) (Gates 1980, p288). Finally, surface temperature is described by an empirical relationship between $T_a$, solar radiation, and steady-state $T_s$ (Fig. 3.2), based upon data obtained during experiments on captive harbour seals (Chapter 4):

$$T_s = 22.222 + 0.436 \cdot T_a + 0.034 \cdot S \quad (n=83,\ r_{adj}^2=0.880) \tag{3.5}$$

Analysis involving flux was restricted to data collected at times of zero precipitation. Equation (3.5) describes heat exchange across dry pelage only. (Seals under experimental conditions generally dried off in less than an hour; the same could not always be said of wild animals, who sometimes forayed into the splash zone while hauling.)

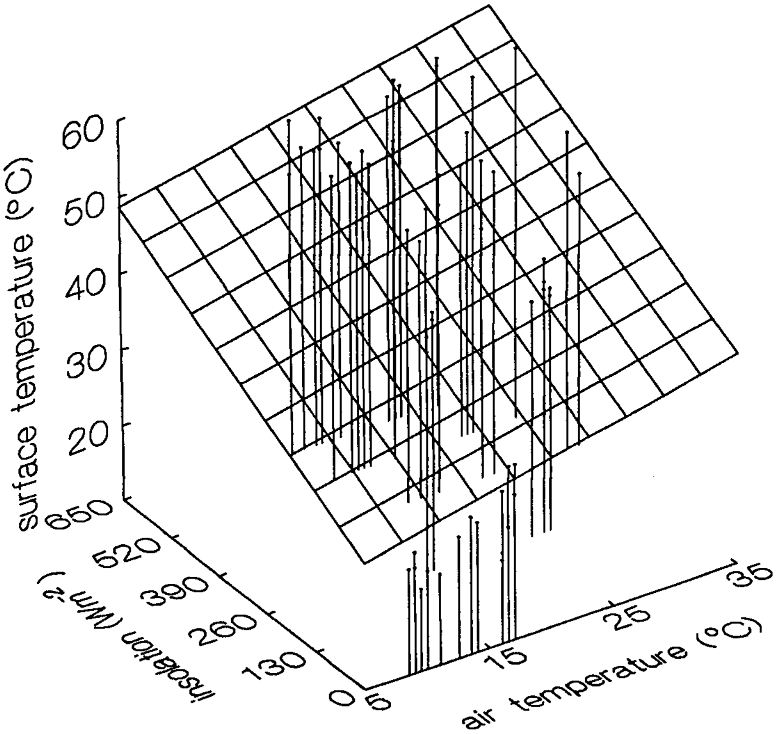

**Figure 3.2** Multiple linear regression of steady-state seal surface temperature on air temperature and incident shortwave radiation, assuming clear sky and dry pelage.

Equation (3.2) is similar in some ways to the "operative environmental temperature" (OET) equations derived by Bakken and Gates (1975) and others (Bakken 1981), which have recently been applied to pinnipeds (Limberger *et al.* 1986). There are, however, very significant differences between the two types of equation. The OET of an animal is the steady-state temperature of an inanimate object having the same morphology and thermal properties as the animal does--essentially, a complete, dead animal. $F_s$, in contrast, deals with heat exchange (not steady-state temperature) across a small piece of a live animal; this obviates the need for a precise description of the thermal geometry of the entire animal (there is no substrate conduction term, for example) , or the alternative assumption that the animal is adequately described by a simple shape (such as a cylinder or sphere). Furthermore, the use of an empirical relationship to describe surface temperature is much less prone to error than a theoretical derivation of the same parameter. The price for such simplicity is that $F_s$ can only be considered a relative index of the thermal relationship between a seal and its environment.

The general relationship between annual hauling activity and flux was initially explored by grouping different levels of flux into a series of discrete categories, and testing for significant differences in annual hauling activity between groups.

Several confounding variables could produce spurious correlations between hauling activity and flux. Seasonal migrations of seals out of or into an area are commonly reported (Brown and Mate 1980, Thompson 1989, Thompson *et al.* 1989); this could change the numbers hauled out coincident with seasonal differences in the thermal environment. Therefore, detailed exploration of the data was restricted to examining the relationship between flux and the transformed proportion of the daily maximum hauled out (hereafter referred to as 'daily haul').

Nonlinear regression techniques were used to describe a quantitative relationship between daily haul and flux during the pupping season. This extends from mid-June to mid-September in Puget Sound and the southern Georgia Strait (Bigg 1969); thermal conditions are warmest during pupping, and hauling activity is high as females give birth on land. This would therefore be the time during which any thermal constraints on hauling would be most readily detected.

During the pupping season, low tide (and the greatest available area for hauling) generally occurs during midday. Furthermore, since the greatest number of seals are in the water (apparently feeding) during darkness (Chapter 2), one might expect a peak in hauling midway between dawn and dusk (i.e., during the warmest part of the day) for reasons that have nothing to do with the thermal environment. Either feeding or tidal effects could produce a spurious correlation between the thermal environment and hauling. Data used in the regression were therefore limited to those collected from 1100 to 1300; i.e., all flux regressions were done on data from a narrow window within which time and tidal phase did not change greatly.

Finally, to explore site-related differences in flux and daily hauling activity, these mid-day data were grouped seasonally and by site; the groups were tested for significant difference using ANOVA (Kruskal-Wallis, 1-way) and, when necessary, Mann-Whitney U-tests (with Bonferroni correction to maintain an overall α-level of 0.05.)

## 3.4 RESULTS AND DISCUSSION

Results of the initial stepwise regressions are presented in Table 3.2. Solar radiation, air temperature, and wind speed all proved highly significant when correlated with annual haul; taken together they account for 37.5% of the total variation in hauling throughout the year at all study sites. Including tidal height in the regression increased the $r_{adj}^2$ to 0.435.

**Table 3.2** Summary statistics of multiple linear regressions of significant environmental variables onto annual haul.

| Variable | Coefficient | S.E. | Tolerance | t | n | r | $r_{adj}^2$ | S.E. of est. |
|---|---|---|---|---|---|---|---|---|
| *Excluding tidal height:* | | | | | | | | |
| constant | 0.189 | 0.028 | - | 6.815 | 745 | 0.614 | 0.375 | 0.234 |
| solar | 0.001 | 0.000 | 0.670 | 13.569 | | | | |
| air °C | 0.014 | 0.002 | 0.723 | 6.870 | | | | |
| wind sp. | -0.012 | 0.003 | 0.843 | -3.547 | | | | |
| *Including tidal height:* | | | | | | | | |
| constant | 0.517 | 0.045 | - | 11.493 | 745 | 0.662 | 0.435 | 0.222 |
| solar | 0.001 | 0.000 | 0.606 | 10.797 | | | | |
| air °C | 0.012 | 0.002 | 0.712 | 6.090 | | | | |
| wind sp. | -0.014 | 0.003 | 0.840 | -4.238 | | | | |
| tide | -0.086 | 0.010 | 0.802 | -8.995 | | | | |

Regression F-statistic = 144.465

All components have $P<0.001$

Since relationships between annual haul and the above environmental factors are generally monotonic (Chapter 2), they can be readily detected using linear regression. However, the linear model is not necessarily the best description of the shape of those correlations; it simply helps ascertain whether some sort of relationship exists.

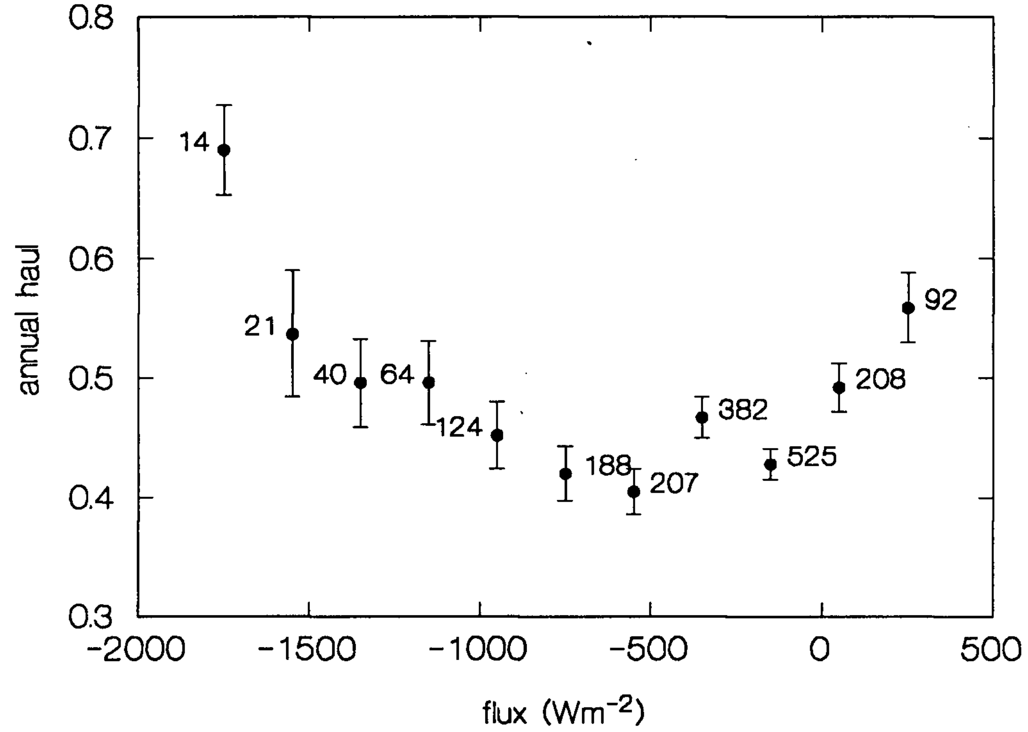

**Figure 3.3** Mean annual haul (arcsine square-root of the proportion of maximum annual haul) during daylight hours of harbour seals under different levels of flux. Standard error and n shown for each mean.

Figure 3.3 illustrates the overall relationship between flux and annual haul. Flux has been broken into a series of discrete groups, each containing a 200Wm$^{-2}$ range of values. Under cold conditions ($F_s$<-500Wm$^{-2}$) there is a significant inverse relationship between between flux and annual haul (Kruskal-Wallis statistic=26.791 with 8 *d.f.* and

$N$=660: $P$=0.001). However, when $F_s$>-500Wm$^{-2}$, the correlation between flux and hauling becomes positive; the hotter the environment, the greater the observed hauling activity (Kruskal-Wallis statistic=20.363 with 3 *d.f.* and $N$=1207: $P$<0.001).

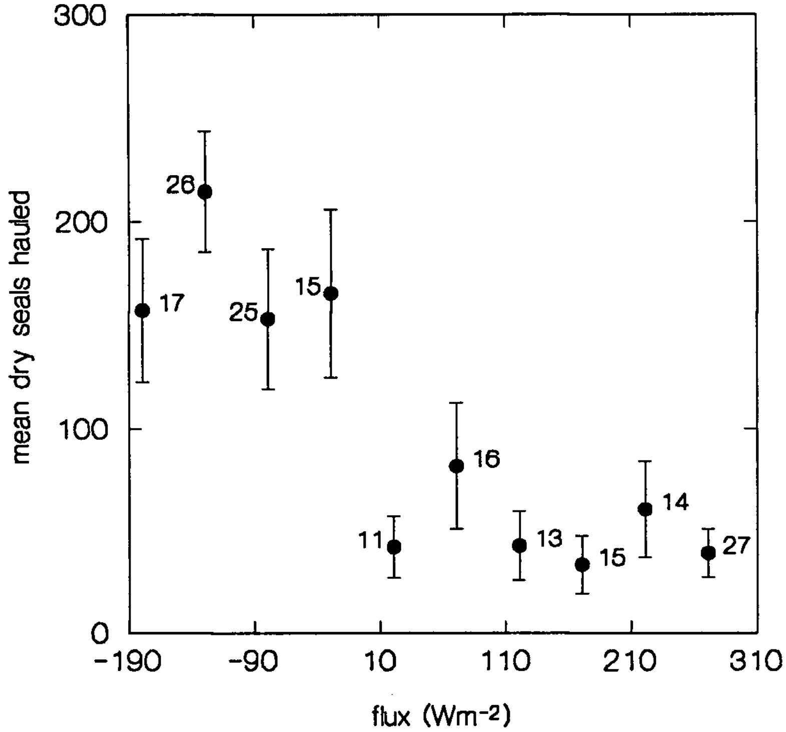

**Figure 3.4** Mean number of dry seals hauled at Gertrude Island under different levels of flux $F_s$. Standard error and n shown for each mean.

This is exactly the opposite to what one would expect if overheating were a significant constraint; under warm conditions, an increase in $F_s$ should be associated with a decrease in hauling activity. However, it is questionable whether this represents a real functional relationship. It could be due to seasonal changes in local abundance and the tendency for seals to forage at night (when $F_s$ is lower) as discussed above. When analysis is limited to only those hauled out seals with dry pelage (and thus less

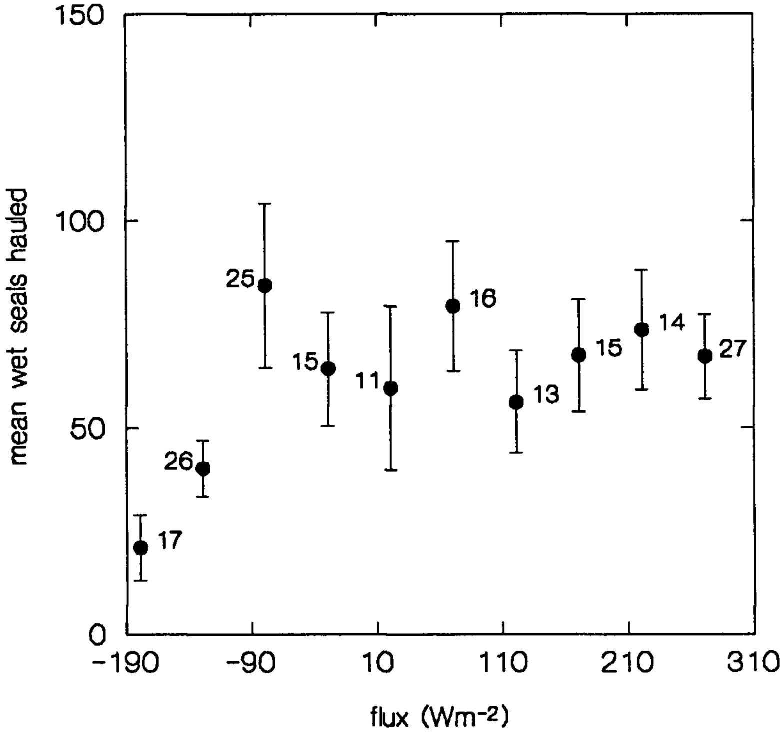

**Figure 3.5** Mean number of wet seals hauled at Gertrude Island under different levels of flux. Standard error and n shown for each mean.

able to benefit from evaporative cooling), a different pattern asserts itself; hauling activity when $F_s$>0 is markedly lower than when $F_s$<0 (Kruskal-Wallis test statistic=38.850 with 11 *d.f.*: $P$<0.001) (Fig. 3.4). Note that, if $F_s$ represents heat exchange between the seal and its environment, positive $F_s$ implies that the animal is gaining net heat, and should therefore overheat[8]. In comparison, there is no such relationship between flux and hauling for wet seals under exactly the same conditions;

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[8] In fact, since $F_s$ is only a relative index of heat exchange, one can not assume that the threshold between heat gain and loss occurs at exactly $F_s$=0 $Wm^{-2}$; judging from experimental work the actual critical value is closer to -70 $Wm^{-2}$ (see Chapter 4).

the only significant trend is a positive correlation between flux and hauling limited to $F_s$<-90 Wm$^{-2}$ (Kruskal-Wallis test statistic=23.055 with 9 *d.f.* and *N*=179: *P*=0.006) (Fig. 3.5).

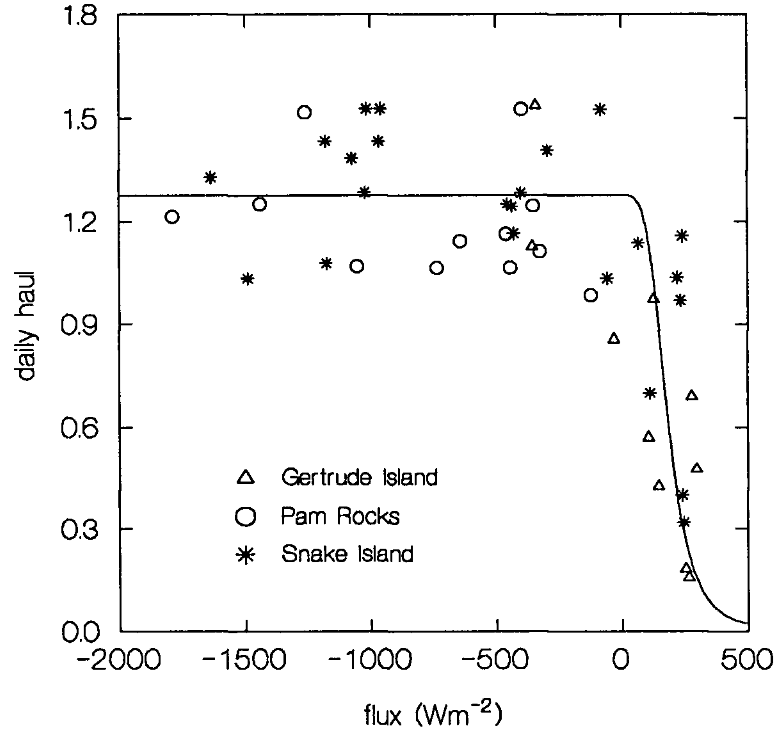

**Figure 3.6** Nonlinear regression of daily haul (arcsine square-root of the proportion of the daily hauled maximum) onto flux $F_s$, for data collected from Julian day 180-240, between 1100 and 1300.

At mid-day during the pupping season, a sharp decline in hauling at high flux levels is evident among all hauled out seals (not just those with dry pelage) (Fig. 3.6). The regression slope of flux vs. daily haul is not significantly different from 0 when flux is less than 0 Wm$^{-2}$ (*n*=32, *F*=0.764, *P*=0.389). Yet there is a strong negative relationship between flux and daily haul when flux is greater than 0Wm$^{-2}$ (*n*=14, *F*=10.082, *P*=0.005

at $\alpha=0.05$).

The lack of a relationship with flux below a certain threshold, coupled with a strong negative relationship under hot conditions, can be described by a declining sigmoid equation of the form

$$\text{daily haul} = \begin{cases} a, \text{ when } F_s<0 \\ a - \dfrac{aF_s^{\,d}}{c^d + F_s^{\,d}}, \text{ when } F_s>=0 \end{cases} \tag{3.6}$$

where a is the maximum value of the function

c is the inflection point of the curve; and

d controls the steepness of the curve.

The coefficients which best fit the data are

a = 1.227;

c = 180.4; and

d = 7.100

This model (Fig. 3.6) is based upon an *N* of 46, has an $r_{adj}^2$ of 0.648, and an associated F-statistic of 234.7. Including additive time-of-day and tidal components in the equation does not improve the fit; this relationship is not an artifact of tide or of any time-dependent behaviour.

The threshold beyond which hauling declines is abrupt (Fig. 3.6). Experimental observations indicate that overheating can occur rapidly in this species (Chapter 4). Under conditions simulating a temperate summer day, it was not uncommon for a harbour seal's core temperature to suddenly rise 1°C in less than 15 minutes, after remaining stable for over an hour.

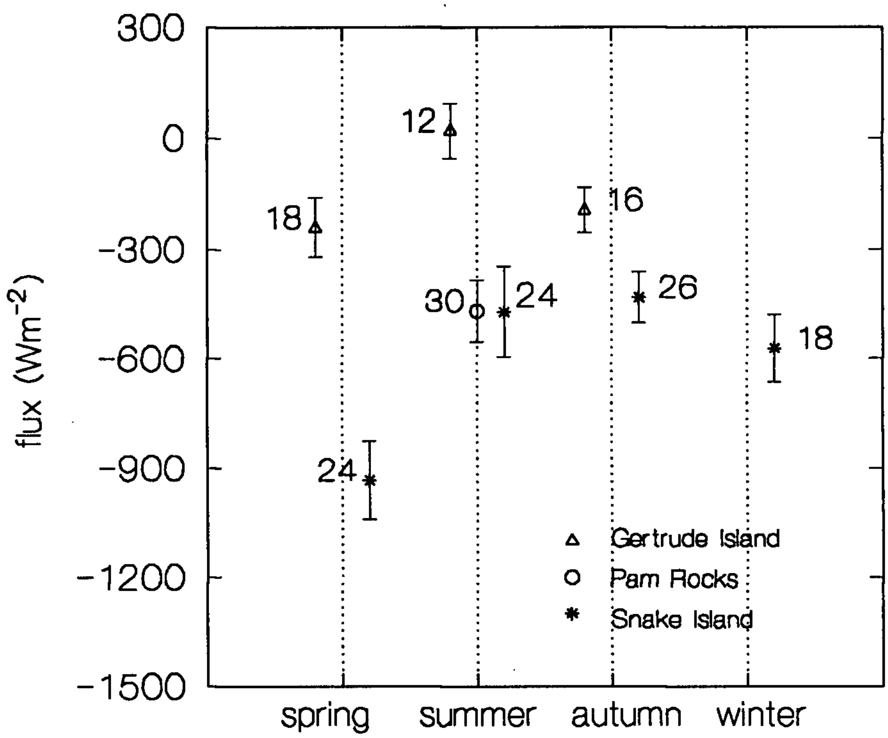

**Figure 3.7** Seasonal differences in mean flux at different sites. Standard error and n is shown for each mean.

Residual and probability plots showed no important violation of the assumptions associated with regression analysis. However, there is considerable "clumping" of points from the same site at different levels of flux (Fig. 3.6). Data collected from Snake Island covers nearly the entire range of the abscissa, from -1700 $Wm^{-2}$ to over 300 $Wm^{-2}$. Mid-day flux levels at Gertrude Island, however, never fell below -300 $Wm^{-2}$, and -100$Wm^{-2}$ is close to the maximum shown in the data from Pam Rocks. There appear to be significant differences in flux between sites.

This is in fact the case (Fig. 3.7). Although thermal conditions during the summer do not differ significantly between Pam Rocks and Snake Island, Gertrude Island is significantly hotter than the other sites (Kruskal-Wallis statistic=12.819 with 2 d.f.: $P$=.002), having a mean midday flux above the critical zone implicit in Figure 3.6. Not surprisingly, hauling activity is lower at Gertrude Island (Kruskal-Wallis statistic=21.009 with 2 d.f.: $P$<.001) than elsewhere (Fig. 3.8).

Inter-site differences in mean daily haul were detected only during the summer. Mid-day hauling data collected from Snake and Gertrude Islands during other times of year (there were insufficient data from Pam Rocks for three-way comparison) show no significant differences (Fig. 3.8) ($P$>0.3). (Gertrude Island is not represented during the winter because all mid-day winter readings taken from that site were associated with precipitation.)

Spring mean flux was significantly different between Gertrude and Snake Islands (Mann-Whitney statistic=346, $P$=.001), and (unlike the summer) this was not associated

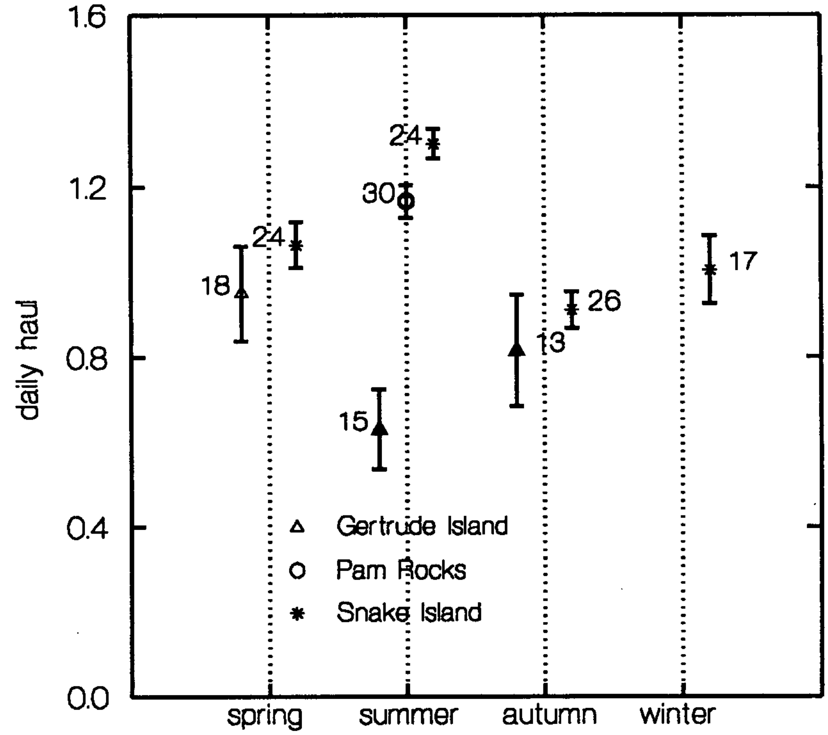

**Figure 3.8** Seasonal differences in mean daily haul (arcsine square-root of proportion of daily maximum hauled) at different sites. Standard error and n shown for each mean.

with any difference in hauling. However, flux levels during the spring do not approach the apparent overheating threshold (Fig. 3.6); below this point one would not expect to see any correlation between flux and hauling.

The coincidence of high flux and low hauling activity at Gertrude may manifest itself in a more obvious fashion. During spring, when flux levels do not approach the threshold at either site, close to the maximum daily haul occurred near noon at both Snake Island and Gertrude Island (Fig. 3.9). This was also the case at Pam Rocks and Snake Island during the summer (Fig 3.10). However, Gertrude Island shows a delayed

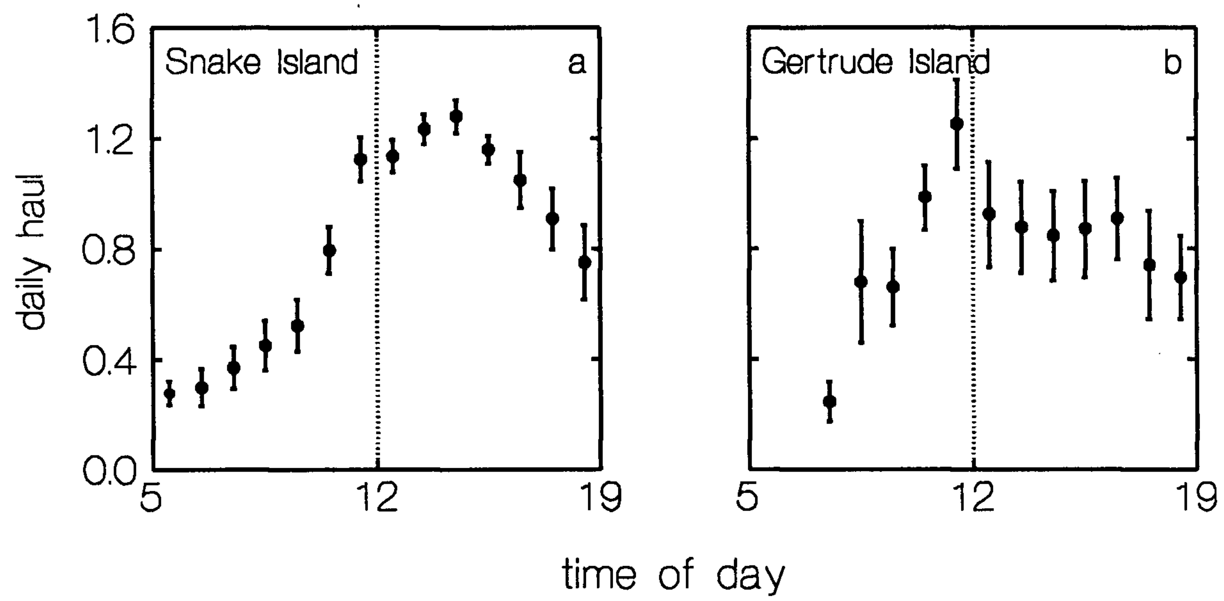

**Figure 3.9** Mean daily haul (arcsine square-root of the proportion of the daily maximum haul) during spring daylight hours at different sites. Standard error shown for each mean.

mid-afternoon peak in hauling during the summer. It is possible that seals may avoid hauling out until the hottest part of the day has passed; simulation modelling suggests that harbour seals are better able to withstand the declining heat of afternoon than the increasing heat of morning (Chapter 5).[9]

The differences between hauling activity at different sites can therefore be explained as a function of site-specific differences in the thermal environment. However, there is relatively little overlap in flux data between sites (although data from different sites agree where they do overlap). The Gertrude flux data occurs almost entirely above the

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[9] Since the data summarised by Fig 3.10 are not filtered for the constraining effects of various environmental variables, the hauling peak is not expected to be strongly skewed to late afternoon (Chapter 2).

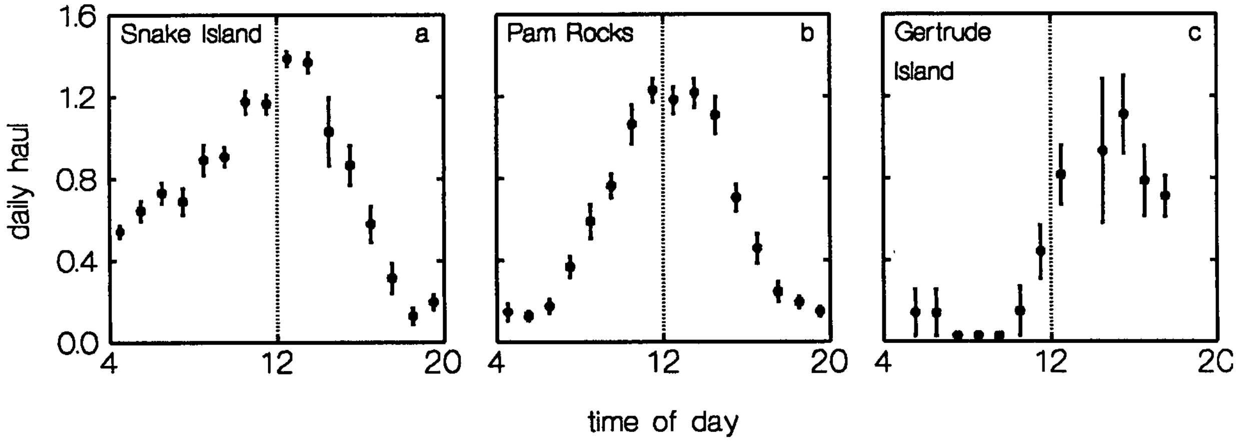

**Figure 3.10** Mean daily haul (arcsine square-root of the proportion of daily maximum haul) during summer daylight hours at different sites. Standard error shown for each mean.

0 $Wm^{-2}$ threshold, while the data from Pam Rocks occurs almost entirely below this level. Since the behaviour of seals at the two sites can not be compared under similar thermal conditions, it is impossible to exclude the possibility of some other site-related effect.

Fortunately the data from Snake Island overlap that of both other sites, and no obvious site-specific differences are apparent (Fig. 3.6). On balance, these results are consistent with the contention that the thermal environment is an important constraint on hauling behaviour in harbour seals, at least during the summer months. Given the central location of the study area within the range of *Phoca vitulina*, such constraints are likely to be geographically widespread. Further, they may be strong enough to significantly deform normal hauling patterns (Fig. 3.10). Since harbour seal surveys often assume a commonly reported mid-day peak in hauling (Boulva and McLaren 1979, Stewart 1984, Thompson *et al.* 1989), this should be of practical interest to census takers.

Thermal conditions on haulout sites appear to constrain, rather than drive, hauling activity in harbour seals. Even during the hottest part of the year, using data selected to minimise the effects of other variables, the thermoregulatory model accounts for only two thirds of the observed variation in hauling. Thermoregulation may be a vital component of any model of hauling behaviour, but it is unlikely to be the only one necessary or the most fundamental one.

Finally, it bears emphasis that this is a correlative study, based on observations made under uncontrolled conditions. It is reasonable to speculate on the functional underpinnings of these correlations, but little can be disproved without resorting to more rigorous studies. By exposing captive seals to the thermal conditions correlated with reduced hauling in wild animals, and monitoring their responses, it should be possible to establish whether a causal relationship actually exists.

# 4. OVERHEATING OF HARBOUR SEALS (*Phoca vitulina*) IN AN INSOLATED THERMAL ENVIRONMENT.

## 4.1 ABSTRACT

Previous studies of wild harbour seals suggest that hauling out behaviour is constrained by the danger of overheating on warm days (air temperature >17°C). Experiments on captive animals have demonstrated a prolonged tolerance for air temperatures as high as 35°C; however, those animals were not exposed to direct sunlight. During the present study, three harbour seals were subjected to controlled thermal conditions which more closely approached their natural environment through the use of a radiant heat source which simulated solar radiation. Seals did not overheat when not insolated or when kept wet. Otherwise, overheating occurred even at relatively low levels of "solar" radiation ($230Wm^{-2}$), although the rate at which this happened varied between individuals. Under more intense insolation ($410$-$630Wm^{-2}$) these differences disappeared. The onset of hyperthermia was characterised by an initial drop in core temperature and voluntary activity, followed by a steep increase in core temperature. During this time, surface temperature exceeded that of the core, effectively preventing

the dissipation of metabolic heat across the body surface. Rate of core temperature change can be expressed as a three-dimensional surface function of core temperature and the thermal environment. Regression analysis was used to fit these data to a theoretical model of homeotherm thermoregulation, with encouraging results ($r_{adj}^2$=0.855). This model may have predictive value when applied to harbour seals in the wild.

## 4.2 INTRODUCTION

The hauling behaviour of harbour seals can be correlated with various aspects of their physical environment. It usually declines as tidal height increases (Krieber and Barrette 1984, Schneider and Payne 1983, Sullivan 1980; but see Calambokidis *et al.* 1979), under strong winds (Schneider and Payne 1983), or during heavy rainfall (Krieber and Barrette 1984). These factors seem to act as constraints on an underlying pattern of hauling behaviour, rather than as driving variables in themselves.

There is strong circumstantial evidence that the danger of overheating while hauled out may be such a constraint. During summer in the Pacific northwest, it is not uncommon to encounter conditions (with air temperatures from 17-25°C) for which the surface of a hauled out harbour seal theoretically absorbs more heat than it emits (Chapter 3). Under these conditions, hauling activity among wild seals drops significantly. This is consistent with theoretical arguments suggesting that phocid seals should be especially sensitive to overheating while on land, as a consequence of their thermal adaptation to the aquatic environment (see Chapter 3).

Other field studies of phocids in potentially stressful thermal environments have also yielded valuable insights (Whittow 1978, White and Odell 1971), but all are limited by lack of control over natural conditions (although simulation models based on field data may extend these limits somewhat (Oritsland and Ronald 1978)). Purely experimental studies of phocid thermoregulation suggest that harbour seals can tolerate prolonged exposure to air temperatures as high as 35°C (Folkow and Blix 1987, Hart and Irving 1959, Matsuura and Whittow 1973). However, these studies have ignored the effects of solar radiation, and are therefore unreliable indicators of wild tolerances (Oritsland and Ronald 1973).

This paper represents a first step towards correcting that limitation. I examined the thermal responses of three harbour seals under controlled conditions simulating a sunlit environment. The goal of the study was to predict changes in core temperature as an empirical function of both environmental and internal heat states.

## 4.3 METHODS

### 4.3.1 Animal Care and Housing

Two harbour seals were captured using a tangle net, in the Strait of Georgia. A third was borrowed from the Vancouver Public Aquarium. This sample ranged in maturity from yearling to adult (Table 4.1), and was representative of the local population in terms of body mass (the average mass of harbour seals in B.C. waters is 45-46 kg (P. Olesiuk, Pacific Biological Station, Nanaimo, B.C., unpublished data). To facilitate comparison with a separate, largely male sample of eleven wild, radio-tagged

**Table 4.1** Morphometric measurements on experimental harbour seals.

| | Attila | Genghis | Thalidomide |
|---|---|---|---|
| Age class | adult | subadult | yearling |
| mass (kg) | 55. | 46. | 31. |
| std. length (m) | 1.15 | 1.20 | 1.00 |
| surface area[1] ($m^{2)}$ | 0.964 | 0.878 | 0.715 |
| area/mass ($m^2kg^{-1}$) | 0.017 | 0.019 | 0.023 |

[1] With flippers open. Based on equation 5.11 in Worthy 1985.

harbour seals (see Chapter 5), all three experimental animals were male.

Seals were housed in an outdoor 3m-diameter pool 1.5m deep, with an open-flow water supply and an adjacent hauling platform of about 4.5m$^2$ (Fig. 4.1). Flow rates were sufficient to completely replace the water in the tank every two hours; water temperature varied from 10-11°C in the summer to 7-8°C in the winter, comparable to local sea surface temperatures. The system was filled with fresh water during the incarceration of one of the seals (Attila), from July to December of 1989; that animal was therefore provided with dietary salt supplements, a salt bath on the haulout platform, and weekly salination of the main tank to simulate marine conditions for 5-6 hr at a time. The other two seals were housed together in a sea-water flow-through system of the same dimensions, from February to early April of 1990.

Seals were fed once daily. Diet consisted mainly of thawed herring (5-8% of body mass) with thiamine and multivitamin supplements (Geraci 1975). Live trout and salmon were periodically introduced into the tank to vary the diet and relieve boredom.

### 4.3.2 Experimental Apparatus and Procedures

Experiments were conducted on an artificial haul-out site that could be subjected to controlled thermal regimes (Fig. 4.1). The haulout surface itself doubled as an experimental chamber; part of the platform could be raised like a drawbridge, becoming in effect a wall of the chamber. It was thus a simple matter to enclose the animals in the chamber with a minimum of stress.

The roof of the chamber was equipped with an array of twelve 480W infrared heat lamps, connected to high-voltage dimmer switches. The radiant heat produced by this array was measured at different switch settings using a Weather Measure R401 mechanical pyronometer, set on the floor of the chamber at several different positions. "Solar" intensity was defined as the mean of these measurements at each setting. The entire array could be moved within the chamber to keep it directly over the tested seal.

Seals were acclimated to the experimental apparatus for a month prior to the running of any tests. Then each seal was subjected to a series of at least five tests, each at a different level of "solar" intensity from darkness ($0Wm^{-2}$) to the maximum radiant output of the array ($627Wm^{-2}$). (This contains the range of thermal conditions associated with a decline in the hauling of wild harbour seals--see Chapter 3.) Table

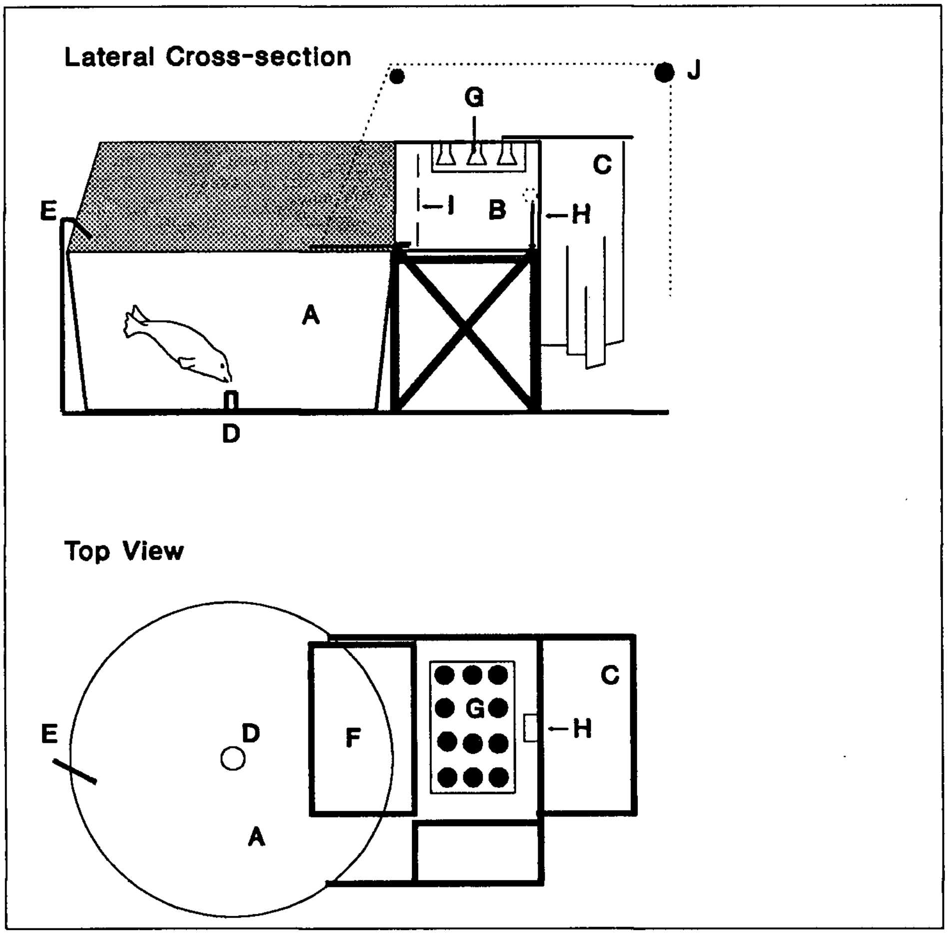

**Figure 4.1.** Seal holding and experimental facility. A) holding tank; B) test chamber; C) observer shelter; D) drain; E) inflow; F) haul-out; G) heat lamp array; H) sensor array; I) haul-out position when raised; J) rope and pulley for raising haul-out.

4.2 provides an indication of the temperatures associated with each treatment, for each month experiments occurred.

Subjects were fasted for at least twelve hours prior to each test to insure that they were post-absorptive. Immediately upon hauling out, the experimental animal was

**Table 4.2** Mean air temperatures (°C) under different "solar" treatments at different times of year.

| | "solar" intensity (Wm$^{-2}$) | | | | |
|---|---|---|---|---|---|
| Month | 0 | 230 | 410 | 530 | 630 |
| Sept. '89 | 15 | 24 | 25 | 28 | 28 |
| Oct. '89 | 8 | 16 | 20 | 26 | 26 |
| Nov. '89 | 7 | 16 | 19 | 19 | 23 |
| Mar. '90 | 12 | 17 | 18 | 18 | 17 |

sealed into the test chamber while still wet[10]. The treatment consisted of exposing the animal to constant "solar" intensity for at least eight hours or until overheating occured, whichever came first. While in the chamber, core temperature was monitored using an AM transmitter (Mini-Mitter Co. Inc., Sunriver, Ore.) with a measured accuracy of 0.2°C. Surface temperatures were obtained without touching the animal, by using an infrared thermometer with an accuracy of ±1°C (Linear Laboratories C-600E); the sensor was held ≤6cm from the surface being measured.

The following variables were measured throughout each run:

air temperature (°C);

substrate temperature (°C);

relative humidity;

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[10] During dry, nonzero "solar" treatments, seals generally dried off in an hour or less.

core temperature (°C);

Estimated percentage of seal's surface that was dry;

Surface temperatures (°C):

- top of head
- foreflipper
- hindflipper
- maximum trunk temperature (usually on the surface exposed to direct radiation)
- minimum trunk temperature (usually on the surface in contact with the floor of the chamber).

Readings were taken every half-hour until core temperature rose more than 0.5°C above it's initial state; thereafter readings were taken every 10-15 minutes.

In an attempt to determine whether responses varied seasonally, Attila was subjected to three complete series of tests from September to November of 1989. Deviation of core temperature from its value at the start of each test (hereafter referred to as "relative core temperature") was compared among months using a repeated measures ANOVA applied to data blocked for time (within treatment) and "solar" intensity.

Attila was also exposed to another monthly series of tests at $0Wm^{-2}$ and $627Wm^{-2}$ "solar" intensity; during these tests he was continuously wetted by a fine spray from a convenient garden hose.

For analytical purposes the thermal environment within the chamber was expressed in terms of $F_s$, an index of heat flux (in $Wm^{-2}$) across the seal's surface. $F_s$ incorporates both air temperature and "solar" radiation (Eq. 3.2). Wind speed (v, in Equation 3.4) was assumed to be $0.1msec^{-1}$ within the chamber, to allow for convective cooling (Gates 1980). The derivation of $F_s$ is discussed in Chapter 3.

## 4.4 RESULTS AND DISCUSSION

### 4.4.1 General responses

Evaporative cooling prevents hyperthermia in wet seals. Regardless of radiant heat intensity, core temperature did not vary more than 0.5°C from baseline whenever Attila's surface was kept wet. This is consistent with field data showing a strong inverse relationship between flux and the number of dry seals hauled out (Fig. 3.4), but no such relationship among wet seals under the same conditions (Fig. 3.5).

Seals did not overheat during tests in which "solar" radiation was $0Wm^{-2}$. However, all radiant treatments eventually resulted in hyperthermia (Fig. 4.2). Overheating followed the same general pattern at all non-zero levels of "solar" intensity (Fig. 4.2); it simply occurred more rapidly under hotter conditions. The pattern itself can be conveniently broken into three stages.

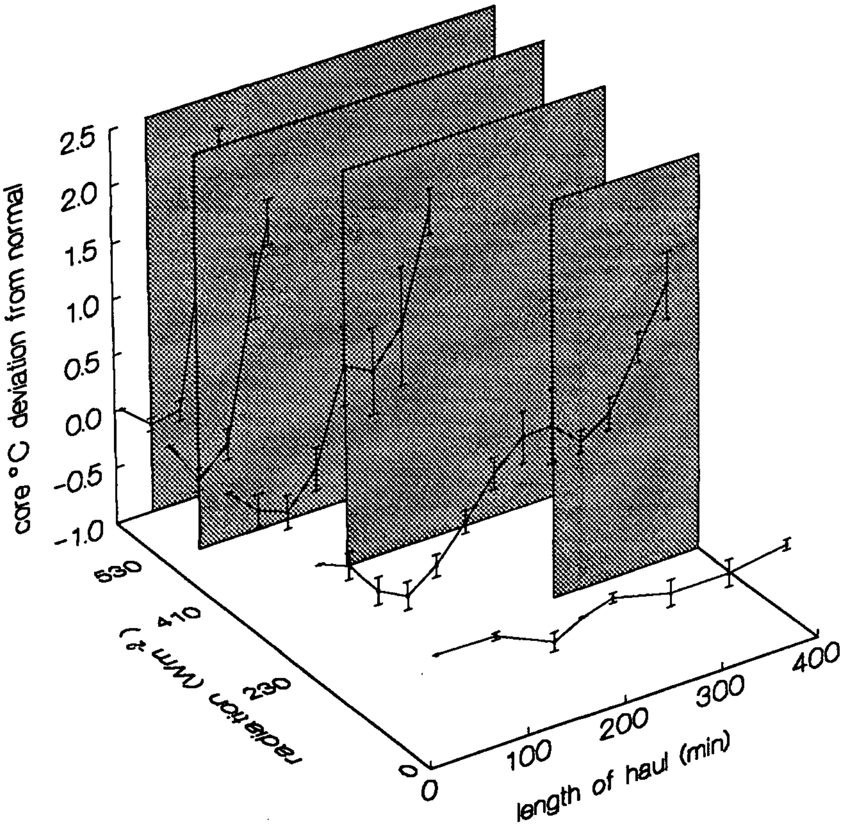

**Figure 4.2** Mean relative core temperature of three seals vs. elapsed time during different "solar" treatments. Shaded areas denote times when mean surface temperature exceeds mean core temperature. Standard errors shown for each mean: N varies from 3-6 per mean.

1) "Resting" is characterised by an initial drop in core temperature of about 0.5°C, and a commensurate reduction in voluntary movement. Seals frequently slept during this phase, which reduced the amount of metabolic heat being produced.
2) "Radiation" begins when core temperature starts to increase again. During this phase, the temperature of the body surfaces exceed that of the core. At this point net heat flow is inward, and the seal is in a "no-win" situation: if it peripherally vasodilates, unwanted surface heat is carried to the core, but if it

vasoconstricts metabolic heat cannot escape. Shaded areas in Fig. 4.2 show the times during which mean pelt temperature exceeded core temperature at each level of "solar" intensity. Although the flippers are often cited as the primary source of heat exchange between the seal and its environment (Hart and Irving 1959, McGinnis 1975), when insolated the flippers radiate at the same temperature as the rest of the body (Fig. 4.3).

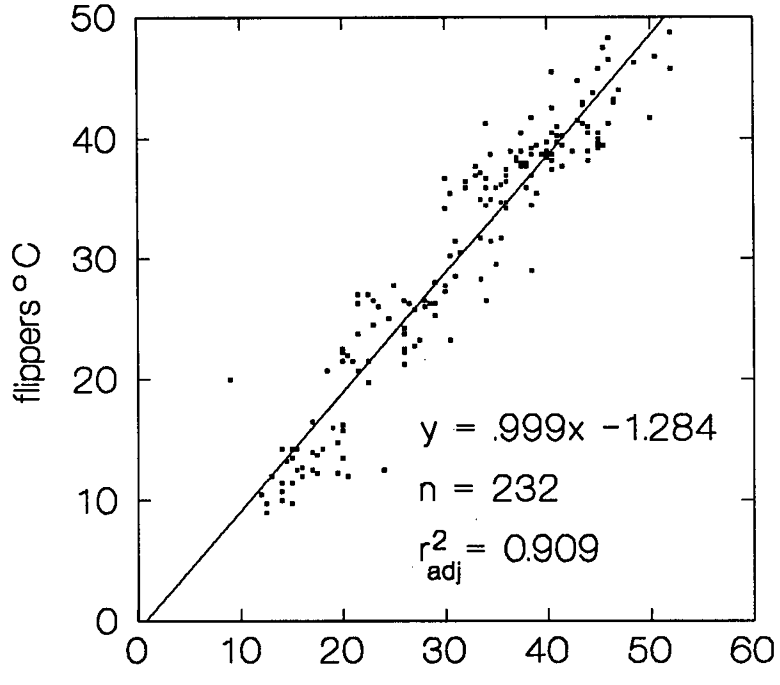

**Figure 4.3** Mean pelt temperature vs. mean flipper temperature for three seals, all "solar" treatments combined.

3) "Redline" is characterised by active promotion of evaporative cooling when core temperature climbs 1.5-2.0°C above normal. The seal salivates profusely, the eyes run, and the bladder and bowels empty (phocid seals do not have functional sweat glands (Montagna and Harrison 1957, Whittow *et al.* 1975)). This wets the animal to a small extent, but the data do not show any associated drop in core temperature. However, experiments were ended at the onset of this phase to minimise discomfort to the animals.

### 4.4.2 Seasonal and Individual differences

Attila's relative core temperature (the deviation of core temperature from normal) did not change significantly between September and November, once time and treatment were accounted for ($P>0.1$). These results are particularly noteworthy since Attila was moulting during the November tests. The metabolism of moulting harbour seals is routinely depressed by 15-20% (Ashwell-Erickson *et al.* 1986), which might be expected to reduce vulnerability to overheating. Apparently this is not so.

There are other reasons for expecting seasonal differences in thermal response. Blubber thickness varies throughout the year in Alaskan harbour seals (Pitcher 1986) and at least one other phocid species (Ryg *et al.* 1990); this should result in seasonally varying thermal properties. In fact, Hart and Irving (1959) reported higher critical temperatures for Atlantic harbour seals in summer than in winter, although that result may have been artifactual; different seals were used during their summer and winter experiments.

Although local conditions from September to November 1989 covered the thermal spectrum from summer to winter, seasonal differences might have appeared if testing had occurred throughout a greater proportion of the year. Some hint of seasonality may be apparent when comparing the thermal responses of different seals to the same treatments at different times of year (Fig. 4.4), but this is inevitably confounded by inherent differences between individuals.

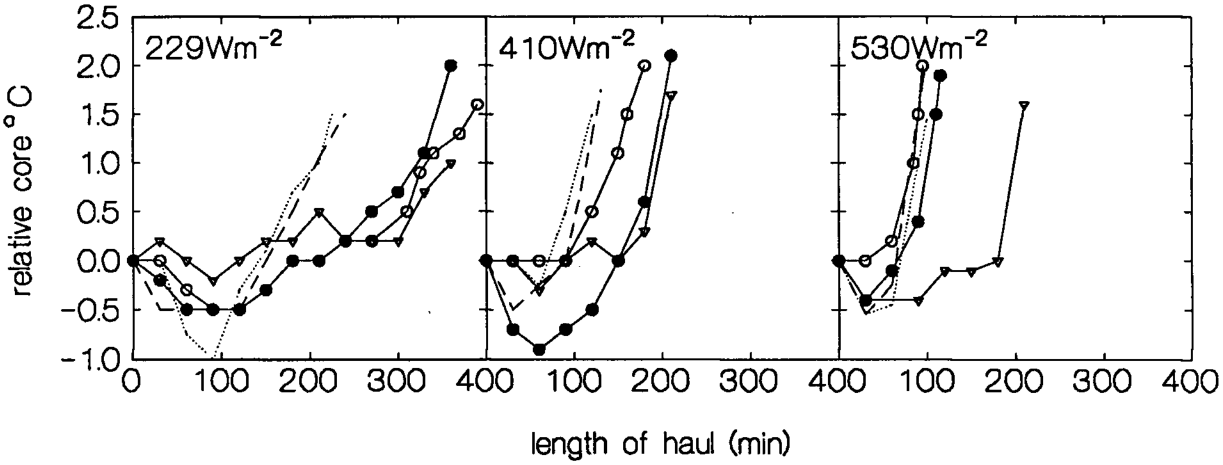

**Figure 4.4** Relative core temperature vs. time for selected "solar" treatments. Dashed line, Genghis; dotted line, Thalidomide; solid line, Attila (open circles, Sept.; filled circles, Oct.; triangles, Nov.).

All three seals reacted similarly under most treatment conditions; however, at the 230Wm$^{-2}$ treatment Attila took almost two hours longer to overheat than either of the other two animals (Fig. 4.4). Large animals have a smaller surface-area-to-mass ratio than small ones, which makes them less vulnerable to their thermal environment; one might therefore expect that Attila (the largest seal) would be the least vulnerable to hyperthermia. However, Genghis and Thalidomide overheated at the same rate, although Genghis' surface area to mass ratio was much closer to Attila's (Table 4.1). This implies that there are other factors involved.

Thalidomide and Genghis had baseline core temperatures which were not significantly different from each other, but which were higher than Attila's (Kruskal-Wallis statistic=19.006, *P*<.001 with 2 d.f.). This implies that Attila had a lower metabolic rate than either of the other subjects. The fact that Thalidomide was a yearling and Ghengis was a subadult may at least partially account for this; juvenile animals have higher metabolic rates than adults. However, Attila was only a young adult, and not much larger than Genghis (Table 4.1); whether this difference is enough to account for the observed variation in heating rates is debatable. The differences between these seals could reflect variation between individuals, seasons, or both. Hart and Irving (1959) could find no seasonal change in thermoneutral metabolic rate for Atlantic harbour seals, but their study also confounded season with individual.

Whatever the differences among individuals, they are most apparent under mild "solar" radiation. As heat load increases, the responses of all three seals converge

(Fig. 4.4).

### 4.4.3 Quantification of the Hyperthermal Response

Thermoneutrality is the state in which a desired core temperature can be maintained without changing resting metabolic rate. Under these conditions, an animal remains in heat balance by adjusting its thermal conductance (e.g., through peripheral vasodilation or vasoconstriction). However, thermal conductance can only change within certain limits; when balance cannot be kept within these limits, core temperature tends to change.

Among large homeotherms, core temperature is regulated by a dual thermostat system which monitors both the external environment and internal heat state (Gordon 1977). Core temperature is monitored by thermoreceptors in the hypothalamus; if it moves beyond inherent upper or lower "set points", metabolic rate changes to restore normal body temperature.

The system must do more than respond to changes in core temperature, however. Because of the inherent thermal inertia of large bodies, it takes time for a thermal imbalance to manifest itself as a temperature change; a compensatory response would take more time to have an effect. This lag between stimulus and response would result in a fluctuating core temperature whenever conditions departed from thermoneutrality (Cossins and Bowler 1987).

To prevent this, the regulating system must be able to anticipate potential changes in deep body temperature. Afferent thermoreceptors in the skin fulfill this need, monitoring changes in the external thermal environment before they exert significant internal effects.

The regulation of core temperature is thus a function of both internal and environmental heat states. Passive transfer of heat between the environment and the animal also depends upon thermal conditions on both sides of the body wall. Rate of change in core temperature can be plotted against relative core temperature and $F_s$; a distance-weighted least squares smooth of these data (Wilkinson 1989, p554-555) produces a three-dimensional surface describing the thermal response of the animal.

There were enough data to construct such a surface for Attila (Fig. 4.5). However, the initial decline in core temperature under nonzero "solar" conditions (Fig. 4.2) introduced a complication. Since core temperature dropped at the start of these runs, initial rate of change was negative. However, when the core reheated back to baseline levels and above, its rate of change was obviously positive; this resulted in opposing rates of change occuring at the same place on the graph. Although these conflicting events were separated in time, there is no time axis in Fig. 4.5.

Since the human brain can not readily comprehend static two-dimensional depiction of four-dimensional relationships, data collected during the initial core decline were excluded from the plot. Figure 4.5 therefore represents Attila's thermal response *after* any initial drop in core temperature. This does not mean that such declines are

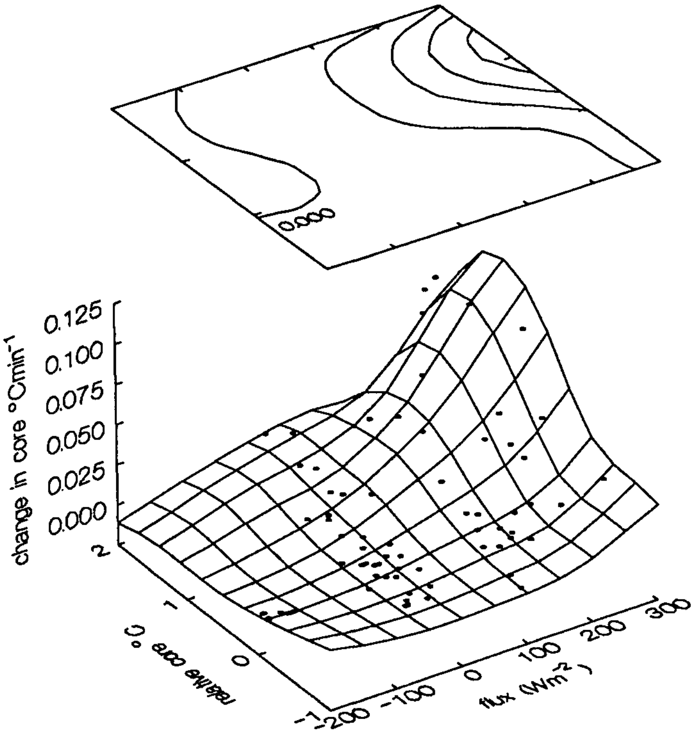

**Figure 4.5** Distance-weighted least-squares surface plot of Attila's rate of core temperature change vs. relative core temperature and flux.

ignored, only that they occur before the relationship depicted in Fig. 4.5 becomes relevant. Thus a trajectory plotted on the response surface might begin at a relative core temperature of -0.5°C, rather than 0°C[11].

Although the surface in Fig. 4.5 is based upon a smoothed plot of actual data, its topography is presumably a function of both active thermoregulatory behaviour and the passive transfer of heat between environment and harbour seal. These processes can be

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[11] If necessary, the actual decline can be described separately to determine the initial relative core temperature of such trajectories--see 5.2.3.4.

described mathematically; it should therefore be possible to describe the response surface as a composite of several simple equations.

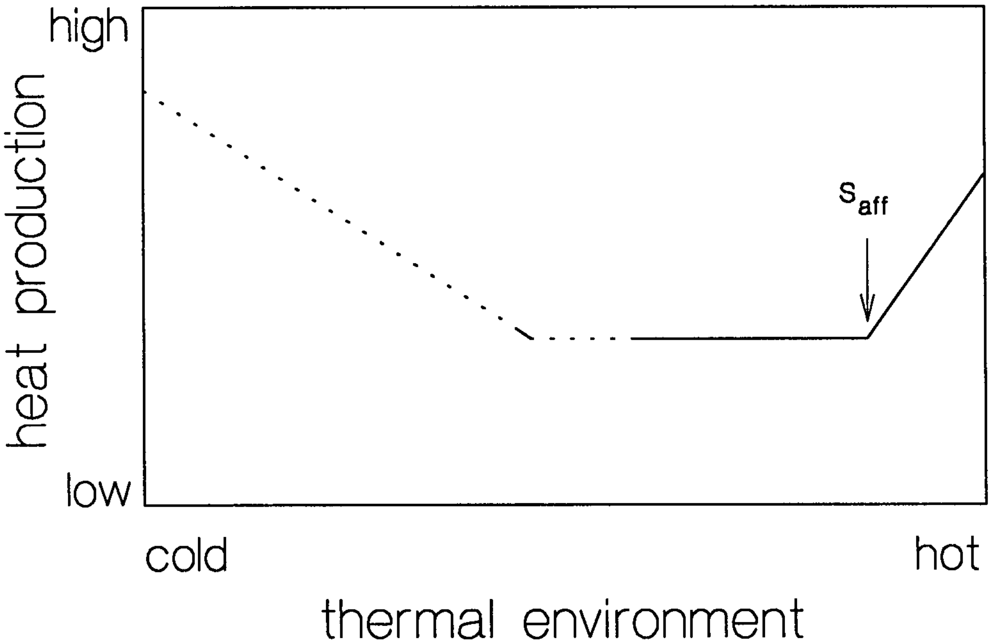

**Figure 4.6** Conceptual relationship between metabolic heat production and the thermal environment. Dotted line denotes the part of the relationship beyond the range of the observed data.

The general relationship between homeothermic heat production and the thermal environment is shown in Fig. 4.6 (Gordon 1977). Metabolic rate increases linearly as the thermal conditions decline below the lower afferent set-point. Within the thermoneutral zone, no metabolic changes are necessary since homeothermy is maintained through changes in thermal conductance and behaviour; near the upper end of this zone, animals tend to minimise voluntary movements (the seals often fell asleep). Once conductance is maximal, however, further increase in external heat causes increased internal heat production. This paradoxical result occurs because active dissipation of surplus heat requires metabolic expenditure, and therefore generates additional heat. Among homeotherms in general, sweating and panting are two common strategies for heat dissipation. Panting in particular generates heat, since it involves continual exercise of the diaphragm and chest musculature (Adams 1971). Harbour seals do not "pant" in the conventional sense; however, their breathing rate appears to increase in conjunction with the "gaping" behaviour observed during incipient hyperthermia. This is probably functionally equivilent to panting.

The shape of this increase in heat production can be linear (as in rodents--Hart 1971), or exponential (Gordon 1977). For simplicity, initial modelling attempts assumed linearity. Furthermore, there was no evidence of a lower thermoneutral limit within the conditions tested, either during these experiments or in the field (Chapter 3). Rate of change in core temperature due to afferent thermoregulatory response ($dC_{aff}$) was therefore described as

$$dC_{aff} = \begin{matrix} 0,\ F_s \leq s_{aff} \\ c(F_s - s_{aff}),\ F_s > s_{aff} \end{matrix} \qquad (4.1)$$

where c is the slope of the increase, and

$s_{aff}$ is the upper afferent set-point ($Wm^{-2}$).

The relationship between heat production and core temperature can likewise be described as a series of line segments (Fig. 4.7). When core temperature is subnormal, a homeotherm will increase metabolic heat production to compensate; the degree of the

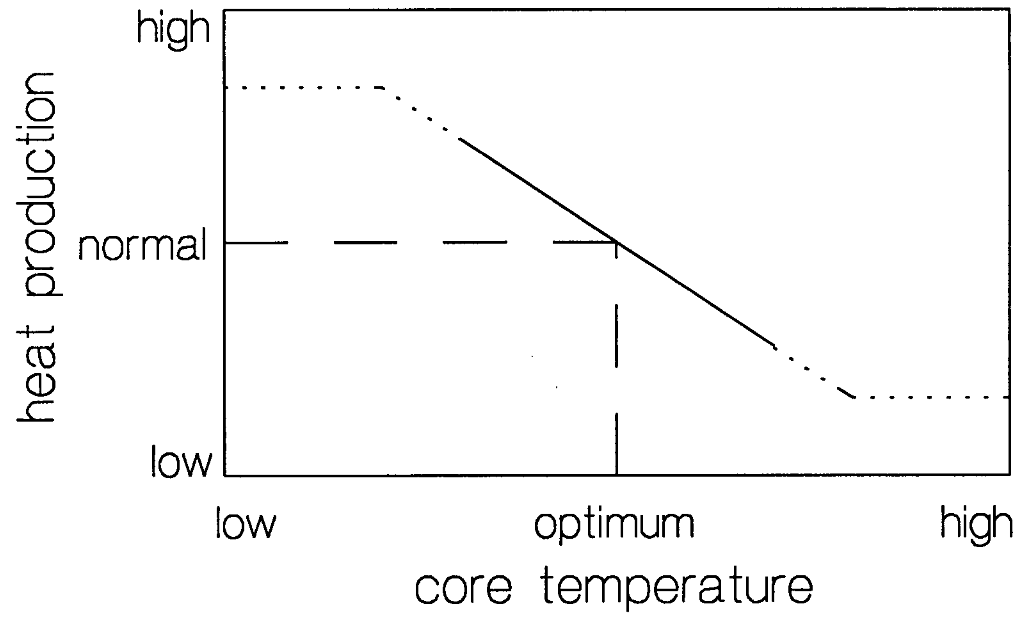

**Figure 4.7** Conceptual relationship between metabolic heat production and core temperature. Dotted lines denote the part of the relationship beyond the range of the observed data; a stable equilibrium exists at the intersection of the dashed lines.

increase is ideally proportional to the difference between actual and optimum core temperature. Likewise, if the core is too hot, heat production should decline, and this decline should also be proportional to the desired change in core temperature. The model thus postulates a straight line with an x-intercept at the optimum core temperature (i.e., a stable equilibrium). Naturally, metabolic rate can only fluctuate within certain limits; if it falls below a minimum level the animal dies, and likewise it cannot increase infinitely. Once again these constraints were not detected during the experiments, since under hot environmental conditions net heat gain increases (see below) and no readings were taken in which a hot core coincided with a cool environment. The rate of core temperature change resulting from departures from the optimum state ($dC_{dfo}$) was therefore described (within the limits of the data) as a simple line:

$$dC_{dfo} = \begin{cases} g(C_a - C_o), & g(C_a - C_o) > dC_{aff} \\ 0, & g(C_a - C_o) \leq dC_{aff} \end{cases} \tag{4.2}$$

where g is the slope of the line;

$C_a$ is actual core temperature (°C); and

$C_o$ is optimum core temperature (°C).

$C_a$ - $C_o$ is equivilent to relative core temperature ($C_{rel}$). (The conditional terms reflect that there is no need for further change if heat production has already increased sufficiently due to the afferent response described in Eq. 4.1)

Superimposed upon this linear relationship are the feedback effects of active heat dissipation (Fig. 4.8), which themselves contribute to the body's heat load. Here these effects are expressed not in terms of environmental heat state but in terms of core temperature. Among carnivores, hyperthermia causes an initial rise in heat production which then flattens out (presumably when the animal reaches its metabolic limit) (Adams 1971). If core temperature continues to increase, the rate of heat production declines again (perhaps representing a breakdown of regulatory effort under extreme heat stress). This general pattern (Fig. 4.8b) is also apparent in the experimental data from Attila (Fig. 4.5), and can be approximated as the difference of two sigmoid

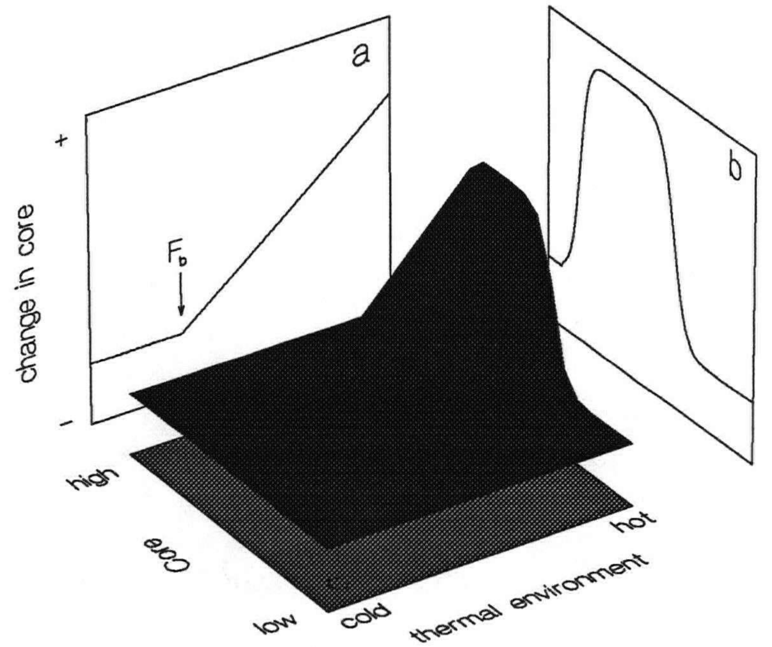

**Figure 4.8** Conceptual model of the hyperthermic part of Attila's thermal response surface. a) heat buildup when flux>$F_b$; b) metabolic heat production as a function of hyperthermic core temperature; c) the interaction of these effects.

curves:

$$dC_{fbk} = M\left[\frac{(C_{rel}+2)^{i1}}{(i2+2)^{i1} + (C_{rel}+2)^{i1}} - \frac{(C_{rel}+2)^{i3}}{(i4+2)^{i3} + (C_{rel}+2)^{i3}}\right] \qquad (4.3)$$

where $dC_{fbk}$ is the rate of change in core temperature due to regulatory feedback (°Cmin$^{-1}$);

M is the maximum value of the function;

i1 determines the steepness of the initial increase in heat production;

i2 is the inflection point of the initial increase in heat production;

i3 determines the steepness of the final decline in heat production; and

i4 is the inflection point of the final decline in heat production.

The constant 2 is added to these components to maintain positive values even when core temperature is up to 2°C below normal; this is necessary to maintain the shape of the sigmoid relationship.

As long as net heat flow is away from the animal, surplus metabolic heat can be dissipated to the environment by increasing the thermal conductance of the body wall. Under conditions which lead to overheating, thermal conductance is at its maximum and is therefore constant; the animal gains heat from the environment at a rate proportional to the difference between its surface and core temperatures. The efficiency with which it can dissipate that heat declines proportional to the same difference; hence, rate of heat buildup increases with $F_s$. The maximum value M of Eq. 4.3 is thus a linear function of the thermal environment, when net heat flow is into the animal:

$$M = \begin{matrix} a(F_s - F_b),\ (F_s - F_b)>0 \\ 0,\ (F_s - F_b)\leq 0 \end{matrix} \qquad (4.4)$$

where a is the slope of the relationship; and

$F_b$ is the level of flux at which net heat flow between the seal and its environment equals $0\mathrm{Wm}^{-2}$ (thermal equilibrium at maximum thermal conductance).

Combining Equations 4.1 through 4.4, a general model describing the overall rate of change in core temperature as a composite function of both core temperature and the thermal environment (dC) has the form

$$dC = dC_{aff} + dC_{dfo} + M \cdot dC_{fbk} \tag{4.5}$$

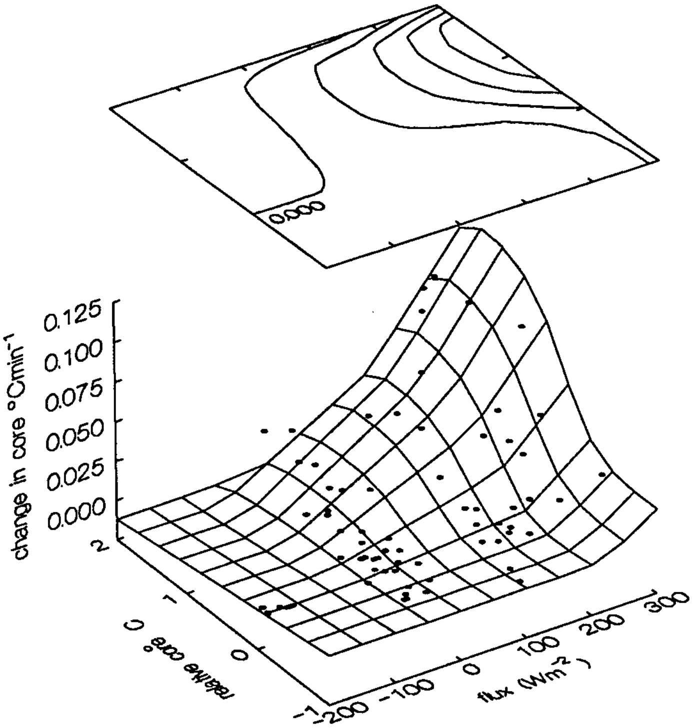

**Figure 4.9** Regression model of Attila's thermal response surface, based on Equation 4.5.

Regression of the experimental data using this general model (Fig. 4.9) produced a very strong fit ($r_{adj}^2$=0.855). Parameter estimates and summary statistics of the fitted model are shown in Table 4.2. Although a large number of parameters were estimated, they are not highly correlated. (Appendix 4).

**Table 4.3** Summary statistics for the regression model of Attila's thermal response surface.

N=83 $r_{adj}^2$=0.855 P<0.001

| Parameter | Estimate | Asymptotic Standard Error | 95% Confidence Limits | |
|---|---|---|---|---|
| | | | Lower | Upper |
| $S_{aff}$ | 196.515 | 0.666 | 195.188 | 197.841 |
| c | $2.73\cdot10^{-4}$ | $7.8\cdot10^{-5}$ | $2.65\cdot10^{-4}$ | $2.92\cdot10^{-4}$ |
| g | -0.006 | 0.002 | -0.011 | -0.001 |
| $F_b$ | -71.546 | 24.173 | -119.650 | -23.442 |
| i1 | 9.564 | 2.438 | 4.705 | 14.423 |
| i2 | 0.321 | 0.072 | 0.177 | 0.464 |
| i3 | 50.073 | 0.000 | 50.073 | 50.073 |
| i4 | 1.851 | 0.038 | 1.776 | 1.927 |
| a | $2.73\cdot10^{-4}$ | $5.00\cdot10^{-5}$ | $2.63\cdot10^{-4}$ | $2.83\cdot10^{-4}$ |

### 4.4.4 Performance of the estimated thermal response surface.

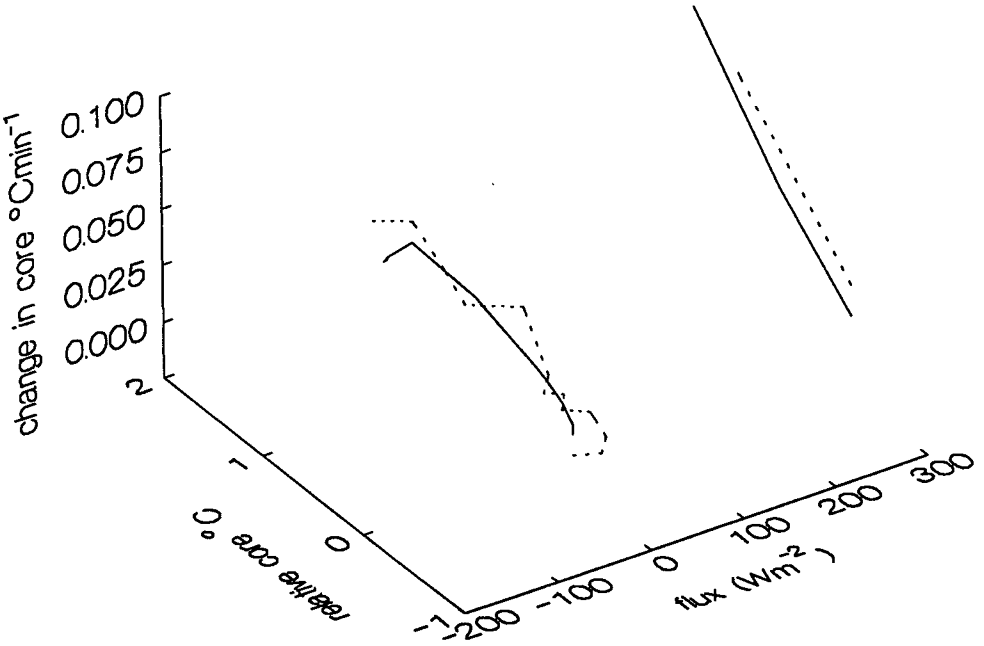

**Figure 4.10** Examples of observed (dotted lines) and predicted (solid lines) trajectories through "thermospace" during two different experimental runs.

Each triplet of experimental data (relative core temperature, $F_s$, and change in core) can be thought of as coordinates describing a point in a three-dimensional "thermospace". The consecutive measurements of an experiment trace a trajectory through this space, which should follow the topography of the thermal response surface. A potential application of Eq. 4.5, therefore, is the prediction of such trajectories; it should be possible to predict how long it would take Attila to overheat in a known thermal environment (Fig. 4.10).

The high $r_{adj}^2$ of the model suggests that in a statistical sense it is more than sufficient for predictive purposes (Draper and Smith 1979). However, such measures are misleading when dealing with time-series predictions because the predictions are not independent. Each estimate of relative core temperature (starting values excepted) is based on a series of previous estimates, each with its own associated error; each estimate therefore adds the error of previous estimates to its own. For this reason, even small consistent errors can produce predictions which diverge greatly from observed reality.

In this case, the main purpose of trajectory prediction is to estimate the time it takes for overheating to occur. In an attempt to estimate this value using iterative computation, I used Eq. 4.5 to simulate trajectories for each of the dry experimental runs to which Attila was subjected. At the start of each trajectory, the model was seeded with observed starting values of flux $F_s$ and relative core temperature $C_{rel}$ (following any initial decline). Thereafter, dC was interatively calculated using the previous estimate of $C_{rel}$ and current observed value of $F_s$. dC was multiplied by the time interval between readings to give the predicted change in core temperature; this change was then used to update $C_{rel}$. When $C_{rel}$ exceeded 1°C, overheating was assumed to have begun.

During the runs in which "solar"=0Wm$^{-2}$, this technique correctly predicted that overheating would not occur. Of the remaining experiments in which "solar">0Wm$^{-2}$,

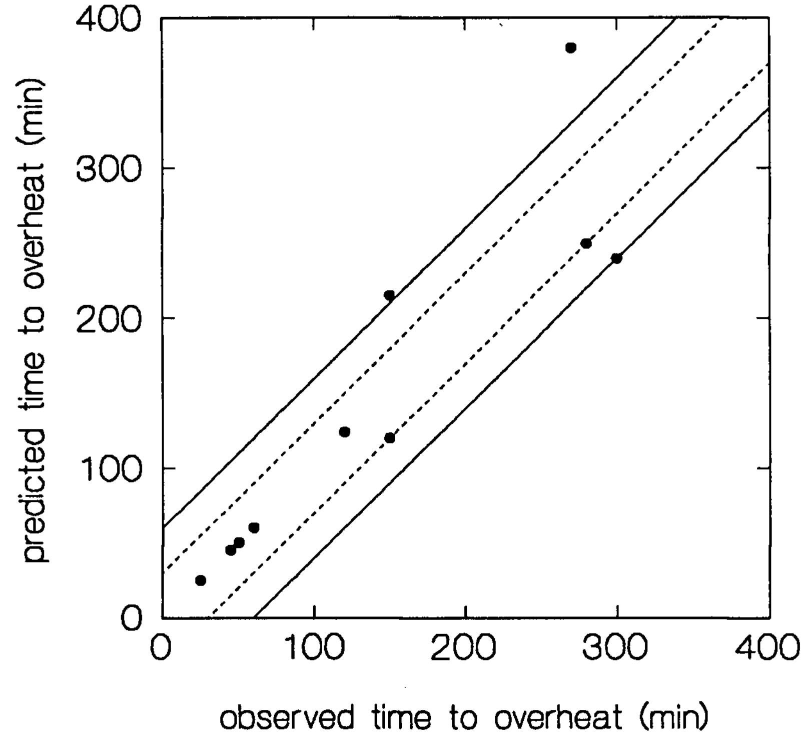

**Figure 4.11** Predicted vs. observed times for Attila to overheat by 1°C during dry, nozero "solar" treatments. Dotted line denotes y=x±30min; solid lines denote y=x±60min.

time to the onset of overheating was predicted within 30min, 8 out of 11 times[12] (Fig. 4.11). Of the remaining predictions, one was accurate within 60min and another within 70min; only one simulation produced a completely unrealistic estimate.

The outlier is not an artifact of the time step used in the iteration[13]; rather, I believe it represents a local weakness in the model. It arises from an experiment in which

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[12] In fact, the accuracy of these predictions may have been greater than 30min; however, since measurements were usually taken at half-hour intervals, more precise estimates could not be made.

[13] Reducing the time step by as much as a factor of 5 did not improve this prediction relative to any of the others.

"solar" radiation was only 230Wm$^{-2}$; as a result $F_s$ was quite low, varying from -62 to -16Wm$^{-2}$ (Appendix 5). This is well within the 95% confidence interval for the estimate of $F_b$, the point (-71Wm$^{-2}$) at which net heat flow between the seal and its environment is 0 (Table 4.3). According to Eq. 4.5, overheating under these conditions should occur very slowly.

One other experiment occured under comparable flux conditions (Appendix 5); the simulation of this trajectory predicted the onset of overheating within 60min. The difference between these two treatments is that in the case of the outlier, there was an initial drop in core temperature of 0.5°C; the decline in the other case was only 0.2°C.

When $F_s$ is much lower than $F_b$, overheating does not occur and the model predicts this. When it is higher, thermal input from the environment rapidly counters the initial decline in core temperature, and again the model performs well. However, when $F_s \approx F_b$, the seal is nearly at thermal equilibrium; overheating very occurs slowly, if at all. Eq. 4.5 predicts that, starting with a relative core temperature of -0.5°C under these conditions, it would take a very long time (440min) for overheating to begin (Fig. 4.11). An additional possibility is that the relationship described by Eq. 4.4 is not linear. If heat build-up near $F_s \approx F_b$ actually follows a saturation curve, for example, the predicted rate of overheating at such flux levels would be too low.

$F_b$ is essentially a critical threshold; whether an animal overheats depends upon with which side of this threshold the thermal environment is on. $F_b$ likely lies within the range of -120Wm$^{-2}$ to -23Wm$^{-2}$ (Table 4.3). However, since its actual value is uncertain, Eq. 4.5 may be unreliable when dealing with predictions within this range.

## 4.5 CONCLUSIONS

These experiments arose from the need to explain a statistical relationship between the natural thermal environment and hauling out in harbour seals (Chapter 3). They support a functional basis for strictly correlative results. The question now arises of how readily these experimental findings can be applied back to a wild situation. Eq. 4.5 could be a useful tool for predicting, in functional terms, the hauling behaviour of harbour seals in their natural environment. This is an obvious avenue for further research.

# 5. A SIMULATION MODEL OF HAULING BEHAVIOUR IN A HARBOUR SEAL.

## 5.1 ABSTRACT

Hauling behaviour in harbour seals can be described as a trade-off between the need to forage and the need to avoid predators. It is constrained by the danger of overheating under warm conditions. The effects of hunger and overheating can be expressed quantitatively and incorporated into a simulation model; here I describe such a model which predicts hauling behaviour of a harbour seal in the Pacific Northwest under a variety of thermal conditions.

The model predicts that overheating can be a constraint under calm, sunny conditions as early as February and as late as November; however, the convective cooling caused by even light winds ($>.5ms^{-2}$) is enough to counteract this effect. Even on the hottest days of the year, the model predicts that overheating should not occur as long as midday winds do not fall below $2ms^{-1}$. Cloud cover also mitigates hyperthermia, although less effectively than wind speed.

Several model assumptions affect its behaviour. It describes the onset of hyperthermia using an empirical relationship which does not account for possible heat

loss to a wet substrate; it therefore describes a more restrictive relationship than is likely the case. It also assumes that a seal suddenly becomes hungry after some fixed time (nominally six hours). The model is sensitive to changes in this parameter; varying it by two hours can dramatically change the predicted duration of hauling events that begin near midnight, although behaviour at other times is not affected.

In light of these limitations, the model performed surprisingly well when used to predict the hauling duration of wild, radio-tagged harbour seals under closely monitored environmental conditions. The tagged seals hauled out primarily in daylight during the winter and at night during summer; this implies that their preferred foraging time also changes seasonally. Under winter conditions, when the model described haul duration solely as a function of hunger and foraging conditions (nocturnal foraging assumed), the correlation between predicted and observed haul duration was very significant ($r_{adj.}^2=0.545$, $P<0.001$), although the model tended to overestimate haul duration (slope of observed vs. predicted values=0.662). There was no such predictive bias under summer conditions, when predicted constraints due to overheating were significant (slope of observed vs. predicted values=1.084), and the correlation was even stronger ($r_{adj}^2=0.602$). However, it was necessary for the model to assume daylight foraging during the summer to obtain this result, since otherwise it drastically underestimated haul duration during late afternoon/early evening. This suggests that the thermal factors which constrain hauling are better described by the model than are the underlying factors (foraging, predation risk) which drive the behaviour.

## 5.2 INTRODUCTION

It has been argued elsewhere in this thesis that hauling behaviour among harbour seals can be described as an interaction between the opposing needs of safety and sustenance. Although it is impossible to prove such a contention using purely observational methods, the behaviour of harbour seals at Snake Island is consistent with this view (Chapter 2). It has also been shown, both through observation of wild populations (Chapter 3) and direct experimentation (Chapter 4), that harbour seals are vulnerable to hyperthermia when hauled out under warm summer conditions. However, neither overheating nor foraging responses occur in isolation, and there has been no investigation of how hauling behaviour is affected by the interaction of these two factors.

This chapter describes the construction and behaviour of a simulation model in which hauling out is described as a simple function of hunger and foraging conditions (i.e., ambient light), modified by thermal constraints which can occur under a wide variety of user-specified environmental conditions. The predictions of the model are compared to the hauling behaviour of three radio-tagged harbour seals from which data could be obtained under monitored environmental conditions, under both summer and winter conditions. The aim of this comparison was to determine whether foraging and the effects of hyperthermia are sufficient to explain observed hauling behaviour under some common environmental conditions.

## 5.3 METHODS

### 5.3.1 Field Data Collection

During early February of 1988, eleven harbour seals were radio-tagged as a part of ongoing studies undertaken by the Washington State Department of Wildlife, at Gertrude Island (Fig. 3.1c). Seals were captured with a modified gill net (set by boat). The mass, girth, length, age class, sex, and colour of pelage of each individual were recorded (Appendix 1). An area of about 10cm diameter on the top of each seal's head was cleaned with rubbing alcohol and blow-dried using compressed air from a SCUBA cylinder. FM transmitters which broadcast only when out of the water (Advanced Telemetry Systems, Isanti, Minnesota) were then glued onto this spot using liberal amounts of quick-setting marine epoxy. In addition to the FM transmitters, each seal was doubly flipper-tagged and had an additional tag of neoprene rubber glued onto the back, between the shoulders. These accessories made visual identification of hauled out animals fairly simple for as long as the tags remained attached. (Flipper tags remain attached indefinitely; FM transmitters and neoprene patches remained attached at most until the annual moult in November, and generally for much shorter periods (Fig. 5.1).)

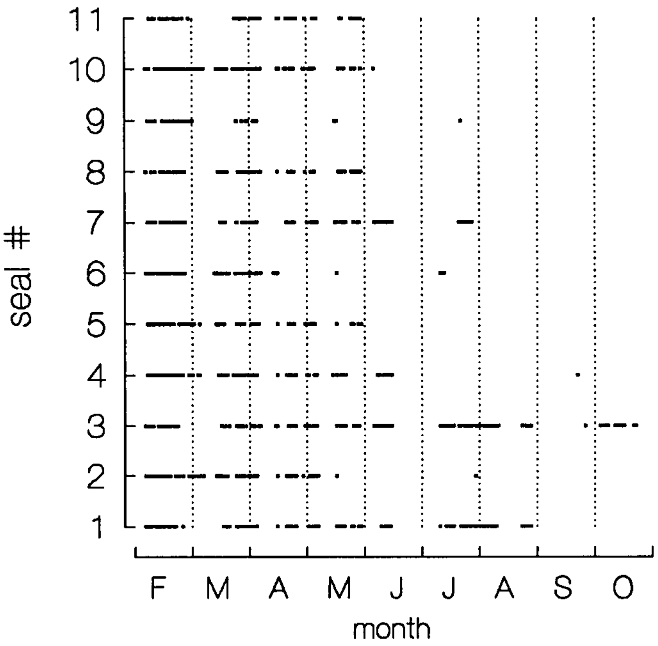

**Figure 5.1** Performance of harbour seal radio-tags over time.

Although only eleven seals were radio-tagged, 36 were captured for morphometric measurements and flipper tagging; tagging operations extended over three days. It was thus possible to establish that the tagging operation itself did not cause seals to abandon the haul-out site for any significant period; in fact, in several cases the same animal was captured on consecutive days.

The haul-out site was monitored from an elevated blind approximately 100m distant. The blind contained an automated scanning receiver, connected to two Yagi antennae set at right angles to each other. The receiver was programmed to scan each transmitter frequency in turn for four-minute intervals, around the clock; output was directed to a 12-pen strip-chart recorder (Esterline-Angus Ltd.). An additional transmitter was left in the blind to test for possible receiver malfunction.

The receiver system was powered by a 12-volt automotive battery with an effective life of about 2 weeks. The entire assembly was checked weekly to replenish the paper and ink supply in the chart recorder, change batteries when needed, and to correct periodic and annoying equipment failures. I also visited the blind for periods of about a week, at approximately monthly intervals, to monitor environmental conditions and to make visual counts of the number of seals hauled out throughout the day (see Chapter 3 for details).

### 5.3.2 Model Layout and Logic

5.3.2.1 Overview The simulation model, Max[14], is written in QuickBasic and is listed (with documentation) in its entirety in Appendix 3. The following subsections describe the overall layout and logic of the model with a minimum of programming detail.

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[14] Named for Max Headroom, a fictional prototype simulation of a human personality.

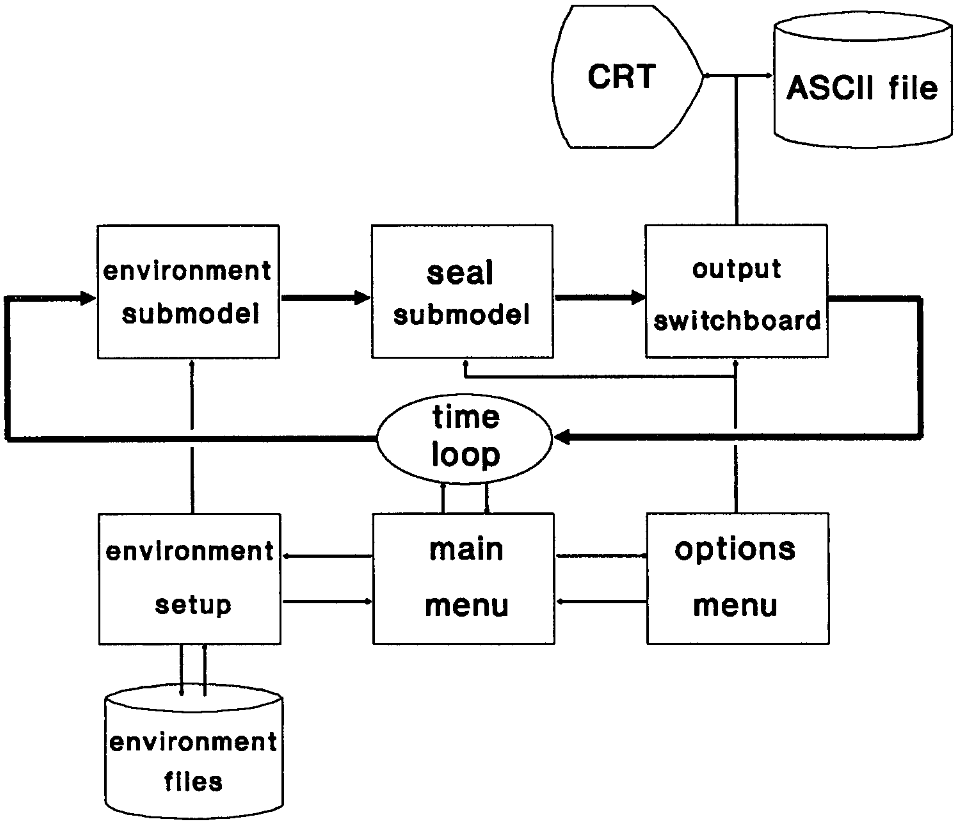

**Figure 5.2** General layout of the simulation model Max, which predicts haul duration of a hypothetical harbour seal under definable environmental conditions.

Max describes the change in core temperature of a hauled out harbour seal exposed to a defined set of environmental conditions over time. The model recursively cycles through a series of discrete time steps, each representing the passage of 0.1h (6 min). At each step it updates relevant aspects of the programmed environment and the core temperature of the seal, and uses that information to decide whether

a) the seal remains hauled out;

b) the seal overheats, and immerses to cool down, or;

c) the seal is hungry, and enters the water to forage (if foraging conditions are acceptable).

Max consists of several interconnected modules (Fig. 5.2). A main menu allows the user to choose between

1) defining or modifying a set of environmental conditions (these can be stored and recalled as ASCII files);
2) an options menu that permits modification of model parameters and output format (see Appendix 2 for details);
3) running the model with current options in place; and
4) exiting the model (which allows the user to edit the program code).

The time loop contains two major subsections[15] (Fig. 5.3):

a) An **environmental submodel** which updates the various aspects of the physical environment, and distils them into values of "flux" $F_s$ ($Wm^{-2}$) (Chapter 3).

b) A **seal submodel** which updates predicted core temperature and decides whether the seal immerses based upon foraging and thermoregulatory considerations.

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[15] The time loop also contains an output switchboard which routes output to the desired destination(s); see Appendix 2 for details.

5.2.3.2 Environmental Setup Max defines the environment in one of two modes. In **static mode**, an initial set of conditions remains constant throughout the run; this permits simulation of experimental, "steady state" conditions. In **fluctuation mode**, the environmental conditions change over time, following a diel cycle. Fluctuation mode is the default.

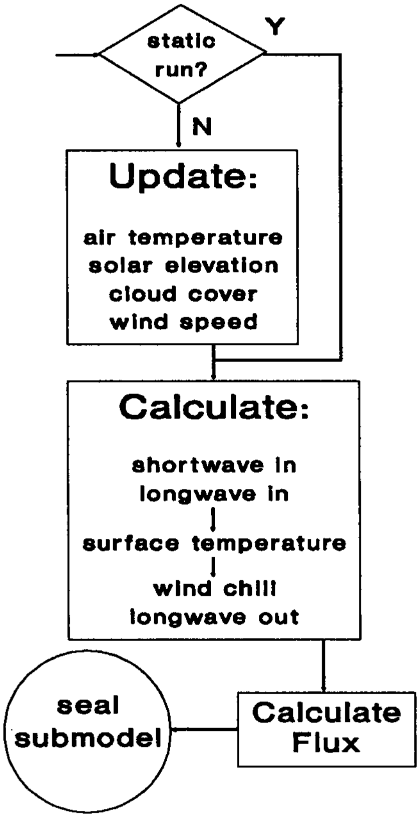

**Figure 5.3** Layout of the environmental submodel of the simulation model Max.

The model requires starting values for a number of environmental variables. The user provides these either by entering them manually or by retrieving a previously-created environmental file. Starting values must be provided for 1) the Julian Day; 2) the time of day at which the seal first hauls; 3) the maximum length of time the model will run (assuming that the model does not force the seal to immerse first); 4) minimum and maximum daily air temperatures; 5) proportion of cloud cover (the chance that the sun will be obscured by clouds at any given time-step); and 6) wind profiles throughout the duration of the run. The model makes no allowance for tidal constraints on hauling, nor for the effects of precipitation.

5.2.3.3 Environmental submodel Max expresses the thermal environment in terms of "flux" $F_s$, a relative index of a harbour seal's thermal environment. $F_s$ describes various components of heat exchange across a horizontal 10cm diameter disk of a live seal's surface, including absorption of shortwave and longwave radiation, longwave emission, and convective heat loss (see Chapter 3 for a detailed derivation). To estimate these components, Max must recalculate air temperature and incident solar radiation at each time step.

**Air temperature** ($T_a$) is defined as a cosine function

$$T_a = \frac{T_{max}\text{-}T_{min}}{2} + T_{min} - \frac{T_{max}\text{-}T_{min}}{2} \cos(0.262t_{lag}) \tag{5.1}$$

where $T_{max}$ is maximum daily air temperature (°C);

$T_{min}$ is minimum daily air temperature (°C);

$t_{lag}$ is time of day - 3h (or time of day + 21h if time<3).

Eq. 5.1 is basically a cosine wave of amplitude $T_{max}$-$T_{min}$, oscillating about a temperature mid-way between these extremes. The term $0.262t_{lag}$ gives the wave a period of 24h, and displaces it along the time axis so that its value is highest at 1500 and lowest at 0300.

Given air temperature and proportional cloud cover (entered as part of "Environmental Setup"), Max uses approximations of atmospheric emissivity (Eq. 3.3)[16] to estimate incident longwave radiation on the seal's surface.

**Incident solar radiation** depends upon a number of parameters including (sine of) solar elevation, time of day, time of year, solar declination, and cloud cover. Solar declination (angular distance from the celestial equator) can be defined as the cosine function

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[16] It is important to note that these approximations are valid only at air temperatures above 0°C (Campbell 1977); the model's descriptive power is thus limited to environments meeting this criterion.

$$D_{sol} = -0.4\cos(0.017205\text{day}) \tag{5.2}$$

where day is Julian day. The sine of the angle of solar elevation ($\phi$) can now be defined as

$$\sin(\phi) = \sin(\text{latitude})\sin(D_{sol}) + \cos(\text{latitude})\cos(D_{sol})\cos 15(t-t_0) \tag{5.3}$$

where t is time of day; and

$t_0$ is time of solar noon (assumed = 12 for modelling purposes).

(All trigonometric quantities are in radians.)

At elevation angles of less than 10°, atmospheric refraction attenuates incoming radiation (Campbell 1977); for simplicity, solar radiation under such conditions is assumed to be negligible. At elevation angles greater than 10°, direct incident shortwave radiation at sea level is described by

$$S_d = S_0 a_{atm}^{1/\sin(\phi)} \tag{5.4}$$

where $S_0$ is the extraterrestrial solar flux density normal to the solar beam, at the distance of Earth from Sol (1360Wm$^{-2}$); and

$a_{atm}$ is the atmospheric transmission coefficient (a decimal fraction, approximately 0.7 on clear days (Gates 1980)).

An additional solar input occurs in the form of sunlight which has been scattered by the atmosphere, and which therefore impinges upon the surface from all angles above the horizon. This can be approximated (List 1971) by

$$S_s = 0.5 \cdot S_0(1-a_{atm}^{1/\sin(\phi)})\sin(\phi) \tag{5.5}$$

Total incident solar radiation is the sum of Equations 5.4 and 5.5. (Sunlight reflected from surrounding topography, usually included in such calculations, is not relevant in this case since the described surface is horizontal.) Field measurements of sunlight made with a mechanical pyronometer show that total measured solar radiation is reduced by about 70% under overcast conditions (Watts, unpublished data). The model accounts for this by multiplying its estimate of solar radiation by 0.3 whenever clouds cover the sun (this occurs whenever a random number falls below the user-defined "Proportion of cloud cover").

In calculating total incident shortwave radiation, it is necessary to estimate $a_{atm}$; this leads to some unavoidable error in the estimate. Of perhaps greater importance is the unknown degree of bias associated with the pyronometer used to measure solar radiation in the field, during other aspects of this research. To permit comparison between model predictions and field observations, solar data collected during a series of eight cloudless days in July were compared to predicted solar radiation during the same times. The resulting linear relationship

$$S_{measured} = 0.704S_{predicted} \tag{5.6}$$

was very strong ($N$=57, $r_{adj}^2$=0.919, $P$<0.001), and was used to calibrate the model's estimate of total incident shortwave radiation.

Once solar radiation and air temperature have been ascertained, it is a simple matter for Max to predict the temperature of the seal surface using an empirical relationship between surface temperature, solar radiation, and air temperature (Eq. 3.2), derived under experimental conditions (Chapter 4).

The above estimates, together with the wind profiles entered into the model by the user, are sufficient for the calculation of $F_s$ as described in Chapter 3. Flux is then passed from the Environmental submodel to the Seal submodel.

5.2.3.4 Seal submodel This part of the time loop (Fig. 5.4) is concerned with two things: whether the hypothesised seal is in danger of hyperthermia, and whether conditions are suitable for foraging.

Change in core temperature is calculated as a function dC of present core temperature and "flux" (Eq. 4.6). This function describes the thermal responses of a young adult male harbour seal of 55kg mass and 0.964m$^2$ surface area, and was empirically derived during an experimental phase of this research (Chapter 4). These experiments suggest that overheating occurs when $F_s > -70$ Wm$^{-2}$, and further that harbour seals can reduce their normal core temperature by about 0.5°C when first exposed to conditions which lead to hyperthermia. Therefore, in addition to using Eq. 4.6 as a predictor of core state, the model assumes that the hypothesized seal will reduce its initial body temperature by 0.5°C when first exposed to $F_s > -70$ Wm$^{-2}$.

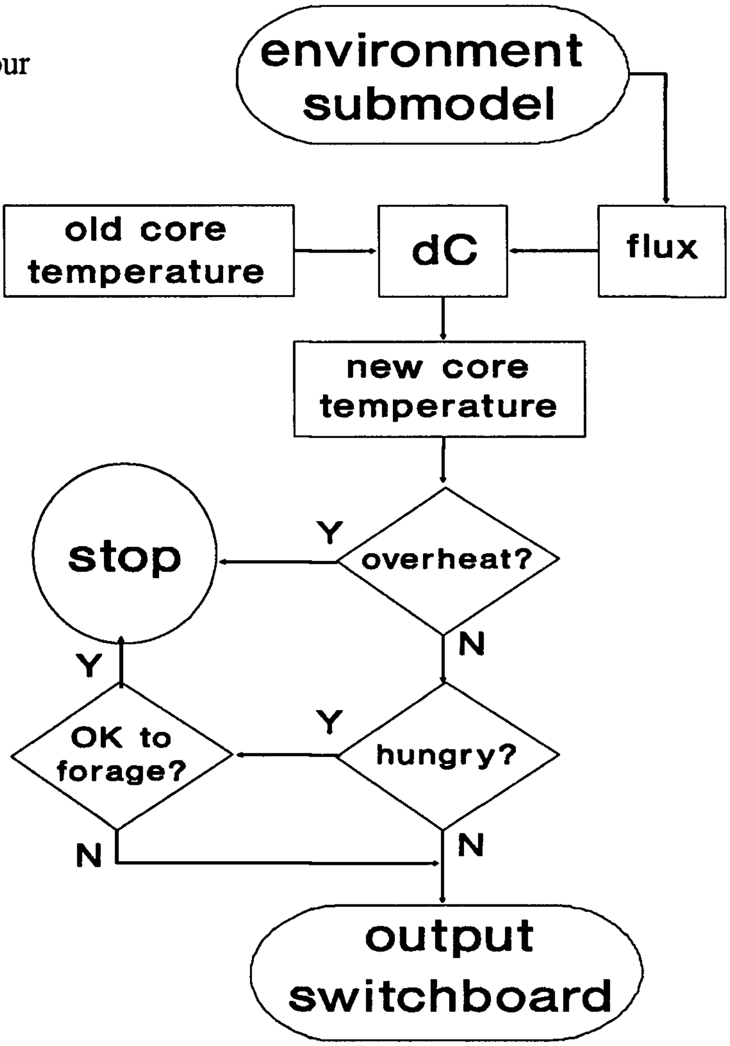

**Figure 5.4** Seal submodel layout for the simulation model Max.

The point at which a hauled out seal becomes hot enough to immerse is not known with any certainty. Harbour seals are reported to have core temperatures which fluctuate more widely than those of terrestrial mammals (Whittow 1987). Seals subjected to hyperthermic stress begin to show visible signs of discomfort (gaping, rolling) when core temperature rises more than 1°C above baseline (Watts, unpublished data); on the other hand, a fluctuation of 0.5°C or less appears to be within the normal range of variation for these animals. The model assumes that the seal immerses when core temperature rises more than a degree above normal, although other threshold values can be specified using the Options Menu. (Other values were used during basic sensitivity analysis of the model; see 5.3.4).

The time it takes for a hauled out harbour seal to grow hungry is known with even less certainty. Harbour seal pups have an initial defecation time (following feeding) of only 5 hours (Helm 1984), but there are reasons for suspecting that this may not be representative of the digestive rates of wild animals. Helm's study animals were fed three times per day, a greater frequency than is likely for wild harbour seals; frequent feeding accelerates digestion rate in pigs (Seerley *et al.* 1962). The elevated metabolic rate of pups relative to adults would also speed digestion.

In any event, hunger is not necessarily contingent on egestion of the previous meal. The seals described in Chapter 4 would eat (albeit half-heartedly) as soon as four hours after being fed to satiation; it was, however, closer to six or seven hours before they would eat with real enthusiasm.

It is always tempting, given the ready availability of telemetry data, to examine the hauling patterns of wild animals for some indication of the onset of hunger. The difficulty is that the model is attempting to predict the behaviour evident in the data set, and should hopefully be able to do so independently, without using the data to "predict themselves". In this case, I resolved the conflict by using data from some seals to refine a model which could be applied the behaviour of others.

Since $F_s$ is a variable which changes seasonally, Max might reasonably be expected to predict resulting seasonal changes in hauling behaviour. However, since the number of seals in the sampled population changed over time (as radio-tags fell off or stopped working), seasonal differences would be confounded with those resulting from the changing complexion of the sample itself. The only way to avoid this was to insure that the sample did not change seasonally. Only three radio-tags remained attached to their respective seals during the period from February to the end of July (Fig. 5.1); the data from these animals were used for model comparison, leaving data from the remaining eight seals available for refining Max.

These eight seals showed a pronounced tendency to haul out for 6-7 hours at a time (Fig. 5.5)[17]. Taking this into account with the other considerations already described, Max assumes that harbour seals become hungry after remaining hauled out for 6 hours. Once again, alternative values can be specified using the options menu; this was done to analyze how sensitive the model is to different estimates of "siesta period" (see 5.3.4).

In fact, the description of hunger as a sensation having only two states is arbitrary and unrealistic. Hunger would be better described using a cumulative probability

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[17] The greatest proportion of "hauling events" actually lasted one hour or less, as seals repeatedly entered and left the water while "settling in" for a more extended haul. These brief occurrences have been excluded from Fig. 5.4.

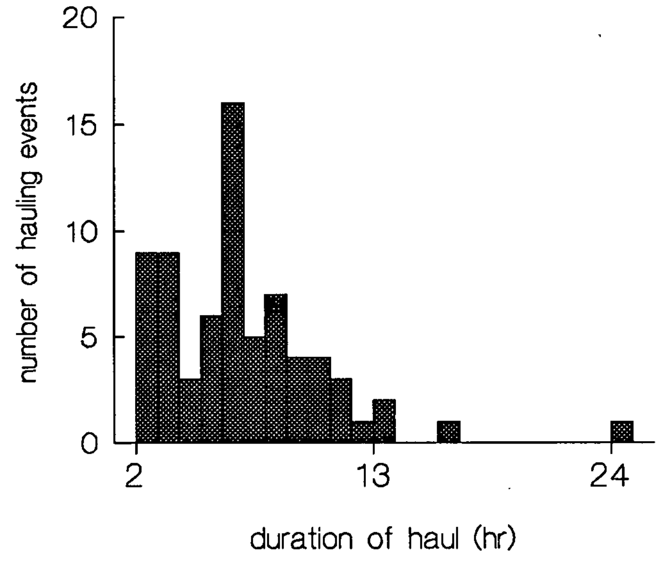

**Figure 5.5** Density plot of night-time haul durations, excluding data from seals used for model corroboration. Daylight hauls (possibly constrained by thermal effects) excluded.

distribution; the chance of leaving the haul-out site to forage at any time would be a function of continuously increasing hunger. However, there are no data upon which to base such a function.

A final assumption was that foraging occurs mainly at night (Chapter 2); a hauled out seal will not enter the water until near sundown, even if it becomes hungry during the day. (Specifically, the model allows hungry seals to forage if the angle of solar elevation is less than 5°; this is effective sundown at Gertrude Island, owing to the presence of topography which eclipses the sun before it reaches the horizon.) If a hauling event is defined as beginning during daylight, it is assumed that the animal was not feeding at sea, but was scared into the water by a disturbance on the haul-out site, or had been forced to immerse for thermoregulatory reasons. By default, then, the seal is assumed to have fasted since sunrise no matter how late in the day it hauls out. However, if the seal hauls after astronomical twilight and before morning it is assumed to have fed and to be satiated when it first hauls.

Once again, this assumption can be altered using the options menu; the alternative is that a seal hauls out sated even if the haul begins during the day. Although daytime foraging would be less efficient than foraging after nightfall (Chapter 2), it may be a reasonable option if thermal constraints prevent an animal from hauling out during the day anyway (see 5.4.3).

### 5.3.3 More Limitations

Max makes other assumptions which are not entirely realistic. When thermal concerns are irrelevant, a seal is assumed to remain hauled out until it becomes hungry; even then it does not immerse unless the sun is below 5° elevation. This results in a predicted linear decline in haul duration with time of day (Fig. 5.6): a seal hauling 5 hours before sundown will remain hauled out until sundown, as will a seal hauling 1 hour before sundown. (As mentioned, this assumes that seals hauling late in the day have not been feeding during daylight hours; see 5.2.3.4.) Hauls beginning just before (and during) twilight will therefore be extremely short as a rule; while hauls that start following twilight will last until the seal grows hungry again, or until the following dusk (if hunger does not set in until after sunrise).

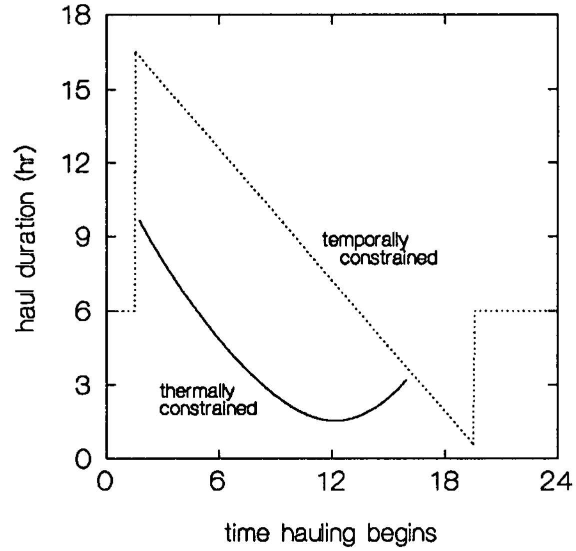

**Figure 5.6** General prediction of haul duration as a function of starting time, assuming that hyperthermal constraints are absent (dotted line) and present (solid line). This example depicts sunrise at 0600 and sunset at 1800.

Such predictions are simplistic; they take no account of changing space limitations due to tidal effects, disturbances on the haul-out site, or a variety of unexplored social interactions (da Silva and Terhune 1988, Davis and Renouf 1987, Godsell 1988, Sullivan 1980) which could limit haul duration. In fact, assuming that the fundamental logic of the model is sound, predicted haul durations are best thought of as a theoretical ceiling, maximum estimates which could be undercut by any of numerous constraints.

The one constraint that is modeled explicitly, and which constitutes the bulk of this thesis, is the effect of overheating in a warm thermal environment. As the effects of that factor are based upon empirical research, one can place somewhat greater confidence in this aspect of the model; however, there are important limitations even here. First, the function dC describes the responses of a single seal with specific morphometric characteristics; larger animals may be less vulnerable to overheating because of their lower surface to volume ratios, and similarly, smaller animals may be more so. Second, although the data upon which dC is based were collected under conditions ranging from summer to winter, data were not collected throughout an entire year. It is therefore possible that seasonal differences in response are not adequately represented (Chapter 4). Perhaps of greatest importance is the fact that the experimental data were collected from a harbour seal on a dry substrate; at Gertrude Island, seals were able to move onto the wet substrate near the water's edge, and could even rest in several inches of water, while still registering as "hauled out" by the automated telemetry equipment. A seal whose surface is kept wet can withstand any natural level of solar radiation without overheating (Chapter 4); this would tend to extend actual haul duration well past limits predicted in the model.

These considerations suggest that the thermal constraints described in the model should lead to minimum estimates of haul duration; seals in reality will not overheat faster than the model predicts, but they may overheat more slowly or not at all. In contrast, the part of the model which describes the underlying hauling cycle is likely to generate maximum estimates of haul duration; seals will not generally haul out for longer periods than predicted by the feeding cycle, but they may for shorter periods.

### 5.3.4 Sensitivity Analysis

The parameters of the model are estimates. For the most part this does not compromise its performance; the calculations involving solar radiation, for example, are based upon straightforward physical and trigonometric relationships, and have been corrected empirically where appropriate (Eq. 5.6). Likewise, the function describing dC (Eq. 4.6) was empirically derived from data which supported a very strong regression.

There are, however, two quantities whose values are more uncertain: the core temperature increase needed to make a seal immerse, and the "siesta period" following feeding, during which the seal presumably feels no hunger. Complicating these uncertainties is the fact that the effects of these parameters might differ depending upon time of day. For example, lengthening the "siesta period" from 6 to 8 hours would have little effect on a haul beginning just after sunrise, since the seal is assumed to fast until dusk regardless of its hunger state. However, the same change would have a dramatic effect on a seal hauling seven hours before sunrise; instead of immersing to forage before dawn, it would not grow hungry until after sunrise and would therefore remain hauled out until the following evening. Furthermore, the fact that day length changes seasonally implies that different siesta lengths might exert different effects throughout the year, even taking time of day into account.

The same sort of argument can be made regarding threshold core temperature elevation. Changes in this value may be irrelevant at night or during cooler parts of the year, when overheating is unlikely to occur; but they could prove critical on a hot August afternoon.

Finally, one cannot rule out the possibility of interaction effects between core temperature elevation and siesta length; changing one could conceivably have an effect on the reaction to the other.

The Options Menu was designed to facilitate the investigation of sensitivity to these uncertain parameters. By varying estimates of siesta length and critical core elevation, changes in the behaviour of the model under any given set of environmental conditions can be assessed. When in "batch" mode, Max automatically performs a series of twelve runs, with start times spaced at two-hour intervals throughout the day. The sets of predictions made using different parameter values can then be compared.

Sensitivity analysis involved systematic "sampling" (computer simulation) of a 3-level complete factorial design. Two independent sets of predictions were made under conditions simulating cloudless days in July and March, to analyze seasonal changes in model sensitivity. Mean observed air temperatures and wind speeds were programmed into the simulation for each of the two months (Table 5.1).

**Table 5.1** Mean environmental parameters used for sensitivity analysis of Critical Core Elevation and Siesta Length.

| Month | Cloud Cover | Wind Speed ($ms^{-1}$) | Min. Air °C | Max.Air °C |
|---|---|---|---|---|
| March | 0%* | 1.5 | 5.0 | 9.6 |
| July | 0% | 0.5 | 12.0 | 26.3 |

*This value assumed for continuity of the sensitivity analysis; actual value was 43%.

The effects of changing each parameter were sampled by increasing and decreasing each value in turn, and comparing results from the "disturbed" runs with those of "nominal" runs (Table 5.2). Although the degree to which parameters are displaced in sensitivity analysis is typically around 10% (Swartzmann and Kaluzny 1987), this was thought to be too conservative given the uncertainty involved in the estimates. Accordingly, critical core elevation was varied by 0.5°C in either direction from the nominal value (1°C), a variation of 50%. Judging from observations made during earlier heat-stress experiments (Chapter 4), it is extremely unlikely that the actual critical value lies outside these limits. Siesta length was varied by 2 hours from the nominal value of 6, a change of 33% in both directions.

At each starting time, the model was run nine times to represent every possible combination of the above changes[18] (including a run in which all parameters were

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[18] A complete factorial design requires $m^n$ runs, where $m$ is the number of values for each parameter and $n$ is the number of parameters being tested.

**Table 5.2** Nominal and disturbed values of Critical Core Elevation (CCE) and siesta length used for model sensitivity analysis.

| | Reduced | Nominal | Increased |
|---|---|---|---|
| CCE (°C) | 0.5 | 1.0 | 1.5 |
| siesta (hr) | 4 | 6 | 8 |

nominal). Since these runs were replicated twelve times around the clock for each of two days (one in March, one in July), a total of 216 runs were analyzed.

The effect of changing a parameter by a given amount is defined as the mean difference in model prediction between runs in which the parameter was disturbed, and those in which it was not. Similarly, the interaction effect of two parameters changed simultaneously is the difference between the effect of the first parameter when the second parameter is disturbed, and its effect when the second parameter is nominal. (Algebraically it makes no difference which parameter is denoted "first" or "second".) I calculated these effects independently for each time of day for each of the two days described, following methods presented in Swartzmann and Kaluzny (1987; pp217-223).

### 5.3.5. Model Corroboration

Because Max predicts that even subtle environmental changes can have a profound effect on the thermal environment (see 5.4.2), comparison of its predictions with telemetry data was limited to those days I was present on Gertrude Island (and thus able to make environmental measurements). Another limitation was that Max describes cloud cover as a random probability that the sun will be overcast at any given moment; it does not deterministically utilize every recorded change in cloud cover as it actually occured. Rather than needlessly complicate the model, I limited the data for model corroboration to observations taken under either uniformly cloudy, or uniformly sunny skies. Days of heavy precipitation were likewise excluded; seals often appeared to be driven from the haul-out site by heavy downpours (this happened frequently during the winter). Finally, to preserve sample integrity across seasons, only data from the three seals which remained radio-tagged at least until July were used for corroboration (5.2.3.4).

The resulting sample set consisted of two blocks of data, one collected during March and the other during July, each spanning about a week. Twenty-four separate hauling events occurred during each period. To assess the performance of the model in comparison to observed hauling durations, Max was programmed to simulate each hauling event, starting at the same time of day and describing the same set of environmental conditions as was actually observed.

There are several ways that model predictions can be compared to data (Swartzmann and Kaluzny 1987; Wallach and Goffinet 1989). Most statistical approaches have been criticized as "too rigorous for the objective of determining model validity" (Parrish and Smith 1990). These authors argue that models are generally intended to predict patterns, rather than the absolute values of specific data; conventional measures of statistical fit would undervalue the utility of any model whose predictions consistently differed from the "validating" data, even though the model may closely mimic the trends inherent in that data.

Parrish and Smith (1990) propose an alternative method (based on the theory of confidence intervals) which is somewhat more forgiving of such differences. Unfortunately, they presume that each parameter predicted by a given model has an associated family of data points with which it can be compared. This is clearly not so in the present case; no two hauling events occurred under exactly the same conditions of wind, temperature, sunlight, and time. Therefore, each predicted haul duration can be compared with only one actual data point.

I was therefore forced to resort to statistical assessment methods despite their objectionable rigour. If a model predicts general trends in a data set, a significant linear relationship should exist between prediction and observation regardless of how well (or poorly) the model predicts the actual data. If the model is good enough to predict the actual data, this line should pass through the origin and have a slope of 1. I therefore used regression analysis, applied separately to each of the March and July data sets, to compare predicted and observed haul durations.

## 5.4 RESULTS AND DISCUSSION

### 5.4.1 Sensitivity Analysis

5.4.1.1 Critical Core Elevation Not surprisingly, changes to this parameter had no effect on model behaviour during the March runs; since overheating did not occur under average March conditions, critical core elevation is irrelevant. (However, the model predicts that under calm, cloudless conditions overheating can occur as early as February: see 5.4.2.)

Changing CCE did have obvious (albeit minor) effects on model behaviour during July, however (Fig. 5.7). Reducing CCE generally led to a reduction in hauling time, since it takes less time for a seal to heat 0.5°C than it does to heat 1°C. This effect was most pronounced during morning or early afternoon hauls, when a hauled out seal would be exposed to increasing flux levels. After 1300, however, this effect disappears; the model predicts that, although core temperature does rise in the afternoon, flux is declining and is not sufficient to cause overheating. This lack of effect continues until the point (during the night) when the seal hauls so close to sunrise that it remains hauled out into the following day. At this point its reduced tolerance to hyperthermia exerts an effect once more.

Increasing CCE produces the opposite effect; it takes longer for a seal to overheat during the day, although once again this is irrelevant during late afternoon/early

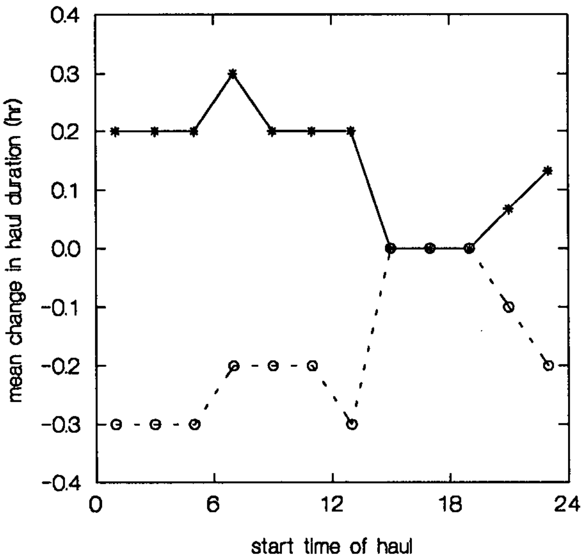

**Figure 5.7** Effect of changing critical core elevation (CCE) on mean predicted haul duration. Solid line, CCE + 0.5°C; dotted line, CCE - 0.5°C.

evening. Whether the threshold value increases or decreases, however, its effects on model behaviour are slight; predicted mean haul duration changes by no more than 0.3 hours. Thus Max is not sensitive to changes in this parameter.

<u>5.4.1.2 Siesta length.</u> As a general rule, changes in siesta length from 4-8 h do not affect model behaviour if hauling begins between midnight and noon (Fig. 5.8). However, they can significantly alter predicted haul duration if hauling occurs during the evening hours, both in March and July.

The trend is the same for both months; during the hours immediately following sunset, hauling is assumed to begin on a full stomach and to continue until hunger sets in. Under these conditions, haul duration is equal to siesta length, and a change in the latter results in an equal change in the former. However, if the hauled out seal becomes hungry near sunrise, even small changes in siesta length have a disproportionate effect on predicted haul duration.

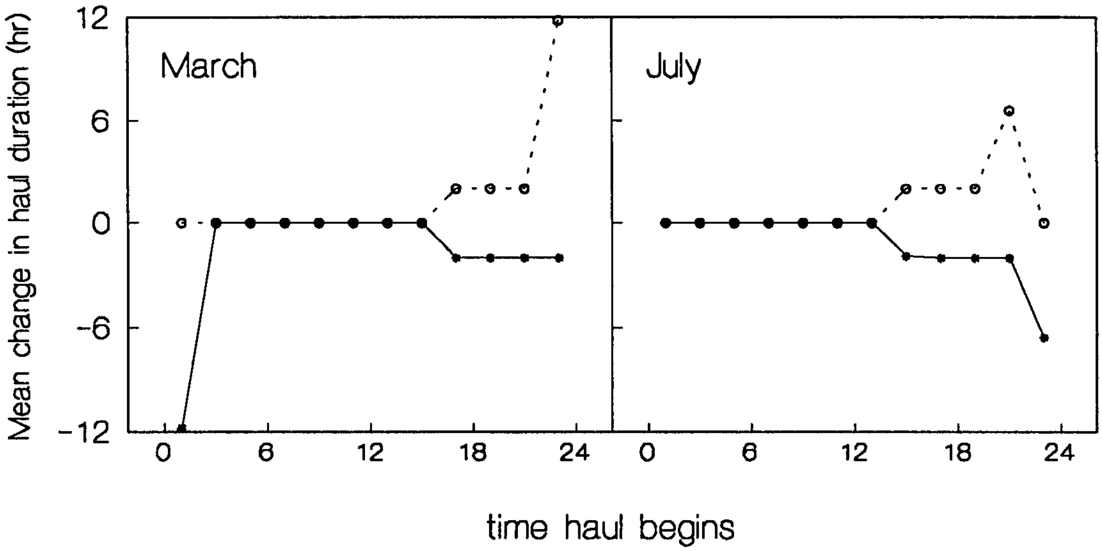

**Figure 5.8** Effect of changing siesta length on predicted mean haul duration during March and July. Siesta length is 6 hr (nominally), 4 hr (solid lines), and 8 hr (dotted lines).

If normal siesta length is such that the seal grows hungry just before sunrise, the model predicts that the seal would immerse to feed at that time. Under these conditions, an increased siesta length would delay the onset of hunger until after sunrise, forcing the hungry seal to remain hauled out until dusk (or until thermal conditions force it to immerse); this adds hours to the length of the haul. Conversely, if nominal siesta length causes a seal to grow hungry in the two hours following sunrise, then shortening it by two hours allows the seal to go foraging before sunrise, which reduces haul duration. These dramatic effects occur when hauling begins near midnight, since a seal hauling at these times would grow hungry during the critical period near dawn (Fig. 5.8).

In summary, the model is much more sensitive to changes in siesta length than it is to changes in critical core elevation. Changing the value of this parameter does not affect model behaviour during most of the day, but during late afternoon and early evening a given change in siesta length will change the predicted haul-out duration by the same amount. There is also a critical range of start times centred at midnight, for which changes in siesta length can drastically alter the model's predictions. If 6 hours is a poor estimate of the time it takes a harbour seal to feel hungry, then Max's predictions during this window should not be trusted.

5.4.1.3 Interaction Effects. Since critical core elevation was irrelevant during the March runs, there were no significant interactions between parameter effects. Although

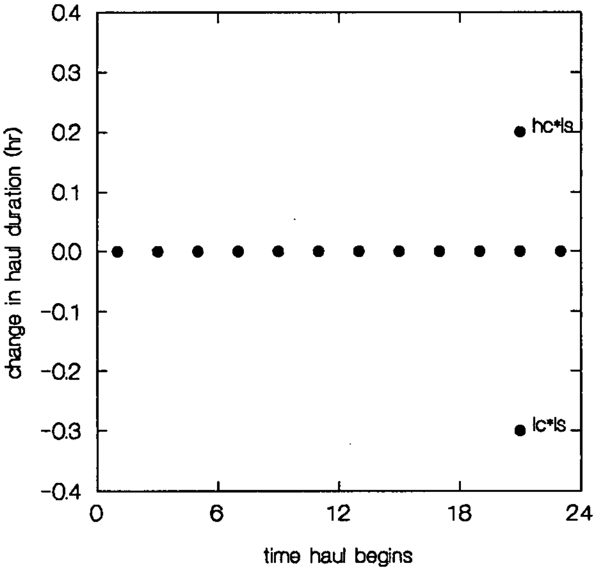

**Figure 5.9** Interactive effects of critical core elevation (CCE) and siesta length on predicted haul duration in July. "hc*ls"--high CCE (1.5°C), long siesta (8 hr): "lc*ls"--low CCE (0.5°C), long siesta.

interactive effects were present in July, their effects were relatively minor (Fig. 5.9). Both occurred within the "critical window", near midnight. Whenever a long siesta period prolongs the haul past sunrise, an increased CCE further increases haul duration (due to the hypothetical seal's increased tolerance to hyperthermia), while a depressed CCE has the opposite effect. These interactions have only a slight effect upon the predictions of the model, however ($\leq$0.3h).

### 5.4.2 Model Behaviour

Although there is undeniable evidence that conditions on the hauling site can force a harbour seal above its thermoneutral zone, I could find no field evidence of a lower thermoneutral limit under local environmental conditions (Chapter 3). This is consistent with other research (Ashwell-Ericksen and Elsner 1980), suggesting that harbour seals can remain thermoneutral under much colder conditions than those encountered in the Pacific Northwest. Locally at least, the thermal environment is irrelevant below a certain heat flux threshold. Below this, the model predicts hauling duration purely as a function of hunger and solar elevation; above it, there is increasing potential for modification of that prediction due to thermal constraints (Fig. 5.6). It would be interesting to discover exactly where, in environmental terms, this cut-off point exists.

According to Max, hyperthermia as a constraint on hauling need not be limited to the summer months. The model predicts that overheating can occur as early in the year as February, and as late as November (Fig. 5.10); however, this is unlikely to occur in the real world, as it is only predicted under cloudless and nearly windless conditions ($0.1 ms^{-1}$). Winds as light as $0.5 ms^{-1}$ are sufficient to prevent overheating at these times of year (according to the model). In fact, under observed conditions typical for the month of March, overheating was never predicted (see 5.4.1).

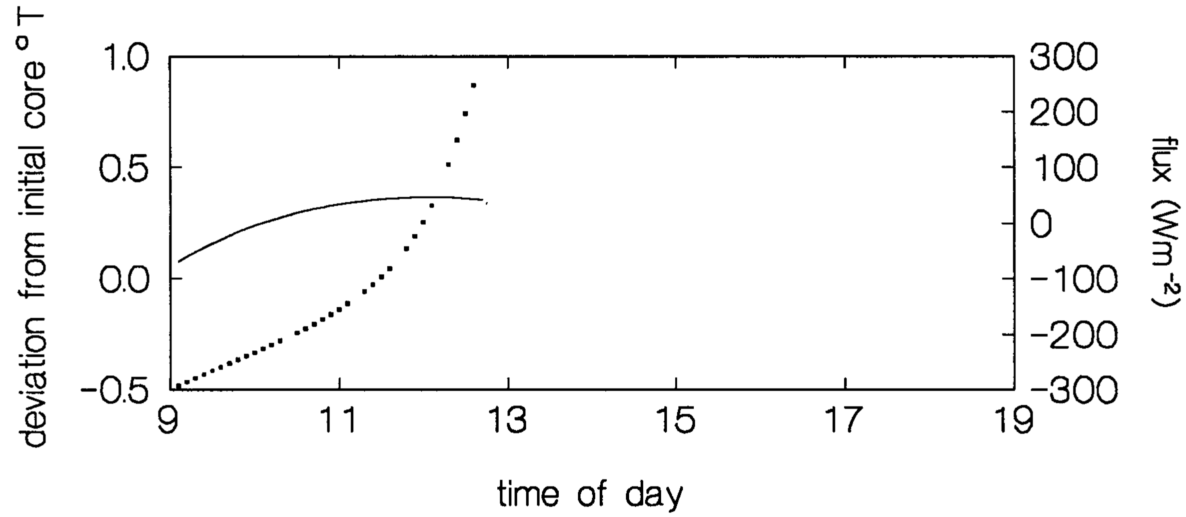

**Figure 5.10** Predicted hyperthermia in a seal hauling during February, under calm, cloudless conditions. Solid line: $F_s$, dotted line: deviation from initial core temperature.

Hyperthermia plays a progressively greater role in governing predicted haul-out behaviour during the spring and summer months. Under clear, calm conditions in August, a seal hauling at 0900 is predicted to overheat in less than two hours (Fig. 5.11a). However, even during the hottest part of the year hyperthermia can be delayed or even prevented by the mitigating effects of wind and cloud. Of these, wind is the most effective in dissipating heat. According to the model, cloud cover can only reduce the amount of shortwave radiation incident on the seal's surface; but even

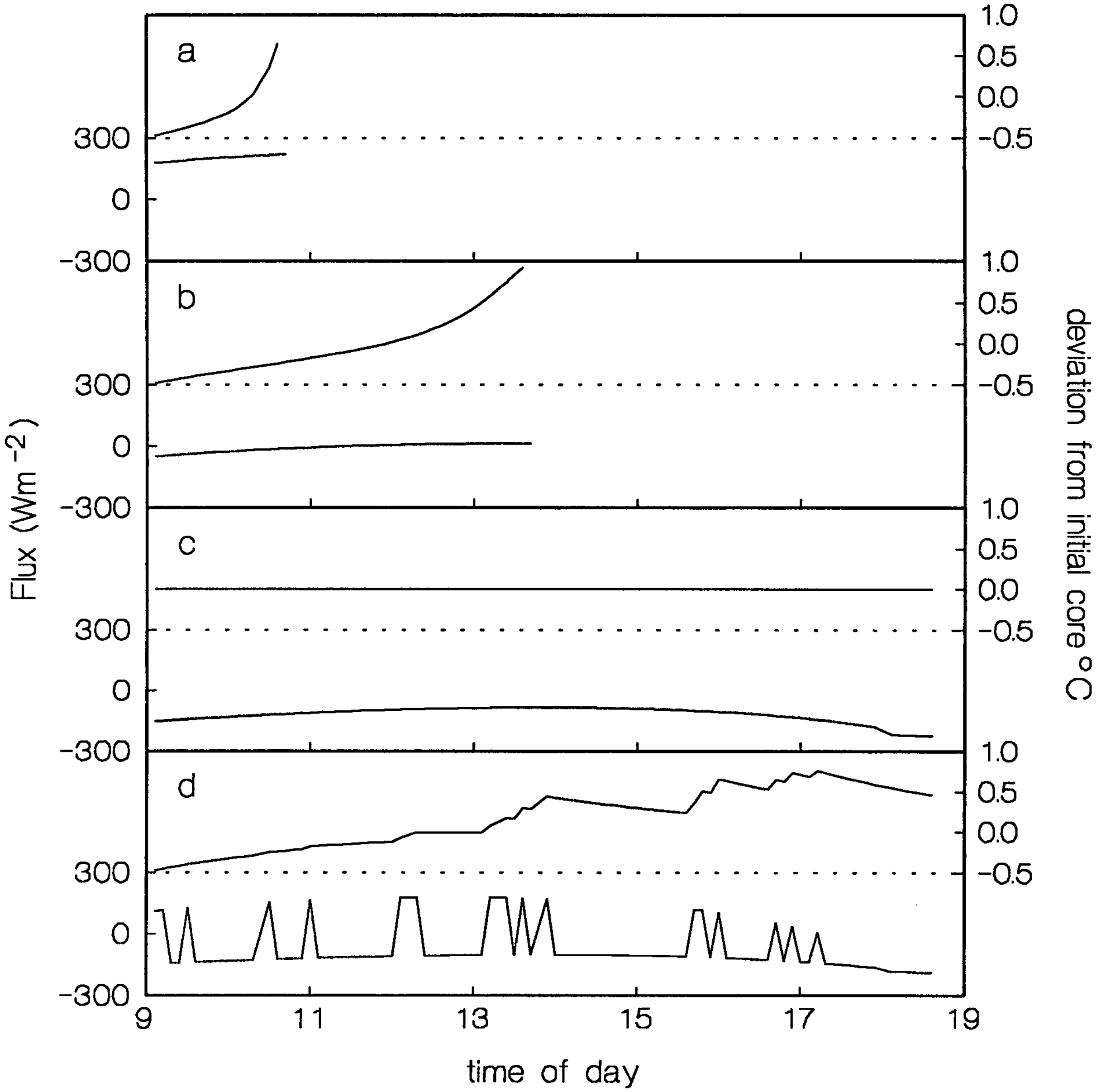

**Figure 5.11** Predicted thermal responses over time for a seal hauling at 0900 on an August day with a maximum air temperature of 27°C and a) clear, calm conditions; b) 1 m/s wind; c) 1.5 m/s wind; and d) no wind, 80% cloud cover.

moderate winds can entirely negate solar input (Fig. 5.12, 5.11b,c), and keep $F_s$ below the critical -70Wm$^{-2}$ threshold even at the height of solar noon. In the case of a seal hauling at 0900 on an August morning, a wind of only 1ms$^{-1}$ can effectively triple the haul duration predicted under calm conditions (Fig. 5.11b), and a wind of 1.5m$^{-1}$ can keep a harbour seal cool enough to remain hauled out for the entire day (Fig. 5.11c). In contrast, cloud cover must be near 80% or greater to prevent overheating under similar (but windless) conditions (Fig. 5.11d).

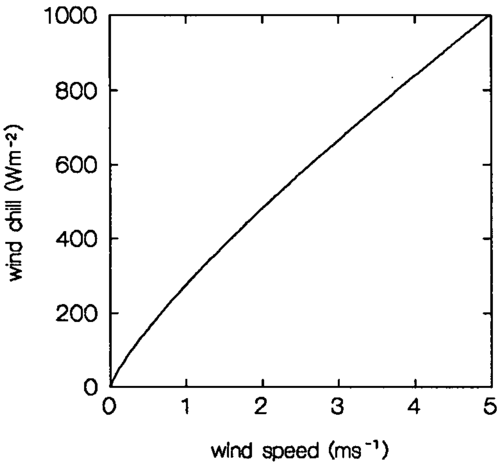

**Figure 5.12** Wind speed vs. convective loss to $F_s$ at an air temperature of 25°C and 640Wm$^{-2}$ incident solar radiation. These conditions approximate the mid-day thermal environment of a typical summer day on Gertrude Island.

### 5.4.3 The Real World: Predicted vs. Observed Hauling Duration

Given the various limitations of the model (5.3.3), its behaviour is surprisingly close to that evident in the field data.

In March 1988 there was a pronounced decline in observed haul duration throughout the day, as predicted (Fig. 5.13). Seals hauling just after sunrise tended to remain hauled out for the longest time, while seals hauling in late afternoon never remained hauled out for more than an hour[19]. Linear regression of observed against predicted duration was highly significant (Table 5.3). The y-intercept was not significantly different from 0 ($P$=0.945); redefining the regression line to pass through the origin produces a line with an $r_{adj}^2$ of 0.524 and a slope of 0.662. The departure of the slope from 1 occurs because the model tended to overestimate haul duration; this resulted in a significant difference between predicted and observed haul durations (paired $t$=-3.541, *d.f.*=23, $P$=0.002, each observation paired to a model prediction by common environmental conditions). Since these predictions are best thought of as upper limits (5.4.3), this is not surprising.

The significant difference between observation and prediction in Fig. 5.13 suggests that there is considerable room for improvement in the model; however, the relative strength of the regression also indicates that the conceptual basis of the model may be

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[19] This late-afternoon restriction was not due to tidal constraints on hauling space; March tides were low during the late afternoon.

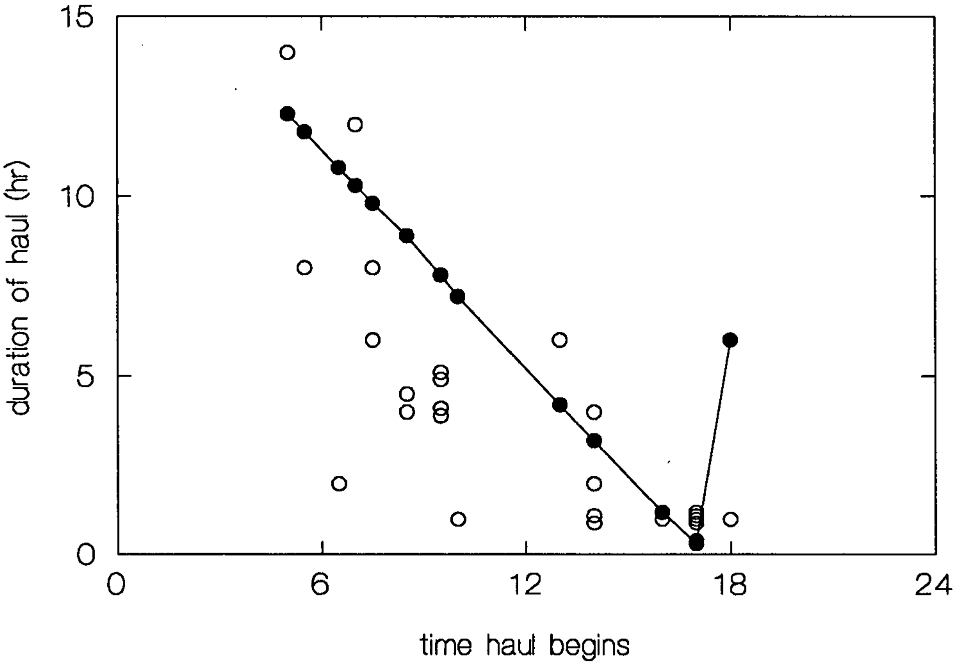

**Figure 5.13** Observed haul durations at different times under known environmental conditions during March (open circles), and corresponding predicted haul durations generated by Max (filled circles).

sound. It is interesting to note that no hauling events were recorded during darkness (Fig. 5.13); this suggests that harbour seals forage primarily at night, at least during the winter months (assuming that they haul out when not foraging--see Chapter 2).

Predicting haulout duration during the winter is relatively simple, since it is based entirely on time of day (relative to solar elevation); all hauls beginning at the same time are predicted to have the same duration. The situation becomes somewhat more complex in July, when thermal constraints exert effects. Then, hauling events beginning at the same time can have radically different predicted durations, depending on the

**Table 5.3** Regressions of observed hauling duration as a linear function of predicted hauling time.

| Month | Daylight Foraging? | n | Regression Coefficient | y Intercept | $r_{adj}^2$ | Std. Error of Estimate | P |
|---|---|---|---|---|---|---|---|
| March | n | 24 | 0.662 | - | 0.524 | 2.471 | <0.001 |
| July | n | 24 | 0.442 | 3.297 | 0.127 | 2.196 | 0.009 |
| July | y | 24 | 1.084 | - | 0.602 | 1.482 | <0.001 |

thermal environment (Fig. 5.14).

The assumption of exclusively nocturnal foraging is not as clearly supported by the July data set as it was by the March data set. The predictions of the model diverge dramatically from July observations from the hours immediately preceding sundown (1500-1900) (Fig. 5.14). The model predicts that seals hauling during the day will always forage at sundown, and seals hauling in late afternoon will therefore remain hauled out for a very short period. This prediction is based on the assumption that harbour seals do not forage during the day, and must therefore be hungry even if they haul out immediately before sundown.

Adhering to this assumption produces a regression which has an extremely low $r_{adj}^2$ (Table 5.3). However, this assumption directly affects the predicted duration of only four hauling events, all occurring in the late afternoon. Seals hauling earlier have more time to spare before sunset, and tend to be constrained by their thermal environment in any event; while seals hauling after dark are not compelled to reimmerse before their siesta period expires.

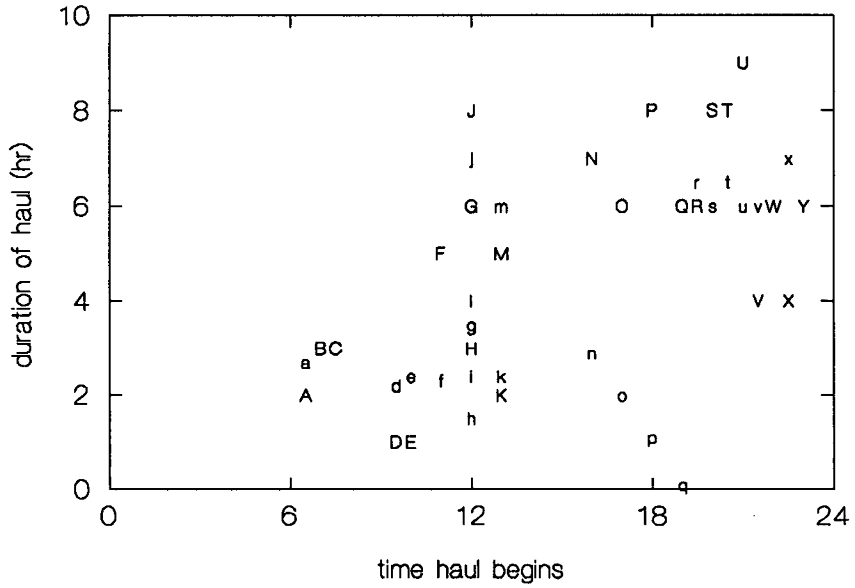

**Figure 5.14** Observed haul duration vs. time under known environmental conditions in July (upper case), and corresponding durations predicted by Max (lower case), assuming no daylight foraging. If no lower case, predicted=observed.

Relaxing the assumption of nocturnal feeding improves the fit of these four points enormously (Fig. 5.15), and consequently improves the overall performance of the entire model. If the model assumes that seals can feed around the clock, then a seal hauling during the day will remain hauled out for a normal siesta period, unless forced to immerse for thermoregulatory reasons. The statistics comparing these modified predictions to the July data are encouraging; a linear regression passing through the origin has a slope of 1.084 and an $r_{adj}^2$ of 0.602 (Table 5.3). (A regression with a nonzero intercept did not give different results, and the intercept itself was not significant, having *P*=0.628). A paired t-test between predicted and observed hauls detected no significant difference between the two (*t*=1.468, *d.f.*=23, *P*=0.156), although this is not a very powerful test given the size and variance of the sample (Peterman 1990).

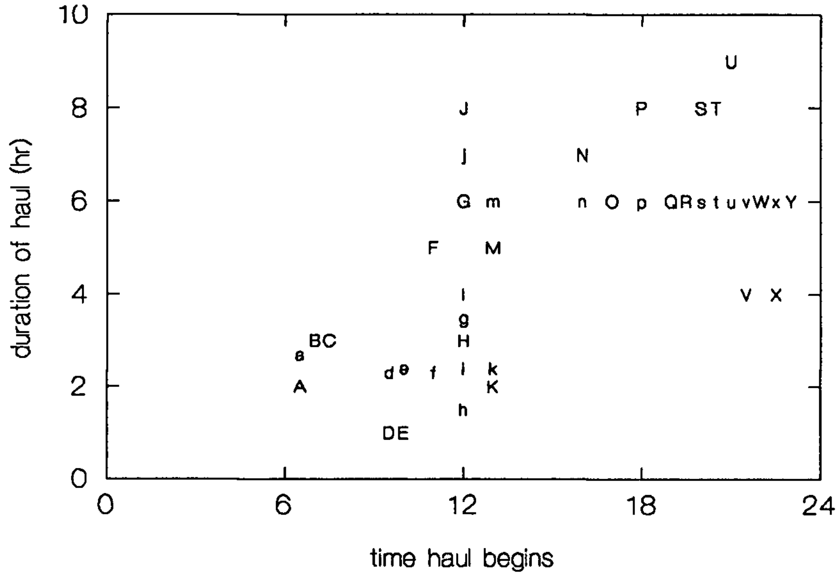

**Figure 5.15** Observed haul duration vs. time under known environmental conditions in July (upper case), and corresponding durations predicted by Max (lower case), assuming daylight foraging. If no lower case, predicted=observed.

Given the greater dependence of the July predictions upon thermal factors (which are better known than those governing the foraging behaviour), it is not surprising that Max should be generally better at predicting the July data set than the March one. However, since this success is contingent upon changing a basic assumption of the model, one might wonder whether there is empirical justification for such a change.

As already noted, all hauling events during the March data set occurred between 0500 and 1800; seals did not haul out during darkness (Fig. 5.13). In contrast, seals in July frequently hauled out between 1800 and midnight (Fig. 5.14). Since the photoperiod is longer in summer than winter, seals hauling out near midnight in July may encounter light levels not much darker than those encountered by seals hauling out near 1800 in March. However, seals who hauled out just before nightfall in March did so for no more than an hour; they invariably spent most of the night immersed. Late-hauling seals in July, on the other hand, typically spent six to eight hours hauled out.

In other words, seals who haul out late on a winter day are back in the water by nightfall. Seals who haul out late on a summer day remain beached all night long.

Why this should be the case is open to debate. There is good reason to expect seals to prefer nocturnal foraging, mainly because prey availability is maximal at night (Chapter 2). It is also reasonable to assume that they maximise the proportion of the day spent hauled out, which minimises predation risk[20] (Chapter 2). Seals might thus

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[20] It should be emphasised that this does not imply concious risk-avoidance on the part of the seals. On hot summer days, seals would grow increasingly restless until one of them would initiate a stampede into the water. Once immersed, they would frequently swim out to sea. If seals felt consiously at risk they would be more likely

forage during the day when hot summer weather restricts their hauling behaviour; they could then remain hauled out at night. This assumes that there is danger from predators around the clock, so it would be advantageous to haul out at any time of day (it is not known whether transient killer whales hunt at night). It also assumes that foraging by daylight, although relatively inefficient, is profitable; this appears likely given the high proportion of shallow water near Gertrude Island (Fig. 2.11) (see Härkönen 1988).

Another way to explain the seasonal difference in hauling patterns is to invoke seasonal changes in prey availability. Perhaps seals forage nocturnally even during the summer, but don't have to spend as much time at it because prey is more plentiful then. A seal may be less inclined to rush into the water at sunset if it knows it can feed to satiation even if it waits until later at night. This possibility can not be ruled out; prey availability certainly seems to influence submigratory movements of harbour seals (Brown and Mate 1980, Thompson 1989, Thompson *et al.* 1989), and there is no reason why it couldn't also affect hauling behaviour.

Since harbour seals feed on such a wide variety of items (2.4.3), it would be virtually impossible to ascertain the prey base available to them at any given time. However, judging from the limited data reported here, the "change in seasonal prey

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to remain immersed as briefly as possible under these conditions. However, even in the absence of such awareness, seals which spend most of their time hauled out (for whatever reason) would have a selective advantage over those which do not. The issue is not how seals perceive the world; but rather, how the world shapes their behaviour.

availability" hypothesis seems unlikely. In the July data set, five hauling events began during the period from 2000 to 2100 (Fig. 5.14), just at or after sunset. Of these seals, three stayed hauled out past sunrise the following morning (which occured at about 0400). Since these animals obviously did not feed during the night, they must have done so during daylight hours--unless they missed feeding for a night, which entails a fast of at least 40 h. This is unlikely given a presumed high abundance of prey and the rate at which captive harbour seals become hungry after feeding (5.2.3.4).

For whatever reason, hauling activity in the July data set is maximal during the night. The most likely explanation is that foraging was taking place during the day, which in turn supports the assumption necessary for Max's optimum performance.

The model described in this paper deals with only a limited subset of the factors that affect hauling behaviour in the real world, and deals with them in relatively simplistic terms. It nonetheless appears to be basically sound, judging by statistical assessments which are considered stringent (at least by modeller's standards--Parrish and Smith 1990). However, it bears repeating that success in fitting a model to observational data can never be said to "prove" the model; any data set can be described by an infinite number of alternative models (Walters 1986).

In Max's case, there are two particularly weak links in need of closer study: the advent of hunger over time, and the processes that govern preferred foraging times. Both of these shortfalls are part of the the hauling/foraging cycle. In fact, it appears that the processes which constrain hauling are somewhat better understood than those which drive it. This is not a desirable state of affairs, but it may be difficult (or at least expensive) to rectify such a basic gap; future researchers have their work cut out for them.

# 6. THE LIMITATIONS OF VOYEURISM

The greatest limitation of the research reported in this thesis is that nobody really knows why hauling occurs in the first place. The simulation model Max is largely founded upon assumptions which, though biologically sensible, are speculative and unproven. This may seem odd, since harbour seals are a frequently-studied marine mammal and the vast majority of such studies have dealt with hauled out animals.

The reason for the popularity of this species as a research subject appears obvious; harbour seals are among the most accessible of the marine mammals. They are abundant throughout a wide geographic range on three continents; although there are other pinniped species which are easier to study at close range, there are none so widely abundant. Harbour seals can generally be observed from shore, and show enough site fidelity to make reliable subjects for observation. The study of aquatic mammals is usually an expensive proposition, yet one can begin an observational study of harbour seals with no more than a pair of binoculars and a note pad. This is perhaps the greatest advantage of harbour seals as a study animal. Unfortunately, it may also be why so much harbour seal research is redundant (see 1.1).

In fact, naturalistic studies of hauled out animals may never provide the answer to the question of why seals haul out. Seals would not haul out unless the terrestrial environment were somehow preferable to the aquatic one. This can not be quantified without assessing the aquatic environment, something no mere haul-out study is equipped to do.

The times at which one chooses to go to bed each night and rise in the morning, as well as any activities occuring between these two actions, are largely determined by events occuring outside the bedroom. No one could reasonably hope to understand the causes of such behaviour by simply peering into a variety of bedrooms night after night; yet this is the essence of many haul-out studies. Most of the activities which decide a seal's success--foraging, mating, and escaping from predators--occur while immersed. Virtually nothing is known about these things. A fundamental assumption of this thesis--that hauling out is driven by the interacting demands of foraging and predator avoidance--can not be tested for lack of data. Yet published studies repeatedly produce the same descriptive results concerning the same aspects of hauling behaviour. Such research may be (relatively) inexpensive, but it is doubtful that it will greatly enhance our general insights into hauling. More might be learned by getting out of harbour seals' bedrooms, and getting into their workplaces.

Fortunately, recent technological advances make it easier to accomplish this. Satellite telemetry can potentially document daily movements at any point throughout a seal's range. (One of the greatest drawbacks of the ground-based telemetry systems now in widespread use is that they only record hauling behaviour on those sites within 10-20km of a receiver.) Harwood *et al.* (1989) optimistically appraise the potential of this technique, while Stewart *et al.* (1989), reporting upon actual field experience with satellite tags, offer a somewhat more subdued evaluation.

Time-depth recorders (TDRs), small sensor-equipped microcomputers which can be attached to pinnipeds, now make continuous records of diving and hauling behaviour for months at a time, and can also be equipped to measure such things as swim speed, location, and even gastric activity (Roger Hill, pers. comm. 1989)[21]. These devices have already collected data relevant to assumptions made in this thesis; at least one harbour seal is now known to have dived continuously for seven hours, to an average depth of 75m (Ellis[22], pers. comm.). Although dives were much shallower during the night, they did not stop at sunrise. This supports the assumption that foraging occurs during the day (at least in the summer), but it throws into doubt the argument that seals may be at a visual disadvantage until nightfall (see Chapter 2).

Using this technology, it is possible to obtain comprehensive data on the foraging activities of harbour seals. This will be of enormous benefit, but it leaves unaddressed one major assumption in this thesis; that hauling is essentially a strategy to avoid predators. To explore this, future research must include not only the harbour seal but its natural enemies.

In the waters around Vancouver Island, the most conspicuous harbour seal predator is the transient killer whale (see Chapter 2). The abundance of these animals changes seasonally, with greatest numbers occurring from late summer through early autumn

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[21] Roger Hill, Wildlife Computers, Woodinville, WA.

[22] Graeme Ellis, Dept. of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C.

(Baird *et al.* 1989); one might therefore expect seasonal changes in hauling behaviour correlated with the local abundance of killer whales. On a finer scale of resolution, the recent memory of killer whales near a particular haul-out site could result in acute changes in hauling behaviour, and might also be reflected in a change in the distance a harbour seal is willing to venture while foraging. Investigation of any such effects would add a great deal to our understanding of the relationship between hauling and predator avoidance. Such studies are currently underway (L. Dill[23], pers. comm.).

However, even these studies would only shed light on the role of a specific and conspicuous predator. Transient killer whales are not abundant throughout the entire range of the harbour seal; along the eastern coast of Canada, for example, they are occasional visitors at best. Atlantic maritime seals are thought to suffer heavy predation by sharks (Boulva and McLaren 1979) (as are Pacific seals, for that matter--Scheffer and Slipp 1944), and it would be extremely difficult to quantify such an impact.

The premise that harbour seals haul out as a means of predator avoidance raises interesting questions on a broader scale. What about species such as the northern fur seal or the harp seal, whose members are pelagic for most of the year and are therefore presumably at risk of predation almost all of the time? Although they do not haul out except to reproduce, it is entirely possible that they are at less risk than harbour seals because of their pelagic lifestyle. A predator should have much less chance of

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[23] Lawrence Dill, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C.

encountering prey spread across the North Pacific, than of encountering prey which concentrates inshore in predictable areas; but this has yet to be investigated. Another interesting issue involves the behaviour of landlocked phocids such as the Baikal seal (*Phoca sibirica*) and the Caspian seal (*Phoca caspica*). Do these animals, neither subject to tidal constraints nor at risk from aquatic predators, haul out following a diel cycle? There do not appear to be any quantitative studies in the literature which address this question. Such a study could go a long way towards supporting or refuting the conjectures I have made in these pages, regarding the relevance of predation to hauling behaviour.

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## APPENDIX 1. MORPHOMETRIC SUMMARIES OF RADIO-TAGGED HARBOUR SEALS FROM GERTRUDE ISLAND

### (Attila included for comparison)

| Seal # | Length (cm) | Mass (kg) | Girth (cm) | Surface Area ($m^2$)[24] | Area/Mass ($m^2$/kg) | Sex | Age Class[25] |
|---|---|---|---|---|---|---|---|
| 01* | 152. | 95. | 113. | 1.281 | 0.013 | M | A |
| 02 | 145. | 77. | 106. | 1.152 | 0.015 | M | A |
| 03* | 154. | 82. | 110. | 1.191 | 0.014 | M | A |
| 04 | 140. | 101. | 114. | 1.326 | 0.013 | M | A |
| 05 | 156. | 111. | 127. | 1.389 | 0.013 | M | A |
| 06 | 160. | 78. | 112. | 1.156 | 0.015 | M | A |
| 07* | 124. | 45. | 88. | 0.874 | 0.019 | F | S |
| 08 | 156. | 89. | 113. | 1.238 | 0.014 | M | A |
| 09 | 153. | 95. | 118. | 1.285 | 0.013 | M | A |
| 10 | 157. | 84. | 108. | 1.202 | 0.014 | M | A |
| 11 | 141. | 73. | 103. | 1.117 | 0.015 | M | A |
| Attila | 115. | 55. | 87. | 0.964 | 0.017 | M | A |

*Used for model corroboration.

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[24] Based on Eq. 5.11 in Worthy (1985).

[25] A=adult, S=subadult

# APPENDIX 2: USER GUIDE FOR THE SIMULATION MODEL MAX

## Introduction

Max is a simulation model written to approximate the hauling behaviour of a hauled out harbour seal under definable environmental conditions. It was originally written in compiled Basic, and runs on IBM-compatible microcomputers under DOS of vintage 2.0 or greater. The machine must have CGA graphics capability if graphical output is desired while the model is running; however, output can be directed to an ASCII file, from where it can be studied in digital form or imported into other graphics-capable programs. Max in its original form must be run using a BASIC compiler[26]; in stand-alone form (i.e, crunched into an .EXE file) it can be run by simply typing MAX(Return).

## Error-trapping

Max is an interactive model which requires extensive keyboard input. This is checked for certain errors before being accepted, which minimises the chance that the model will crash due to user error. In most cases the program beeps when it detects an input error, then allows the user to re-enter the botched data; however, in some cases the message "Redo from Start" is displayed instead.

---

[26] Interpreted BASIC can also be used, but the model will run very slowly.

The input errors Max checks for include:

> Entering character data when numeric data is called for, or vice versa;
>
> Entering inconsistent data, for example entering a "minimum air temperature" value which is greater than the "maximum air temperature" value;
>
> Entering illegal options, for example trying to answer a "yes/no" question with anything other than "y" or "n", or trying to choose option 7 from a menu that offers only 4 choices;
>
> Asking Max to access a file which does not exist. Max will only forgive this particular error once per run: the next time it will crash.

In some cases, Max uses the BASIC VAL function to extract useful information out of illegal input, and may simply assume that a particular value is 0. It does so without comment. Thus, a wind speed entered as "4er" will be read as 4, whereas one of "er3" will be accepted as "0".

The set of possible user errors borders on the infinite, and Max does not guard against them all. In the event of a crash, the model can simply be re-run.

## Running Max

There are four options available from the Main Menu:

1. Environmental Setup
2. Options Menu
3. Run Simulation, and
4. Exit.

**Environmental Setup** allows the user to define (or recall) the desired environment: it must be used before selecting Option 3. After selecting Option 1, Max asks

**Data from file (f) or current (c)?**

If you choose to retrieve data from an environmental file (these can be identified in DOS by their .ENV extensions), you are prompted for the file's name (don't include the ".env").

The screen now shows a list of environmental variables and their default values. If you are defining an environment for the first time, the defaults will all be zeroes or blanks; otherwise they will be the values recalled from the environmental file, or whatever values you entered the last time you were in the Environmental Setup option. You must now go through each variable on the list. To leave the default value unchanged, hit <RETURN> when the cursor reaches that value; otherwise, simply type in the new value.

Variables on this screen include

Flux or steady-state: the first choice lets the model run through a diurnal cycle in which environmental variables fluctuate "naturally"; the second forces Max to freeze all environmental variables at their initial levels for the duration of the run (this essentially duplicates idealised experimental conditions in which thermal conditions are held constant).

Julian Day: day of the year at which run begins.

Start time: time of day the simulated haul is to begin. This is to be entered as a decimal fraction, i.e., nine-thirty a.m. would be entered as 9.5, not 0930.

Length of run: the maximum number of hours that Max is to simulate, assuming that the model seal doesn't stop hauling itself first.

Minimum/maximum air temperature. Minimum air temperature must be greater than 0°C, to meet a model assumption about atmospheric emissivity.

Proportion of Cloud Cover: the decimal fraction of the sky that is overcast. This figure is also used to determine the chance that clouds will obscure the sun at any given moment.

Overcast: this only appears when the 'steady-state' option is in effect. Enter "y" if you want the sun to be overcast for the duration of the steady state run, and "n" otherwise.

Once the variable list has been completed, the heading

**Wind profile: enter elapsed time, then a space, then wind speed (m/s)**

appears on the screen, followed by two columns of numbers. Again, these will all be zeroes if you are editing a new environment for the first time. Enter 0, a space, then the initial desired wind speed. Hit <RETURN>. These values will be echoed near the left-hand side of the display. Then enter the elapsed time after which you want the wind speed to change, a space, and the new wind speed (for example, if you want the wind to change to 4 m/s after 7 hours elapsed time, enter "7 4<RETURN>").

Max will accept up to 60 changes in wind speed throughout the run. To exit this part of the environmental editor, enter an elapsed time greater than the maximum time the model is to run; for example, if you have told Max to simulate the passage of 24 hours, entering a wind speed change occuring at 25 hours elapsed time will get you out of the editor.

You will now be given the option of saving your defined environment to a file for later recovery. If you take this option, you will be prompted for a file name of up to 8 characters. Remember that Max automatically adds the .ENV extension.

You should now find yourself back in the Main Menu.

The **Options Menu** allows you to define various output parameters, as well as change the feeding behaviour and thermal responses of the seal. As with the Environmental Setup option, you are presented with a number of parameters and their default values; just hit <RETURN> when you come to any value you do not wish to change. Here, your options include

Output interval: the frequency with which output is sent to a file or the screen. Max uses a time-step of 0.1 hours, so output interval can be no smaller than this. Increasing it produces cruder plots, but the savings in graphics computation may save some time on slower machines. Generally this parameter is best left at the default.

Output to screen (y/n): if you want graphical output, say so here.

Output to file (y/n): if you want the output to be sent to an ASCII file for use in other programs, take this option. Output can be directed to screen and file simultaneously. If you answer "y" to this option, you will eventually be prompted for a choice of file name. Note also that *the default choice resets to "n" after each run; you can not send data from a number of runs to the same file.*

Batch run (y/n): if you accept this option, Max will perform a series of twelve runs using the defined environment, each starting at a different time of day (odd hours, from 1 to 23). Under these conditions Max ignores the Start Time value entered in "Environmental Setup". At the end of each run, summary data (julian day of haul, start time, duration, and replicate number: see below) are appended to an ASCII file called DURAHAUL.DAT. This option is used for sensitivity analysis applications. Rather than testing environmental effects on the behaviour of the seal, different sets of behavioural parameters are repeatedly tested under the same set of environmental conditions (see Chapter 5). Since the environmental data is not variable, it is not sent to the output file.

At this point, if you have selected file output you will be prompted for a file name. If you have selected the batch option you will be prompted for the number of "reps"; this is simply the number of replicates you wish performed at each starting time[27].

You are now presented with choices regarding the seal's behaviour:

Critical core elevation: how far above normal core temperature has to rise before the seal immerses for thermoregulatory reasons.

Feed the seals (y/n): Choosing "n" causes all foraging considerations to be bypassed, and hauling is modeled solely as a function of the thermal environment.

Daylight feeding (y/n): Choosing "y" allows the model to assume that seals hauling out during the day have recently fed; choosing "n" tells Max that feeding only occurs when solar elevation is less than 5°.

Hours to get hungry: the length of the "siesta period" following feeding, during which a hauled out seal will not to enter the water to forage.

---

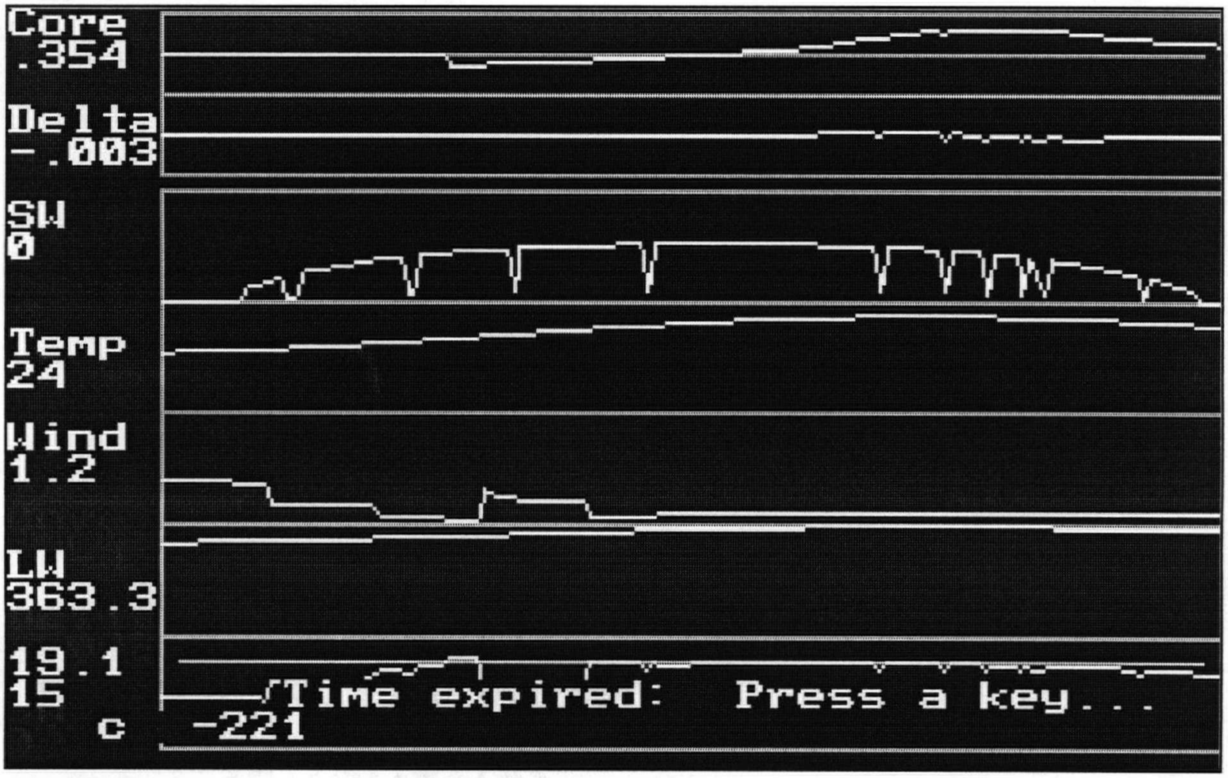
[27] Since Max is a largely deterministic model, it may seem a waste of time to replicate runs. Partial cloud cover does cause random variations in the thermal environment, however; the replication option is included for such cases.

Once the environment has been defined and the appropriate options selected, the model can be run. When **Run Simulation** has been selected in conjunction with the "output to screen" option, a series of graphs and numbers appear on the display (Fig. A1). Each graph consists of a plot of a particular variable over time, accompanied by a label and digital readout of the current value of that variable. From top to bottom, the plotted variables are

Core temperature deviation from normal (°C);
Delta (the rate of change in core temperature (°Cmin$^{-1}$);
Total incident shortwave radiation (Wm$^{-2}$);
Air temperature (°C);
Wind speed (ms$^{-1}$);
Total incident longwave radiation (Wm$^{-2}$);
Net flux ($F_s$, in Wm$^{-2}$).

Core and flux plots both have reference lines drawn at y=0, in addition to the actual data plot.

Flux, the lowest variable on the display, is not labelled explicity, and its digital readout is located within the plotting area; this is to leave space for time of day and elapsed time readouts at the bottom left-hand corner of the screen (time of day is on top). In addition, the letter "c" appears in this area whenever clouds block the sun during the simulation.



```
Time expired: Press a key...
```

**Figure A1** Screen output generated by Max during the course of a typical run.

The run ends when a) the seal overheats, b) the seal leaves the haulout site to forage, or c) the specified run time expires. Additionally, the run can be aborted by hitting any alphanumeric key during execution. Appropriate messages appear in the lowest plot area when any of these events occur.

At this point the user has two options. Hitting the "c" key will cause the model to continue running where it left off. (This is only useful when the run was prematurely aborted or run time has expired; trying to continue the run after a seal has overheated or immersed to feed is pointless, since the seal has left the haulout site.) Hitting any other key recalls the Main Menu.

# APPENDIX 3: PROGRAM CODE FOR THE SIMULATION MODEL "MAX"

## Annotated Variable List

### Graphics variables:

| | |
|---|---|
| CU(6) | Vertical location of digital readout showing current value for each of the variables being plotted |
| HP(6) | The origin of each of the seven graphs plotted on the output screen. |
| NX(6), NY(6) | X and Y coordinates for the new points to be plotted for each of 7 output variables (indexed from 0-7) |
| OX(6), OY(6) | X and Y coordinates for the last points already plotted for each of the output variables. |
| YINC(6) | Y increment (in pixels) for plotting a 1-unit change in eachj of the variables being graphed. |
| Z | Loop counter for plotting each of the variables in turn |

### "Book-keeping" variables

| | |
|---|---|
| BR$ | "y" if running in batch mode, "n" otherwise |
| ES | 0 if Environmental Setup option hasn't been used yet, 1 otherwise |
| FI$, FE$ | Names of user-defined ASCII files for input and output |
| FLAG | 0 if elapsed time is 0, 1 otherwise. Used for one-time-only setting of certain variables, and plotting initial graphics axes |
| FREQ | Length of simulated time step, in tenths of an hour |
| MM$, MM | MM holds the chosen Main Menu option; accepted as MM$, then converted to numeric format after error-trapping |

| | |
|---|---|
| OF$ | "y" if output to be sent to ASCII file, "n" otherwise |
| OS$ | "y" if output to be graphically plotted on screen, "n" otherwise |
| QQ, RP | Loop counters used when running in batch mode |
| REPS | Number of replicate runs desired when running in batch mode |
| SOURCE$ | In Environmental setup, is "f" if input source is an ASCII file and "c" if the user simply wishes to edit the current environmental settings |
| SP$, LSP$ | Strings of blank space, used to erase prior digital readout before overwriting with new values |
| X$, V$ | Generic variables for accepting character input from the keyboard (used in a variety of contexts; after error-trapping, these are generally converted into numeric variables) |

## Time-keeping variables

| | |
|---|---|
| ATM | The simulated time of day exactly 3 hours behind HOUR; used for calculating air temperature cosine function |
| ELAP,LELAP,OVERLAP | Different measures of elapsed time (you need three to handle complications like time going from 2300 to 0000 during a run which crosses midnight, and to allow elapsed time to continue incrementing without resetting to 0 if you decide to continue the simulation after specified runtime has expired. Don't worry about these; you'll never have to deal with them. |
| HOUR | Simulated time of day at current moment in run (decimal fraction) |
| RUNT | total simulated run time in hours |
| START,STTIME | Simulated hour of the day that run begins (decimal fraction: no military time here). I don't exactly remember why I needed two variables to express the same quantity (I think it had something to do with batch mode), and I'm too nervous to take one of them out now to find out. |

## Physical and environmental constants

| | |
|---|---|
| LABS | Longwave absorbance (and emissivity) of seal surface |
| LAT | Latitude |
| S0 | Extraterrestrial flux density at 1 AU |
| SABS | Shortwave absorbance of seal surface |
| SBC | Stefan-Boltzmann constant |

## Environmental variables

| | |
|---|---|
| ATEMP | air temperature |
| CLOUD | Proportion of sky covered by cloud, and the probability that the sun will be overcast at any given time-step |
| DEC | solar declination |
| DSOL | direct incident shortwave |
| EA | emissivity of clear sky |
| EAC | emissivity of sky with clouds |
| ET$ | Elapsed time counter for changes in wind speed: see WIND |
| FLUXFLAG | 0 until flux exceeds -70 for the first time, 1 thereafter |
| H | Wind chill |
| OVERC$ | Only used when running in static mode: "y" if sun is overcast, "n" otherwise |
| RAND | random number from 0-1, compared against CLOUD to determine if sun is overcast |
| TMIN, TMAX | Minimum and maximum air temperature |
| TS$ | Loop counter for changes in wind speed: see WIND |

| | |
|---|---|
| SELEV | Sine of solar elevation |
| SOLAR | Total incident shortwave radiation |
| SSOL | Scattered incident shortwave radiation |
| STATE$, STATE | character and numeric indices of whether the environment is running in static mode or fluctuation mode |
| SURFT | Surface temperature of seal |
| V | Wind speed |
| WDI | tracks elapsed time for WIND array |
| WIND(1,60) | An array of up to 60 combinations of elapsed time (val(et$)) and wind speeds (val(ts$)). V is always some value of WIND(val(et$),val(ts$)). If wind is defined as 0, it defaults up to 0.1 since some convection occurs in even the calmest air |

## Seal variables

| | |
|---|---|
| CORE | Current core temperature deviation from starting value |
| DAYFD$ | "y" if daylight foraging is desired, "n" otherwise |
| DELTA1-DELTA4,DELTA | Various pieces of the empirical core-response function derived in Chapter 4 |
| FD$ | "y" if any feeding behaviour is to be included, "n" otherwise |
| FLUX | heat-exchange index between seal surface and environment: see Chapters 3,4 |
| FEDFLAG | 1 if conditions are suitable for foraging, 0 otherwise |
| FORAGE | 1 if seal has gone foraging: 0 otherwise |
| HAUL | 1 if seal is hauled out: 0 otherwise |

| | |
|---|---|
| HICORE | Positive deviation from initial CORE (0) necessary to cause seal to abandon haul-out due to overheating |
| HUNGER | Hours it takes for seal to become hungry ("siesta period") |
| OH | 2 is seal has overheated: 0 otherwise |

## Source Code

```
5 KEY OFF

REM Error trapping
ON ERROR GOTO snafu

20 REM ARRAY CREATION

70 DIM wind(1, 60), NX(6), NY(6), HP(6), OX(6), OY(6), YINC(6), y(6), cu(6):
80 FOR z = 0 TO 6: READ HP(z), YINC(z), cu(z): NEXT

REM COORDINATES FOR PLOTTING LIMITS ON EACH GRAPH

90 DATA 11,2,2
100 DATA 31,50,5
110 DATA 73,.023,8
120 DATA 94,.63,12
130 DATA 129,2.3,15
140 DATA 145,.04,19
150 DATA 163,.014,23


170 REM INITIALIZATION OF PHYSICAL CONSTANTS

190 labs = .97: LAT = 49 * 3.14 / 180: S0 = 1360
200 sbc = 5.6697 * 10 ^ -8: TRANS = .7: sabs = .87: sp$ = " LSP$ = "                              "

REM DEFAULT VALUES FOR BOOK-KEEPING VARIABLES

210 os$ = "y": OF$ = "n": br$ = "n": freq = .1: fd$ = "y": reps = 1: es=0

REM DEFAULT VALUES FOR SEAL VARIABLES

215 hicore = 1: hunger = 6: dayfd$ = "y"

230 GOTO menu

250 REM GRAPHICS OUTPUT SUBROUTINE----------------------------------------------------
REM SET UP GRAPHICS SCREEN AND PLOTTING AXES

260 IF flag = 1 THEN 310 ELSE : SCREEN 1: LINE (40, 1)-(319, 21), 2, B:
                                    LINE (40, 21)-(319, 41), 2, B: LINE (45, 11)-(314, 11), 2
```

```
270 LINE (40, 45)-(319, 185), 2, B: LINE (40, 73)-(319, 73), 2:
                                                            LINE (40, 101)-(319, 101), 2

280 LINE (40, 129)-(319, 129), 2: LINE (40, 157)-(319, 157), 2
285 LINE (45, 163)-(314, 163), 2
290 LOCATE 1, 1: PRINT "Core": LOCATE 4, 1: PRINT "Delta": LOCATE 7, 1:
                                              PRINT "SW": LOCATE 11, 1: PRINT "Temp"

300 LOCATE 14, 1: PRINT "Wind": LOCATE 18, 1: PRINT "LW": LOCATE 22, 1

REM ASSIGN VARIABLES TO GRAPHS

310 y(0) = core: y(1) = delta: y(2) = solar: y(3) = atemp: y(4) = v: y(5) = lrad:
                                                                              y(6) = flux
320 FOR z = 0 TO 6: GOSUB 350: NEXT: LOCATE 21, 1: PRINT sp$: PRINT sp$:
                                    PRINT sp$: LOCATE 21, 1: WRITE INT(hour * 10) / 10:
                                                        WRITE INT(OVERLAP * 10) / 10

330 IF rand <= cloud THEN LOCATE 23, 4: PRINT "c": ELSE :
                                                            LOCATE 23, 4: PRINT " "

340 flag = 1: GOTO 1600

350 REM PLOT COORDINATES FOR EACH VARIABLE

360 NX(z) = 40 + INT((elap / runt) * 279):
                                      NY(z) = HP(z) - (INT(y(z) * 1000) / 1000 * YINC(z)):
                                      IF elap = 0 THEN PSET (NX(z), NY(z)), 3: GOTO 380

370 LINE (OX(z), OY(z))-(NX(z), NY(z)), 3
380 OX(z) = NX(z): OY(z) = NY(z): IF z < 6 THEN LOCATE cu(z), 1:PRINT sp$:
                              LOCATE cu(z), 1 : IF z < 2 THEN WRITE INT(y(z) * 100) / 100
                                    IF z >= 2 AND z < 6 THEN WRITE INT(y(z) * 10) / 10

385 IF z=6 THEN LOCATE cu(z),6: PRINT sp$+" ":LOCATE cu(z),7: WRITE INT(y(6))
386 RETURN


400 REM OPTIONS MENU--------------------------------------------------------------------------

420 CLS : PRINT : PRINT : PRINT TAB(30); "Welcome to  M-M-Max!": PRINT :PRINT
430 LOCATE 7, 7: PRINT "Output interval (down to .1 hour) "; : PRINT freq
440 LOCATE 8, 18: PRINT "Output to screen (y/n)  "; : PRINT os$
450 LOCATE 9, 20: PRINT "Output to file (y/n)  "; : PRINT OF$
455 LOCATE 10, 25: PRINT "Batch run (y/n)  "; : PRINT br$


460 LOCATE 7, 40: INPUT x$: IF LEN(x$) > 0 THEN freq = VAL(x$):
```

```
                                                    IF freq < .1 THEN 460 ELSE :
                                                        freq = INT(10 * freq) / 10

470 LOCATE 8, 40: INPUT x$: IF LEN(x$) > 0 THEN os$ = x$:
                                  IF os$ <> "y" AND os$ <> "n" THEN BEEP: GOTO 470

480 LOCATE 9, 40: INPUT x$: IF LEN(x$) > 0 THEN OF$ = x$:
                                 IF OF$ <> "y" AND OF$ <> "n" THEN BEEP: GOTO 480

482 LOCATE 10, 40: INPUT x$: IF LEN(x$) > 0 THEN br$ = x$:
                                  IF br$ <> "y" AND br$ <> "n" THEN BEEP: GOTO 482

484 IF OF$ = "y" THEN PRINT TAB(16); "Name of file (<=8 chars)"; : INPUT FI$:
                                          IF LEN(FI$) > 8 THEN FI$ = LEFT$(FI$, 8)

486 IF br$ = "y" THEN PRINT TAB(16); "How many batch reps"; : INPUT reps
500 IF OF$ = "y" THEN FI$ = FI$ + ".max"
    IF br$ = "n" THEN reps = 1

LOCATE 15, 17: PRINT "Critical Core elevation "; : PRINT hicore
LOCATE 16, 20: PRINT "Feed the Seals (y/n)  "; : PRINT fd$
501 LOCATE 15, 40: INPUT x$: IF LEN(x$) > 0 THEN hicore = VAL(x$):
                                    IF STR$(hicore) <> " " + x$ THEN BEEP: GOTO 501

502 LOCATE 16, 40: INPUT x$: IF LEN(x$) > 0 THEN fd$ = x$:
                                  IF fd$ <> "y" AND fd$ <> "n" THEN BEEP: GOTO 502

IF fd$ = "n" THEN 510
    LOCATE 17, 18: PRINT "Daylight Feeding (y/n)  "; : PRINT dayfd$
    LOCATE 18, 21: PRINT "Hours to get hungry "; : PRINT hunger
503     LOCATE 17, 40: INPUT x$: IF LEN(x$) > 0 THEN dayfd$ = x$:
                             IF dayfd$ <> "y" AND dayfd$ <> "n" THEN BEEP: GOTO 503

504     LOCATE 18, 40: INPUT x$: IF LEN(x$) > 0 THEN hunger = VAL(x$):
                                    IF STR$(hunger) <> " " + x$ THEN BEEP: GOTO 504

510 GOTO 1680


530 REM SET UP TIME LOOP

542 FOR rp = 1 TO reps

REM IF RUNNING IN BATCH MODE, REPLICATE WHOLE RUN 12 TIMES WITH  REM
DIFFERENT START TIMES

545 IF br$ = "n" THEN 550
FOR qq = 1 TO 23 STEP 2: start = qq
```

```
REM OPEN APPROPRIATE ASCII FILES FOR OUTPUT

550 IF OF$ = "y" THEN OPEN FI$ FOR OUTPUT AS #1
555 IF br$ = "y" THEN OPEN "durahaul.dat" FOR APPEND AS #2

REM INITIALISE TIME-KEEPING AND SEAL STATUS VARIABLES

560 core = 0: flag = 0: fluxflag = 0: hour = start
565 sttime = hour: wdi = 0
566 forage = 0: haul = 1
570 elap = 0: OVERLAP = elap: lelap = 0

REM BEGIN TIME LOOP---------------------------------------------------------------------------------

DO WHILE haul = 1 AND lelap <= runt * 5

REM UPDATE ELAPSED TIME
elap = lelap / 5: IF lelap > 0 THEN OVERLAP = OVERLAP + .1

REM ENVIRONMENTAL DRIVER----------------------------------------------------------

REM IF RUNNING IN STEADY-STATE MODE AND INITIAL ENVIRONMENT
REM HAS ALREADY BEEN DEFINED, SKIP ENVIRONMENTAL DRIVER
IF state$ = "s" AND flag = 1 THEN GOTO seal

REM TIME OF DAY:
620 hour = hour + .1: IF hour >= 24 THEN hour = hour - 24
630 IF hour > 3 THEN ATM = hour - 3 : ELSE : ATM = hour + 21

REM AIR TEMPERATURE:
640 atemp = (TMAX - tmin) / 2 + tmin - ((TMAX - tmin) / 2) * COS(.262 * ATM)

REM ATMOSPHERIC EMISSIVITY:
650 rand = RND(1): EA = .72 + .005 * atemp:
                                        EAC = EA + cloud * (1 - EA - 8 / atemp)

REM SOLAR ELEVATION:
660 DEC = -.4 * COS(jday * .017205):
selev = SIN(LAT)*SIN(DEC)+COS(LAT)*COS(DEC)*COS(3.14*15*(hour - 12) / 180)

760 REM WIND SPEED:
770 IF elap > wind(0, wdi + 1) THEN wdi = wdi + 1
780 v = wind(1, wdi): IF v = 0 THEN v = .1

870 REM INITIALIZE INCIDENT SHORTWAVE RADIATION:
REM (No reflected, since patch is assumed the be facing upwards)
890 dsol = 0: ssol = 0

REM DIRECT SOLAR FOR SOLAR ELEVATION ANGLES >10°:
```

```
900 IF selev > .173561 THEN dsol = S0 * TRANS ^ (1 / selev):

REM SCATTERED INCIDENT SHORTWAVE RADIATION:
ssol = .5 * S0 * (1 - TRANS ^ (1 / selev)) * selev

REM RANDOM SEED FOR CLOUD COVER:
920 RANDOMIZE TIMER: rand = RND

REM TOTAL INCIDENT SHORTWAVE RADIATION (NO REFLECTED COMPONENT,
REM SINCE PATCH IS ASSUMED TO BE FACING UPWARDS):
930 solar = dsol + ssol

REM CORRECTED TOTAL INCIDENT SHORTWAVE, CALIBRATED REM FOR DIFFERENCE
BETWEEN MEASURED AND PREDICTED VALUES:
940 solar = .704 * solar: IF rand <= cloud THEN solar = .2 * solar

1020 REM INCIDENT LONGWAVE RADIATION:
1030 lrad = EAC * sbc * (atemp + 273) ^ 4

1050 REM SURFACE TEMPERATURE (based on empirical data at steady state):
1070 surft = 22.222 + .436 * atemp + .034 * solar

1110 REM CONVECTION EFFECTS (for a flat plate, .1m in diameter):
1120 h = 5.85 * v ^ .8 / (.1 ^ .2)


REM SEAL DRIVER-------------------------------------------------------------

1270 REM FLUX
     REM (Note longwave absorptivity and emmisivity are the same (labs)):
flux = sabs * solar + labs * lrad - labs * sbc * (surft + 273) ^ 4 - h * (surft - atemp)

REM IF SEAL IS RUNNING INTO FLUX>-70 FOR THE FIRST TIME,
REM LET CORE DROP 0.5°C TO COMPENSATE:
SEAL: IF fluxflag = 0 AND flux > -70 THEN core = -.5: fluxflag = 1

1350 REM EMPIRICAL CORE RESPONSE FUNCTION:
    delta1 = 0: IF flux > 196.34 THEN delta1 = .00028 * (flux - 196.34)
    delta2 = 0: IF -.006 * core > .00028 * (flux - 196.34) THEN delta2 = -.006 * core
    delta3 = 0: IF flux >= -71.162 THEN delta3 = ((core + 2) ^ 9.4 / (2.32 ^ 9.4 +
                              (core + 2) ^ 9.4) - (core + 2) ^ 50 / (3.852 ^ 50 + (core + 2) ^ 50))
    delta4 = delta3 * .00027 * (flux - (-71.162))
    delta = delta1 + delta2 + delta4

REM UPDATE CORE TEMPERATURE:
1370 core = core + freq * 60 * delta: IF core < -.5 THEN core = -.5

1390 REM IS SEAL OVERHEATING?
1400 oh = 0:
```

```
1410 IF core > hicore THEN oh = 2: haul = 0

REM IF FEEDING OPTION DISABLED, SKIP THE FOLLOWING SECTION:
IF fd$ = "n" THEN 1570

REM IF SEAL FEEDS AT DAWN OR DUSK, END RUN:
IF elap > 0 THEN GOTO probfeed
   fedflag = 0: IF selev < SIN(3.14 * -13 / 180) THEN fedflag = 1

REM LET SEAL FEED DURING THE DAY IF THE OPTIONS MENU SAYS SO:
   IF dayfd$ = "y" THEN fedflag = 1:

probfeed: REM IF SEAL HAULS DURING DARKNESS, ASSUME IT'S JUST FED:
          REM START SIESTA PERIOD.
    IF fedflag=1 AND elap>hunger AND selev<(3.14 * 5 / 180) THEN forage=1:haul=0

REM IF OPTIONS MENU DOESN'T LET SEAL FEED DURING THE DAY, THEN
REM ASSUME A SEAL HAULING DURING DAYLIGHT HOURS IS HUNGRY COME
REM SUNDOWN: NO SIESTA PERIOD.
        IF fedflag = 0 AND selev < (3.14 * 5 / 180) THEN forage = 1: haul = 0

REM OUTPUT SWITCHBOARD---------------------------------------------------

REM IF NO OUTPUT IS SCHEDULED FOR THIS TIME STEP,
REM SKIP TO THE NEXT SECTION:
1570 IF elap / freq <> INT(elap / freq) THEN 1615

1580 REM PRINT OUTPUT VARIABLES TO APPROPRIATE DESTINATIONS
    REM  (SCREEN OR ASCII FILES):
590 IF os$ = "y" THEN 250
1600 IF OF$ = "y" THEN PRINT #1, hour, elap, core, delta, oh, flux, v, atemp, solar,
                                                          lrad, h * (surft - atemp)
1605 IF OF$ = "y" AND os$ = "n" THEN PRINT hour, elap, core, delta, oh, flux, v,
                                                 atemp, solar, lrad, h * (surft - atemp)

REM STOP PROGRAM IF ANY KEY IS HIT:
1615 IF os$ = "y" THEN v$ = INKEY$: IF v$ <> "" THEN haul = 0

REM INCREMENT TIME
1620 lelap = lelap + .5
LOOP

REM END TIME LOOP-----------------------------------------------------------------


REM PRINT APPROPRIATE MESSAGES AT END OF RUN:
1630 LOCATE 22, 10: PRINT LSP$: LOCATE 22, 10:
IF br$ = "y" THEN 1655
   IF oh = 2 THEN PRINT "Overheated:  ";
```

```
   IF forage = 1 THEN PRINT "Gone Fishing:  ";
   IF forage = 0 AND oh <> 2 THEN PRINT "Time expired:  ";
PRINT "Press a key..."

REM K TO SEE IF A MEANINGFUL KEY HAS BEEN HIT:
1640 v$ = INKEY$: IF v$ = "" THEN 1640

REM CONTINUE THE RUN IF SPECIFIED:
1650 IF v$ = "c" AND os$ = "y" THEN flag = 0: SCREEN 2: SCREEN 0: GOTO 570

REM PRINT ELAPSED TIME AND VARIOUS RELATED TIDBITS TO ASCII FILE, IF
REM RUNNING IN BATCH MODE:
1655 IF os$ = "n" AND OF$ = "n" AND br$ = "y" THEN PRINT rp, jday, sttime, elap

REM SHUT DOWN GRAPHICS SCREEN AND CLOSE FILES AS NEEDED:
1660 IF os$="y" THEN SCREEN 2: SCREEN 0: IF OF$="y" THEN CLOSE #1: OF$="n"
1665 IF br$ = "y" THEN PRINT #2, jday, sttime, elap: CLOSE #2

REM LOOP BACK TO NEXT START TIME IF RUNNING IN BATCH MODE
IF br$ = "n" THEN 1667
NEXT qq

1667 NEXT rp

1670
1680 REM Main Menu--------------------------------------------------------------------------------

menu:
1700 CLS : CLOSE
1710 PRINT : PRINT : PRINT:PRINT: PRINT TAB(40); "MAIN MENU":PRINT:PRINT
1720 PRINT TAB(30); "1. Set up environment"
1730 PRINT : PRINT TAB(30); "2. Options Menu"
1740 PRINT : PRINT TAB(30); "3. Run simulation": PRINT :
                                                          PRINT TAB(30); "4. Exit"

1750 PRINT : PRINT : PRINT TAB(30); : INPUT "Choose: "; MM$
1760 IF VAL(MM$) <> 1 AND VAL(MM$) <> 2 AND VAL(MM$) <> 3 AND
                                  VAL(MM$) <> 4 AND VAL(MM$) <> 5 THEN 1700

1770 MM = VAL(MM$): CLS

REM CHECKS TO MAKE SURE THAN ENVIRONMENT HAS BEEN EDITED REM BEFORE
RUNNING; IF NOT, KICKS BACK TO MENU
IF NOT (mm = 3 AND es = 0) THEN CLS : ON mm GOTO 2210, 400, 530, 1780

IF mm = 3 AND es = 0 THEN BEEP: BEEP: LOCATE 20, 23:
PRINT "No environment ready: Hit any key"
1775 LET v$ = INKEY$: IF v$ = "" THEN 1775
    GOTO menu
```

```
1780 END

2190 REM ENVIRONMENTAL SETUP----------------------------------------------------------

2210 CLS : LOCATE 2, 30: PRINT "ENVIRONMENT SETUP"
2220 LOCATE 4, 9: PRINT "Data from file(f) or current(c)"; : INPUT SOURCE$
2230 IF SOURCE$ <> "c" AND SOURCE$ <> "f" THEN BEEP: GOTO 2220
2240 IF SOURCE$ = "c" THEN LOCATE 5, 28: PRINT "Name of file  " + FE$: GOTO

2260 REM SPECIFY WHAT FILE YOU WANT TO ACCESS IF APPROPRIATE:
2270 LOCATE 5, 28: PRINT "Name of file"; : INPUT FE$: FE$ = FE$ + ".env":
                                                OPEN FE$ FOR INPUT AS #2:GOTO 2280

REM ERROR-TRAP FOR BAD FILE SPECIFICATION:
snafu: IF ERR = 53 THEN BEEP: BEEP: LOCATE 10, 18:
      PRINT "Try a file that actually EXISTS, Bozo:"
      LOCATE 11, 17: PRINT "One more mistake and the program crashes."
      GOTO 2270

REM READ ENVIRONMENTAL VARIABLES FROM ASCII FILE

2280 state$ = "f": INPUT #2, state, jday, start, runt, tmin, TMAX, cloud:
                                          IF state = 0 THEN state$ = "s": INPUT #2, OVERC
2300 FOR i=0 TO 60: INPUT #2, wind(0, i), wind(1, i): NEXT: CLOSE #2: GOTO 1680

REM SET UP MENU: PRINT ENVIRONMENTAL VARIABLES,
REM AND ACCEPT NEW INPUT TO REPLACE THEM IF NECESSARY

2310 PRINT : PRINT TAB(12); "Flux (f) or steady-state (s)  "; : PRINT state$
2320 state = 0: IF state$ = "f" THEN state = 1
2330 PRINT TAB(30); "Julian Day "; : PRINT jday
2340 PRINT TAB(30); "Start time "; : PRINT start
2350 PRINT TAB(27); "Length of run "; : PRINT runt
2360 PRINT TAB(17); "Minimum air temperature "; : PRINT tmin
2370 PRINT TAB(17); "Maximum air temperature "; : PRINT TMAX
2390 PRINT TAB(9); "Proportion of cloud cover (0-1) "; : PRINT cloud
2400 IF state$ = "s" THEN PRINT TAB(26); "Overcast (y/n) "; : PRINT OVERC$
2410 LOCATE 7, 45: INPUT x$: IF LEN(x$) > 0 THEN state$ = x$
2411 IF state$ <> "f" AND state$ <> "s" THEN 2410
2420 state = 0: IF state$ = "f" THEN state = 1
2430 LOCATE 8, 45: INPUT x$: IF LEN(x$) > 0 THEN jday = VAL(x$): IF jday > 365 OR jday
< 1 OR jday <> INT(jday) THEN 2430
2440 LOCATE 9, 45: INPUT x$: IF LEN(x$) > 0 THEN start = VAL(x$): IF start < 0 OR start
>= 24 THEN 2440
2450 LOCATE 10, 45: INPUT x$: IF LEN(x$) > 0 THEN runt = VAL(x$):

REM REM TEMPERATURE MUST BE >0°C, OR THE ATMOSPHERIC EMMISSIVITY REM
FORMULA ON LINE 650 CRAPS OUT:
```

```
2460 LOCATE 11, 45: INPUT x$: IF LEN(x$) > 0 THEN tmin = VAL(x$):
                                                              IF tmin <= 0 THEN 2460

2470 LOCATE 12, 45: INPUT x$: IF LEN(x$) > 0 THEN TMAX = VAL(x$):
                                                          IF TMAX <= tmin THEN 2460
2490 LOCATE 13, 45: INPUT x$: IF LEN(x$) > 0 THEN cloud = VAL(x$):
                                                  IF cloud < 0 OR cloud > 1 THEN 2490
2500 IF state$ = "s" THEN LOCATE 15, 26: INPUT "Overcast (y/n) "; x$:
  IF LEN(x$) > 0 THEN OVERC$ = x$: IF OVERC$ <> "y" AND OVERC$ <> "n" THEN 2500
2510 OVERC = 0: IF OVERC$ = "y" THEN OVERC = 1

2620 REM WIND PROFILE: WRITE IT OUT AND ACCEPT NEW INPUT IF
     REM NECESSARY

2640 FOR i = 0 TO 40 STEP 20: CLS :
          PRINT TAB(5); "Wind profile: enter elapsed time, then a space, then wind speed (m/s)"
2650 IF i = 0 THEN PRINT TAB(27); "(Start with elapsed time=0)": PRINT
2660 FOR j = 0 TO 19: LOCATE 4 + j, 37: WRITE wind(0, i + j), wind(1, i + j):
                                                              NEXT: FOR j = 0 TO 19
2665 et$ = STR$(wind(0, i + j)): ts$ = STR$(wind(1, i + j))
2670 LOCATE 4 + j, 35: INPUT x$:

                  IF LEN(x$) > 0 AND INSTR(2, x$, " ") = 0 THEN BEEP: BEEP: GOTO 2670
                                IF LEN(x$) > 0 THEN et$ = LEFT$(x$, INSTR(x$, " ") - 1):
                                            ts$ = RIGHT$(x$, LEN(x$) - INSTR(x$, " "))

2675 PRINT et$, ts$
2680 wind(0, i + j) = VAL(et$): wind(1, i + j) = VAL(ts$):
                                           IF wind(1, i + j) = 0 THEN wind(1, i + j) = .1
2690 IF wind(0, i + j) >= runt THEN i = 41: j = 20
2700 NEXT: NEXT

REM SAVE ENVIRONMENTAL VARIABLES TO ASCII FILE IF REQUIRED

2760 CLS : PRINT : PRINT TAB(19); "Save to a file? (y/n)"; : INPUT SV$:
                                             IF SV$ <> "y" AND SV$ <> "n" THEN 2760
2770 IF SV$ = "n" THEN 1670
2780 PRINT TAB(16); "Name of file (<=8 chars)"; : INPUT FE$:
                                          IF LEN(FE$) > 8 THEN FE$ = LEFT$(FE$, 8)
2790 FE$ = FE$ + ".env": OPEN FE$ FOR OUTPUT AS #2: CLS : PRINT : PRINT :
                               PRINT : PRINT : PRINT : PRINT TAB(30); "Saving " + FE$
2800 PRINT #2, state, jday, start, runt, tmin, TMAX, cloud:
                                                 IF state = 0 THEN PRINT #2, OVERC
2820 FOR i = 0 TO 60: PRINT #2, wind(0, i), wind(1, i): NEXT
2830 CLOSE #2: GOTO 1670
```

# APPENDIX 4: ASYMPTOTIC CORRELATION MATRIX OF REGRESSION COEFFICIENTS FOR ATTILA'S THERMAL RESPONSE SURFACE

| | $s_{aff}$ | c | g | $F_b$ | i1 | i2 | i3 | i4 | a |
|---|---|---|---|---|---|---|---|---|---|
| $s_{aff}$ | 1.000 | | | | | | | | |
| c | -0.016 | 1.000 | | | | | | | |
| g | 0.007 | -0.402 | 1.000 | | | | | | |
| $F_b$ | 0.024 | -0.515 | 0.617 | 1.000 | | | | | |
| i1 | -0.019 | 0.094 | -0.121 | -0.051 | 1.000 | | | | |
| i2 | -0.041 | 0.219 | -0.147 | -0.168 | -0.550 | 1.000 | | | |
| i3 | -0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 1.000 | | |
| i4 | 0.017 | -0.423 | 0.135 | 0.110 | 0.074 | -0.288 | 0.000 | 1.000 | |
| a | 0.032 | -0.547 | 0.411 | 0.782 | -0.393 | 0.285 | 0.000 | 0.022 | 1.000 |

# APPENDIX 5: PREDICTED AND OBSERVED TRAJECTORIES OF DRY EXPERIMENTAL TREATMENTS IN "THERMOSPACE"

Readings taken within the first hour of each test were excluded from analysis, to allow for initial decline in core temperature.

Readings denoted by asterisk (*) were not observed in the real world. In these cases Attila overheated earlier than predicted, so the time simulated by the model exceeded that of the actual experiment.

| | | Relative Core Temperature (°C) | |
|---|---|---|---|
| elapsed time (min) | flux ($Wm^{-2}$) | observed | predicted |
| 0 | -199 | 0.0 | - |
| 60 | -195 | -0.1 | -0.1 |
| 120 | -195 | -0.1 | -0.1 |
| 150 | -195 | -0.1 | -0.1 |
| 240 | -193 | 0.0 | 0.0 |
| 300 | -191 | 0.0 | 0.0 |
| 360 | -191 | 0.0 | 0.0 |
| 420 | -191 | 0.0 | 0.0 |
| | | | |
| 0 | -168 | 0.0 | - |
| 30 | -179 | -0.1 | - |
| 60 | -166 | 0.0 | 0.0 |
| 90 | -166 | -0.1 | 0.0 |
| 120 | -166 | -0.1 | 0.0 |
| 150 | -166 | -0.1 | 0.0 |
| 180 | -163 | -0.1 | 0.0 |
| 210 | -161 | -0.1 | 0.0 |
| 240 | -161 | -0.1 | 0.0 |
| 270 | -161 | -0.1 | 0.0 |
| 300 | -159 | -0.1 | 0.0 |
| 330 | -159 | -0.1 | 0.0 |
| 360 | -157 | -0.1 | 0.0 |
| 390 | -157 | -0.1 | 0.0 |

| elapsed time (min) | flux ($Wm^{-2}$) | Relative Core Temperature (°C) observed | Relative Core Temperature (°C) predicted |
|---|---|---|---|
| 0 | -57 | 0.0 | - |
| 30 | -36 | 0.2 | - |
| 60 | -31 | 0.0 | 0.0 |
| 90 | -27 | -0.2 | 0.1 |
| 120 | -22 | 0.0 | 0.1 |
| 150 | -20 | 0.2 | 0.2 |
| 180 | -19 | 0.2 | 0.4 |
| 210 | -19 | 0.5 | 0.5 |
| 240 | -14 | 0.2 | 0.7 |
| 270 | -19 | 0.2 | 0.9 |
| 300 | -19 | 0.2 | 1.2 |
| 330 | -16 | 0.7 | 1.4 |
| 360 | -16 | 1.1 | 1.6 |

This run generated the outlier in Fig. 4.11:

| | | | |
|---|---|---|---|
| 0 | -62 | 0.0 | - |
| 30 | -39 | -0.2 | - |
| 60 | -31 | -0.5 | -0.5 |
| 90 | -27 | -0.5 | -0.4 |
| 120 | -25 | -0.5 | -0.3 |
| 150 | -22 | -0.3 | -0.3 |
| 180 | -21 | 0.0 | -0.2 |
| 210 | -16 | 0.0 | -0.1 |
| 240 | -19 | 0.2 | 0.0 |
| 270 | -19 | 0.5 | 0.1 |
| 300 | -16 | 0.7 | 0.1 |
| 330 | -16 | 1.1 | 0.3 |
| 360 | -16 | 2.0 | 0.4 |
| *440 | -16 | - | 1.2 |

| elapsed time (min) | flux (Wm$^{-2}$) | Relative Core Temperature (°C) observed | Relative Core Temperature (°C) predicted |
|---|---|---|---|
| 0 | -40 | 0.0 | - |
| 30 | -21 | 0.0 | - |
| 60 | -7 | -0.3 | -0.3 |
| 90 | 2 | -0.5 | -0.2 |
| 120 | 7 | -0.5 | -0.1 |
| 150 | 12 | -0.3 | -0.1 |
| 180 | 15 | 0.0 | 0.1 |
| 210 | 17 | 0.0 | 0.3 |
| 240 | 17 | 0.2 | 0.5 |
| 270 | 22 | 0.2 | 0.9 |
| 310 | 28 | 0.5 | 1.6 |
| 325 | 28 | 0.9 | 1.8 |
| 340 | 30 | 1.1 | 1.8 |
| 370 | 30 | 1.3 | 1.8 |
| 405 | 28 | 2.0 | 1.9 |
| | | | |
| 0 | 57 | 0.0 | - |
| 30 | 88 | -0.7 | - |
| 60 | 101 | -0.9 | -0.9 |
| 90 | 108 | -0.7 | -0.7 |
| 120 | 112 | -0.5 | -0.6 |
| 150 | 117 | 0.0 | -0.5 |
| 180 | 117 | 0.6 | -0.3 |
| 210 | 117 | 2.1 | -0.2 |
| *275 | 117 | - | 1.5 |
| | | | |
| 0 | 65 | 0.0 | - |
| 30 | - | 0.0 | - |
| 60 | - | 0.0 | - |
| 90 | 135 | 0.0 | 0.0 |
| 120 | 135 | 0.5 | 0.3 |
| 150 | 135 | 1.1 | 1.1 |
| 160 | 135 | 1.5 | 1.5 |

| elapsed time (min) | flux ($Wm^{-2}$) | Relative Core Temperature (°C) observed | Relative Core Temperature (°C) predicted |
|---|---|---|---|
| 0 | 53 | 0.0 | - |
| 30 | 97 | 0.0 | - |
| 60 | 110 | -0.3 | -0.3 |
| 90 | 135 | 0.0 | -0.1 |
| 120 | 192 | 0.2 | 0.0 |
| 150 | 192 | 0.0 | 0.4 |
| 180 | 180 | 0.3 | 1.8 |
| 210 | 174 | 1.7 | 2.8 |
| | | | |
| 0 | 117 | 0.0 | - |
| 30 | 159 | -0.4 | - |
| 90 | 172 | -0.4 | -0.4 |
| 120 | 174 | -0.1 | -0.2 |
| 150 | 177 | -0.1 | -0.1 |
| 180 | 186 | 0.0 | 0.1 |
| 210 | 186 | 1.6 | 0.9 |
| *214 | 186 | - | 1.1 |
| *221 | 186 | - | 1.6 |
| | | | |
| 0 | 142 | 0.0 | - |
| 30 | 191 | -0.4 | - |
| 60 | 205 | -0.1 | -0.1 |
| 90 | 213 | 0.4 | 0.3 |
| 110 | 219 | 1.5 | 1.1 |
| 115 | 216 | 1.9 | 1.5 |
| | | | |
| 0 | 166 | 0.0 | - |
| 30 | 174 | 0.0 | - |
| 60 | 230 | 0.2 | 0.2 |
| 85 | 235 | 1.0 | 1.2 |
| 90 | 238 | 1.5 | 1.6 |
| 95 | 238 | 2 | 2.1 |

| elapsed time (min) | flux ($Wm^{-2}$) | Relative Core Temperature (°C)<br>observed | predicted |
|---|---|---|---|
| 0 | 183 | 0.0 | - |
| 35 | 234 | -0.3 | - |
| 60 | 252 | -0.1 | -0.1 |
| 90 | 257 | 0.2 | 0.7 |
| 120 | 255 | 1.8 | 2.5 |