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RINGED SEAL WINTER ECOLOGY AND EFFECTS OF NOISE DISTURBANCE

by

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with

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ABSTRACT

Ringed seals abandon subnivean breathing holes and lairs at higher than normal rates in response to seismic (Vibroseis) surveying and, probably, other human-made noises. The significance of such abandonment was assessed in a telemetric study of lair occupation by ringed seals.

Temporal and spatial haul-out patterns of 13 radio-tagged seals were recorded from early March through early June in the Beaufort Sea and in Kotzebue Sound. Both male and female ringed seals haul out in more than one, and as many as four, alternative subnivean lairs. At least one lair was used by more than one seal. Distances between lairs used by individual seals were as great as 4 km with numerous breathing holes between those sites.

The percentage of once-hourly monitoring periods in which seals were hauled out in lairs increased from 11.5% in March to 17.8% in April, 20.4% in May, and 27.2% in June. Individual haul-out bouts averaged 5.4 hours; nonhaul-out bouts averaged 18.9 hours. Post-parturient females hauled out most regularly and did so in significantly longer bouts during the nursing period than before or after that period. Diel haul-out patterns tended to be weak or absent in March and April but became pronounced with midday peaks in late May and early June.

Heat dissipated from the underlying sea water maintained air temperatures in subnivean lairs above -10°C despite outside equivalent wind chill temperatures lower than -35°C. The presence of a seal in a lair increased the air temperature by at least 3°C and by as much as 10°C. Air temperature in one lair averaged 27.0°C warmer than outside windchills in March, 26.2°C warmer in April, and 16.4°C warmer in May. After the first week of May, outside wind chill temperatures tended to be warmer than internal lair temperatures.

Ringed seals abandoned subnivean lairs and breathing holes that were within 150 m of seismic lines significantly more often than they abandoned sites at greater distances from seismic lines. Radio-tagged ringed seals departed lairs by diving into the water in greater than 50% of instances when helicopters flew over at or below an altitude of 305 m. Seals departed lairs in response to snow machines operating at distances of 0.5 to 2.8 km. An operating Vibroseis and associated equipment caused a seal to exit a lair at a distance of 644 m. People moving on foot or skiis generally did not cause seals to depart lairs until within 200 m. Seals departed significantly more often in response to people walking than in response to skiers. In all cases where seals departed lairs in response to human-made noises, they subsequently returned to the lair and hauled out. The seal that departed in response to seismic equipment on the ice may have abandoned his lair five days later.

The effectiveness of aerial surveys of basking ringed seals could be increased by telemetrically monitoring haul-out patterns during the basking season.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (continued)

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INTRODUCTION

Background

Ringed seals, of all northern pinnipeds, are recognized as the most adapted to areas of annual sea ice cover (McLaren 1958; Smith and Stirling 1975; Burns 1970). These small phocids can inhabit areas of complete ice cover by virtue of their ability to make and maintain breathing holes through the ice by using the strong claws on their foreflippers. Some of these holes are covered by snow drifts, into which the ringed seals excavate lairs where they haul out to rest and give birth.

The female gives birth to a single pup in a subnivean lair in late March to mid April (McLaren 1958; Smith and Stirling 1975; Lukin and Potelov 1978). Each pup retains its white, wooly lanugo pelage for most of the 4 to 6 week nursing period, during which time they develop a thick blubber layer. Nursing overlaps with mating, which occurs in late April and May (McLaren 1958). At that time, the rutting males become odoriferous, a condition referred to as "tigak" by Inupiaq-speaking Eskimos. The odor is imparted to the snow at breathing holes and lairs used by the males.

Subnivean lairs have been attributed with providing protection from predators (McLaren 1958; Smith 1980) and extremely cold temperatures (Lukin 1980). The lairs generally are abandoned in late May, and the adults then begin to bask in the sunlight as they molt. After the ice breaks up, generally in late June or July, the seals mainly are pelagic until they again inhabit the ice the following winter.

The existence of ringed seal lairs was known long ago to the Eskimo people, who used dogs to locate them (Hall 1866; Stefansson 1913). Only recently, however, have those structures been investigated by biologists. Lukin and Potelov (1978) investigated the distribution and abundance of pupping lairs in the White Sea using a trained dog to locate those structures. Smith and Stirling used Labrador retrievers to locate subnivean seal structures (breathing holes and lairs) in the Canadian arctic (Smith and Stirling 1975). They and their co-workers have investigated the distribution and abundance of the structures and predation on ringed seals (Smith and Stirling 1975; Smith 1976; Smith and Stirling 1978; Smith 1980; Smith and Hammill 1981).

Shore-fast ice has been considered the most important habitat for breeding ringed seals (McLaren 1958; Burns 1970; Smith 1973a). In the Chukchi and Beaufort Seas, the fast ice also is used as a substrate for petroleum exploration and development activities, including seismic surveying and gravel island construction. To a large degree, those activities take place on ice that is believed to be optimal ringed seal habitat (Burns and Kelly 1982).

Relevance to Problems of Petroleum Development

Petroleum exploration and development may affect ringed seals through: (1) direct contact with crude oil from a spill; (2) destruction or displacement of prey; or (3) displacement from portions of their habitat due to noise disturbances. Effects of contact with, and ingestion of, crude oil included temporary soiling of the pelage, eye irritation, kidney lesions, and possible liver damage (Smith and Geraci 1975; Geraci and Smith 1975). Six ringed seals immersed for 24 hours in crude oil shortly after capture survived, but three held in captivity for a longer period died within 71 minutes of immersion, apparently as the combined result of stress and exposure to the oil (Smith and Geraci 1975). Indirect effects on the seals through impacts on prey populations are difficult to assess and predict but generally are considered to be of minor importance (Sekerak 1979; Craig 1984; Truett 1984).

Disturbance by noise is likely to be more widespread in time and space, but the long term significance of such disturbance is difficult to predict or assess. Burns and Eley (1978) suggested that low numbers of ringed seals in the immediate vicinity of coastal villages was due to displacement through noise disturbance as well as to hunting pressure. Based on aerial surveys in 1970, Burns and Harbo (1972) concluded that "ringed seals were not appreciably displaced" by under-ice seismic exploration (dynamite method), although their surveys were not well stratified with respect to experimental (seismic) areas and control (nonseismic) areas (Burns and Kelly 1982). Aerial surveys conducted in June of 1975, 1976, and 1977 also were not designed to test for displacement of ringed seals by industrial activities, but reanalysis of those data suggested that densities of seals in areas subjected to seismic exploration was approximately half of the density in undisturbed areas (Burns and Kelly 1982). In 1981, this project conducted aerial surveys specifically designed to assess the impact of on-ice seismic activity on ringed seal distribution and numbers (Burns *et al.* 1981; Burns and Kelly 1982). Those surveys also suggested displacement of ringed seals by on-ice seismic exploration, but the results were confounded by an early ice break-up and a questionable relationship between seal distribution in winter and in the June survey period.

Also in 1981, Kelly (with the aid of Dr. Thomas Smith and his colleagues) trained a Labrador retriever to locate subnivean seal structures by smell. In the spring of 1982, the Labrador was used to survey subnivean seal structures in areas of seismic exploration and in control areas. Each structure was examined repeatedly to determine whether it remained in active use by a seal. Seals abandoned 29.2% of the structures ($n = 48$) within 150 m of seismic lines and 10.8% of the structures ($n = 37$) beyond 150 m of the same seismic lines (Burns and Kelly 1982). A log-likelihood ratio goodness of fit test indicated that the difference was significant ($G = 5.530$, $df = 1$, $0.01 < p < 0.025$). Abandonment rates did not differ significantly with distance from control lines ($G = 0.071$, $df = 1$).

Three ringed seals were radio-tagged in 1982, and their daily and seasonal haul-out patterns were monitored by means of the radio signals. A brief summary of those results was reported by Burns and Kelly (1982).

While local displacement of ringed seals occurred in areas of seismic exploration, assessment of the impacts at the population level required additional information. Major concerns were (1) the significance of different geographical areas to overwintering ringed seals, (2) the ecological importance of lair use by seals, (3) responses of individual seals to noise disturbances, and (4) the nature of the acoustic environment of seals in areas with and without industrial activity. The first of these concerns was addressed by Burns and co-workers in Part I of RU 232, and the second and third are the subject of this report; the fourth was addressed by TRACOR, Inc., as RU 636.

To address these different concerns simultaneously, an additional Labrador retriever was trained in the art of "seal sniffing." Lil, a three year old bitch was trained, with the aid of Clyde, the experienced Labrador. Her training took place initially along the Seward Peninsula in early March 1983 and continued "on the job" in the Beaufort Sea.

Objectives

The ecological importance of lair use and the responses of individual ringed seals to noise disturbance were studied telemetrically over three years. The objectives were:

(1) To determine the number of subnivean lairs utilized by individual ringed seals and the spatial distribution of those lairs.
(2) To determine the patterns of daily and seasonal use of subnivean lairs by ringed seals.

(3) To determine the thermal advantage realized by ringed seals occupying subnivean lairs.
(4) To determine how lair occupancy is affected by noise disturbances including seismic exploration.

Additionally, we supported the acoustic measurements of RU 636 by locating subnivean seal structures and aiding with logistics.

Study Areas

Telemetric studies were conducted in the vicinity of Reindeer Island (70°29.1'N, 148°21.5'W), Beaufort Sea in 1982 and 1983 and in southern Kotzebue Sound (66°04'N, 162°26'W), Chukchi Sea in 1984 (Figure 1). The Beaufort Sea study area was subjected to seismic exploration (Vibroseis method) during the month before radio-tagging was begun in 1982. The area was subjected to a simulated seismic survey, after most study animals had been radio-tagged in 1983. Kotzebue Sound was chosen as the study area in 1984 because it was not impacted by industrial activities and could serve as a control area. Kotzebue Sound offered the additional advantage of higher densities of seals, thus expediting the tagging and tracking procedures.

The 1982 and 1983 study area in the Beaufort Sea encompassed the shore-fast ice within an approximately 13-km radius of Reindeer Island (Figure 2). Water depth in the study area was generally less than 15 m and increased only gradually offshore of Reindeer Island. The island is composed of sand and gravel as are most of the bottom sediments in the vicinity.

The sea around the island usually is ice covered from October to July with annual ice attaining a thickness of 2 m. Variable numbers of large pressure ridges trend more or less parallel to the shoreline and are most numerous seaward of the barrier islands. Snow drifts adjacent to surface deformations, such as pressure ridges and grounded floes, predominantly run northeast to southwest, since the prevailing winds are out of the northeast. Except for those drifts, snow depth generally is less than 20 cm, which is the minimum required for lair excavation by seals (Smith and Stirling 1975; Burns and Kelly 1982).

Water circulation under the fast ice is very slow with currents mostly less than 2 cm/sec. (Barnes and Reimnitz 1973). Water temperature under the ice remains very close to the freezing point which decreases with increasing salinity through the winter months (Newbury 1983).

Kotzebue Sound, the 1984 control area, averages 13 to 16 m in depth with a sand and gravel bottom. Water temperature under the ice was measured at -2°C. The Sound typically is covered with annual ice from November to July (Barry 1979), and in April we found the ice to average 1.5 m in thickness. Between freeze-up and break-up, the ice is very stable since its enclosure in the Sound mostly protects it from the force of the drifting pack. Except for narrow (1 to 3 km) bands of flat ice along the shoreline, the ice in most of the Sound was deformed by ridges and hummocks, most of which were 1 to 2 m in height with some reaching 9 m in height. Snow accumulation was extremely low in 1984 and seldom reached 20 cm except in the southern part of the Sound. There, consistent westerly winds resulted in drifts of accumulated snow on the east and west sides of ice deformities. The northern part of the Sound, however, was subjected to winds from various directions, resulting in few snow drifts deeper than a few centimeters. Telemetric studies of ringed seals took place in the vicinity of Ninemile Point in the southern part of the Sound (Figure 3).

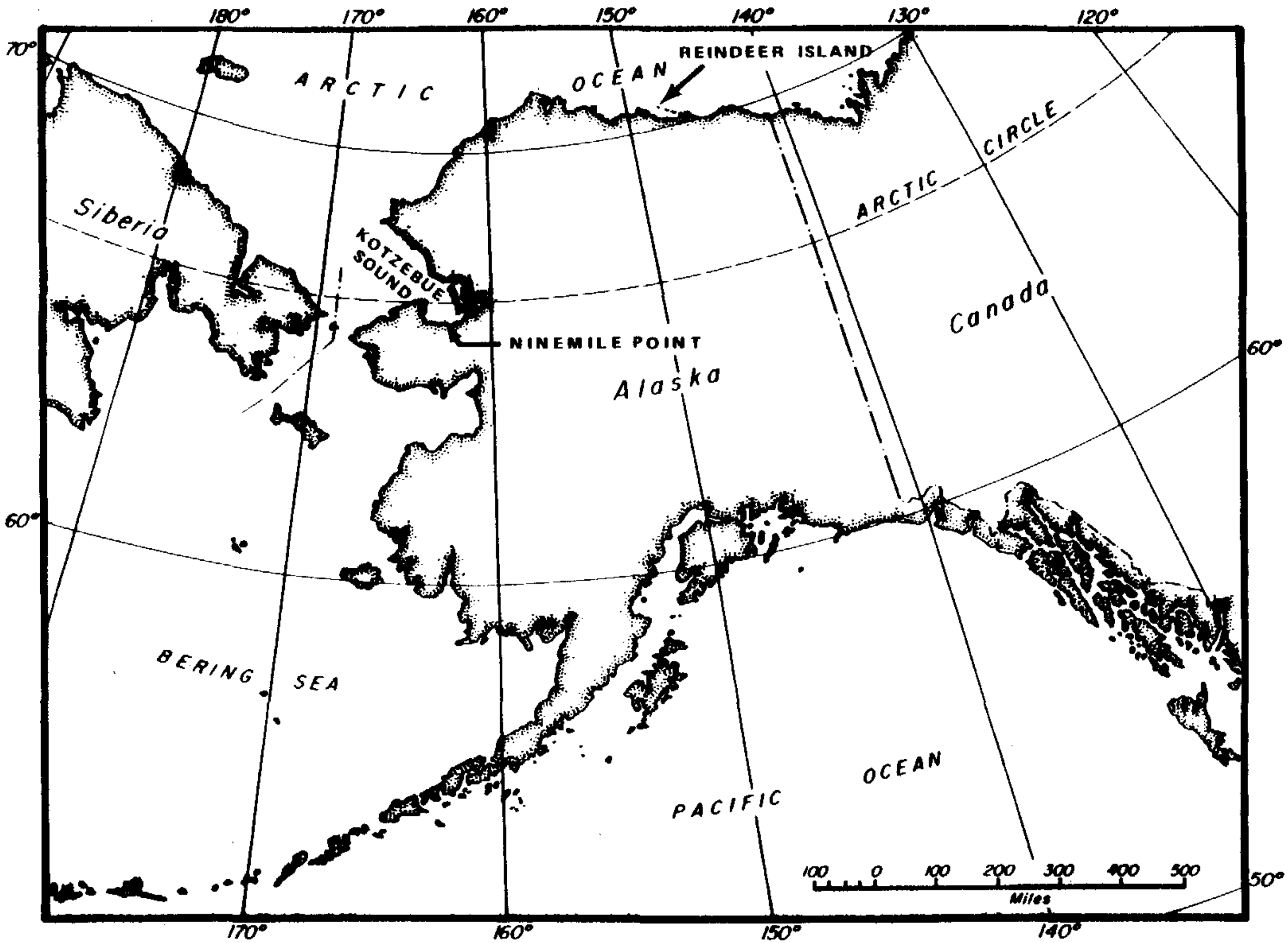

Figure 1. Locations of study areas; Reindeer Island (1982 & 1983) and Ninemile Point, Kotzebue Sound (1984).

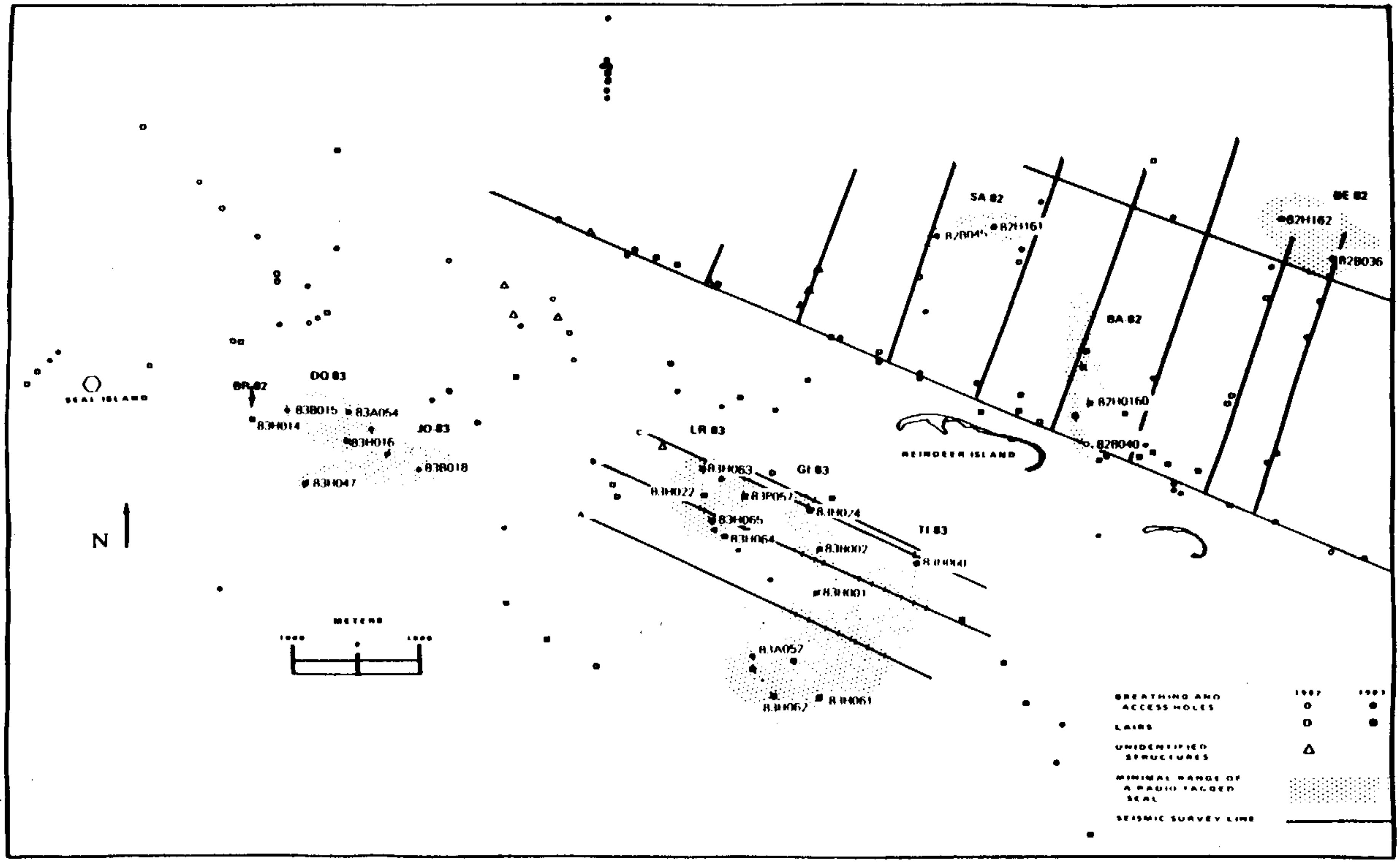

Figure 2. Reindeer Island study area showing locations of seal structures found by trained dogs and seismic survey lines vibrated in 1982 (north of island) and 1983 (south of island).

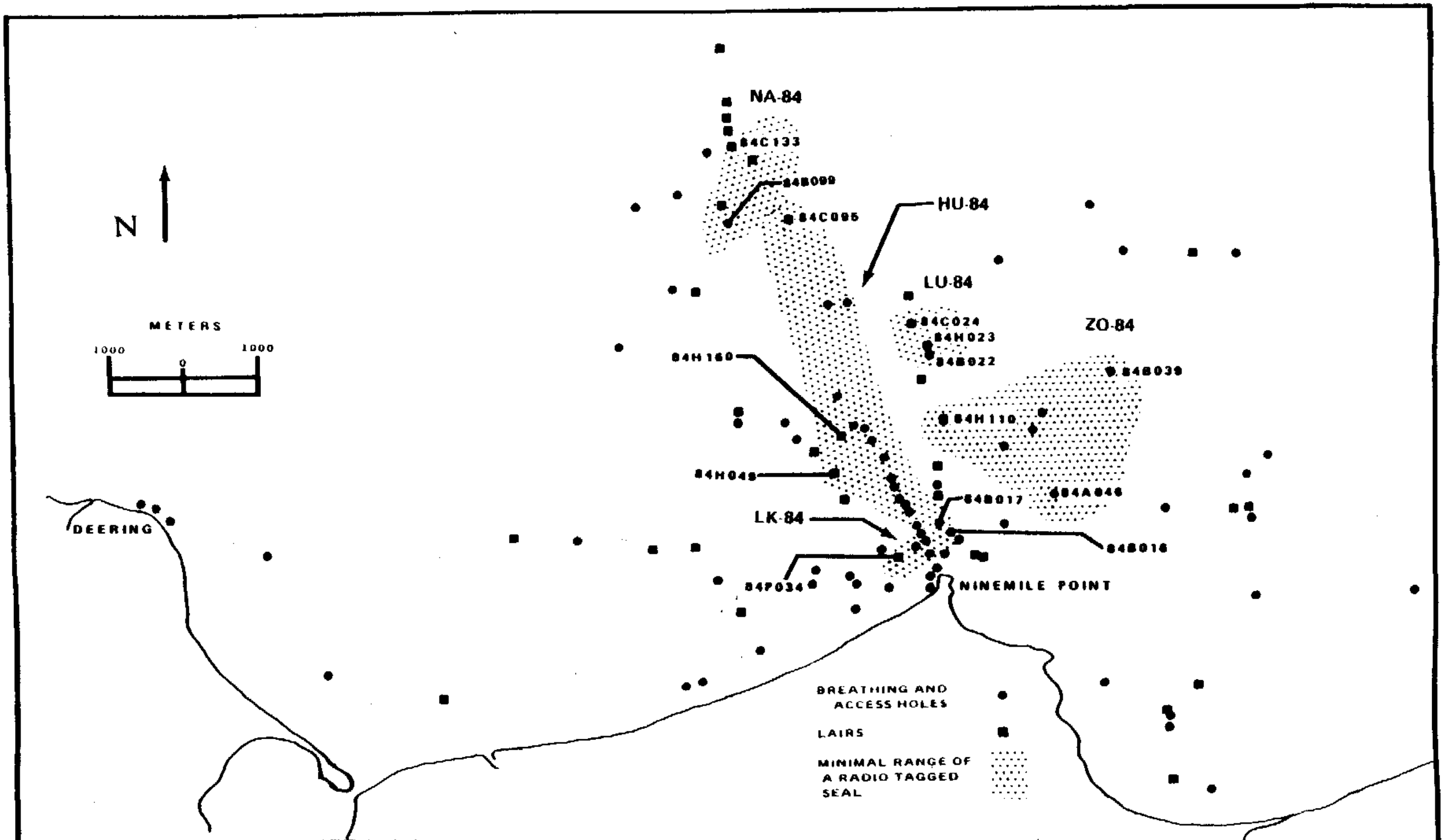

Figure 3. Ninemile Point, Kotzebue Sound study area showing locations of seal structures found by trained dogs in 1984.

METHODS

Subnivean structures (breathing holes and lairs) were located in the vicinity of camps established for around-the-clock monitoring of radio transmitters. Three camps were employed in 1982 (Figure 2): one on the ice approximately 1.2 km northeast of Reindeer Island (20 - 29 April), the second on the ice approximately 3.7 km north of that island (30 April - 22 May), and the third on Reindeer Island itself (23 - 29 May). Two monitoring camps were employed concurrently in 1983 (Figure 2): one on Reindeer Island (20 March - 6 June) and the other on Seal Island (70°29.5'N, 148°41.6'W), which is a man-made gravel island (14 April - 30 May). In Kotzebue Sound, one camp on Ninemile Point (66°04.0'N, 162°27.5'W) was utilized from 2 March - 16 May 1984 (Figure 3). All camps, with the exception of Seal Island, utilized 5 by 5 m portable huts fitted with oil heaters. At Seal Island, we monitored from an oil-drilling camp operated by Shell Western E & P, Inc.

Field studies consisted of (1) locating and mapping subnivean seal structures, (2) radio tagging and monitoring the haul-out behavior of seals, (3) monitoring the internal temperature of lairs, (4) testing the reactions of tagged seals to seismic exploration and other noise disturbances, and (5) monitoring the number of radio-tagged seals hauled out during visual aerial surveys in the early basking season.

Locating and Mapping Seal Structures

In 1982, the selection of areas searched for subnivean structures was dictated mainly by the distribution of seismic survey lines (Burns and Kelly 1982). In the next two years, we selected areas on the basis of ice and snow conditions that appeared most favorable for subnivean lairs.

A series of snow machine trails, ranging from 1.6 to 12.0 km in length, were established in each area to be searched. Subnivean structures were located on or near the trails by a trained Labrador retriever. The retriever was directed to run ahead of a snow machine along these trails. When the dog detected seal odor, he/she would follow the scent to its source and indicate the location of the structure by digging in the snow above it. Whenever possible, the dog was run perpendicular to the wind direction to maximize the area of detection.

We probed each site with aluminum rods (1 cm diameter) and, in most instances, uncovered a part of the structure to examine and measure it. Structures that we excavated were carefully re-covered. Structures were classified as either:

(1) **breathing holes**, holes maintained in the ice by seals for obtaining air but not large enough to be used for emergence from the water.

(2) **basking holes**, holes through which seals emerged from the water but not within a lair.

(3) **access holes**, holes through which seals emerged from the water into lairs.

(4) **resting lairs**, single-chambered cavities excavated in the snow above a hole in the ice.

(5) **complex lairs**, multi-chambered cavities excavated in the snow above a hole in the ice.

(6) **pupping lairs**, lairs in which was found positive evidence of a pup's presence. Evidence included the actual presence of a live or dead pup, after-birth and blood at a birth site, lanugo hair, and "pup tunnels" (tunnels too small to accommodate seals larger than pups).

(7) **unidentified structures**, breathing holes or lairs not identified to specific type.

The location of each seal structure was mapped by triangulation using bearings to at least two landmarks of precisely known location. Each structure was assigned an identification number that was recorded with the date and time of discovery. Measurements of each structure included snow depth, percentage deformation of the ice within a 200 m radius, and the diameter of the hole maintained by the seal. At lairs, the length, width and depth of each chamber were measured as well. The height of ice deformities that produced the snow drift and the compass orientation of the drift also were recorded. Evidence of tigak odor, pupping, and/or signs of arctic foxes or polar bears was noted. The condition of the hole in each structure was indicative of the recency of its use, since the ice must frequently be abraded from the hole to prevent its freezing over. Generally, a hole will freeze over within one day if unattended. Not infrequently, lair access holes were found partially frozen, indicating that the seals were using them merely as breathing holes. The status of each structure was recorded as: (1) **open**, if it was maintained by a seal to maximal diameter; (2) **partially frozen**, if it was frozen such that less than the maximal diameter was open; (3) **frozen**, if the entire hole was refrozen; (4) **obstructed**, if the lair had an open or partially frozen hole but access to the lair was obstructed, for example by a collapsing ceiling. Each time a structure was examined, the nature and extent of examination were noted.

The number of subnivean structures per unit area were calculated for the areas most intensively searched in 1983 and 1984, assuming that all structures were located. Although those areas were searched repeatedly and in a variety of wind conditions, the resulting estimates of density can only be considered minima.

Radio Tagging and Monitoring

Seals were snared at breathing holes, weighed, and their minimal age determined from counts of claw annuli. Alternating light and dark bands on the claws are laid down annually, and counting those bands provides an indication of age up to about the tenth year (McLaren 1958). After that, wear at the claw tip generally removes the earliest annuli. One or two of the most proximal annuli are covered by soft tissue and not visible in live seals with intact claws. We recorded ages as X+, where "X" is the number of annuli visible, and "+" indicates that the seal is older than "X" by at least one year.

The transmitters were glued (fast curing epoxy) to the pelage of the dorsum in a manner similar to that described by Fedak *et al.* (1983). We chose an attachment site on the dorsum midway between the tail and the point of maximal girth, so the transmitter would not interfere with the seals' passage through holes in the ice. Also, because that area on the back is the last to shed hair in the annual molt (Fay *et al.* 1983; pers. obs.), the transmitter could be expected to stay attached until late June.

The transmitters were Model L2B5 manufactured by Telonics Inc., Mesa, Arizona. Each transmitter weighed approximately 100 g with dimensions of 50 by 35 by 25 mm. Transmitter frequencies were between 164.000 and 165.999 MHz, with pulse widths of 15 to 18 milli-sec and pulse rates of 75/min. After each transmitter was glued firmly in place, the seal was released at the breathing hole at which it had been captured.

The receiving system in 1982 was a Telonics TR-2 receiver, TS-1 scanner, two-element Yagi antenna (4 dBd gain); in 1983 and 1984, five-element antennas (9 dBd gain) were used. Each site was equipped with two antennas, one in the horizontal and one in the vertical plane, mounted on rotating masts, 7.25 m above the ice.

The frequency of each deployed transmitter was monitored half-hourly in 1982 and hourly in 1983 and 1984. At each monitoring, the antennas were rotated through 360 degrees. Signals were receivable only when the transmitters were above the ice surface, thus indicating that the seals were out of the water. Signal reception varied with orientation of the transmitting and receiving antennas and with local ice deformities. Reception of the signals ranged from 3 to greater than 8 km Whenever feasible, signals were "ground-truthed" to determine the location of lairs and basking sites. Ground-truthing was accomplished by skiing or walking around the signal source while monitoring the signal via a hand-held directional antenna. Generally, we were able to ski or walk within 200 m of an occupied lair without alarming the seal and causing it to dive from the lair.

In addition to the hourly monitoring, 458 hours of continuous monitoring were accomplished with a Telonics TDP-2 digital processor and a strip chart recorder in 1983. Up to five frequencies were monitored simultaneously, resulting in over 1,000 "seal hours" of continuous monitoring.

For the investigation of diel haul-out patterns, local times were converted to "sun time," in which 1200 hours is defined as the time when the sun is at its greatest angle of inception (Stirling *et al.* 1982).

The seal-borne transmitters were monitored also during seven aerial surveys of basking ringed seals, between 29 May and 4 June 1982. Those surveys were flown in a Bell 204 helicopter at altitudes of 150 to 1100 m. Seal-borne transmitters were monitored also between 24 March and 13 May 1983 from altitudes of 300 to 1200 m during 22 helicopter flights. All surveys were conducted between 1000 and 1700 hours (local time), to coincide with periods of maximal numbers of seals on the ice (Burns and Harbo 1972; Smith 1973b). Most of the aerial monitoring was done on flights between Deadhorse, Reindeer Island, and Seal Island. Four flights (11 April, 4, 5, and 6 May 1983) were designed specifically to survey for haul-out sites outside of the range of the monitoring camps. Those surveys were over the shore-fast ice from Pingok Island (70°39.5'N, 149°30.0'W) to Narwhal Island (70°24.0'N, 147°30.0'W). The Seal Island camp was established when a lair of one of the radio-tagged seals was located in this way within reception range of that island but outside the range of Reindeer Island. In 1984, we monitored the seal-borne transmitters from the air whenever aircraft support was available. Aerial surveys of Kotzebue Sound south of Cape Blossom were flown on 21 and 29 March, 6 April, and 14, 15, 16, and 17 May. The aircraft used for those surveys were a Bell 204 helicopter, a Cessna 185, and a Cessna Super Cub. Survey altitudes generally were 900 m with portions of some as low as 125 m. All aircraft were fitted with a pair of Yagi antennas, one on each side.

Monitoring Lair Temperatures

Air temperature within lairs and ambient temperature were monitored with Telonics L2B5 transmitters fitted with thermistors. Temperatures were coded as pulse period (time between pulses) which was measured on a digital processor (Telonics, TDP-2). Accuracy was ±0.5°C.

The temperature sensor (50 by 35 mm) of each transmitting thermistor was inserted through a hole in the roof of the lair. The transmitter was suspended such that it protruded less than 10 mm below the inner surface of the lair, at the point of maximal height of the ceiling. The insertion hole was then sealed with snow and filled to the original roof thickness.

Ambient air temperature was measured in 1983 via a transmitting thermistor mounted 1 m above the lair. In 1984, ambient air temperature was measured via a telethermometer (Yellow Springs Instruments, 42SC), the sensor of which was mounted 1 m above the snow near the monitoring camp. Wind speeds were measured by hand-held anometer, 2 m above the snow at the camp.

Temperatures were monitored at 1- to 2-hour intervals in 13 lairs for periods ranging from 1 to 8 weeks. When removing the thermistors, a thorough examination was made of the lairs to determine their status and the nature and extent of any recent seal activity.

Reactions of Seals to Noise Disturbances

A simulated seismic survey was conducted on the south side of Reindeer Island in 1983 in order to test the direct effects on the radio-tagged seals. Approximately 20 km of "shot-line" were surveyed by TRACOR and NOAA personnel on snow machine and on foot on 20 April 1983 (Figure 2).

The seismic survey involved a convoy of a drill truck, a bulldozer, the vibrator truck (Vibroseis), and a fuel truck. The drill truck carried a power auger which bored holes through the ice, generally every 67 m along the survey lines, to test the ice thickness. The bulldozer, a D6 Caterpillar, leveled ice along the survey lines. Every 67 m, the Vibroseis vibrated the ice ten times in 16 second sweeps from 10 to 70 Hz. The fuel truck followed at the end of the convoy. Underwater sounds, airborne sounds, and vertical and horizontal vibrations produced by the convoy were measured by TRACOR at an abandoned lair site, a few meters north of line D (Figure 2).

Lines A and B were vibrated on 21 April, lines C and D were vibrated on 22 April (Figure 2). Line A was vibrated a second time on 27 April. We attempted to monitor the frequencies of the radio-tagged seals throughout the seismic surveys but were unable to do so during much of the period due to radio interference from TRACOR's transmitting equipment.

Reactions of seals to human-made noises from other than seismic equipment were recorded whenever possible. While locating lair sites utilized by radio-tagged seals and in the course of normal field activities, we recorded the responses of radio-tagged seals to the sounds of various human activities. When people and/or equipment approached lairs containing radio-tagged seals, the closest point of approach and the seal's response (departed or remained in lair) were noted.

RESULTS

Locating and Mapping Seal Structures

Clyde, the Labrador retriever trained in 1981, located most of the structures (breathing holes and lairs) in our 1982 effort. In locations that he indicated the presence of seal odor, we almost always were able to verify that a seal structure or odor was present. In optimal scenting conditions, he located seal structures from as far as 1,500 m.

Most searches in 1982 were conducted in the vicinity of Reindeer Island (Figure 2). From approximately 295 km of survey lines (including some repeats of the same lines), the dog located 157 seal structures, an average of 0.53 seal structures per kilometer searched. Search conditions varied widely, hence the effective transect width along each search line also varied and was not readily determined. The number of structures/linear kilometer searched thus is not convertible to structures per square kilometer but is only a crude index for comparative purposes. Of the 157 structures located, 72 were breathing holes (including 2 that were basking holes open to the surface when found), 73 were lairs, and 12 were not identified by type (Table 1).

Most of the seal structures investigated in 1983 and 1984 were located by Lil, a female Labrador retriever. In locations that she indicated the presence of seal odor, we consistently found seal structures. Under optimal scenting conditions, she detected seal structures from as far as 3,500 meters.

Table 1. Percentages of ringed seal breathing holes and lairs found by trained dogs.

Structure type	Beaufort Sea 1982 %	Beaufort Sea 1983 %	Kotzebue Sound 1984 %
Breathing holes	50.0	35.0	69.0
Lairs	50.0	65.0	31.0
Pupping lairs[1]	12.3	5.4	8.2
Sample size	145	57	157

[1] Percentage of total number of lairs showing positive evidence of a pup's presence.

Table 2. Estimated densities of subnivean seal structures in two areas of repeated search efforts.

	Beaufort Sea (1983)	Southern Kotzebue Sound (1984)
Area of repeated searches (km^2)	42	27
Breathing holes/km^2	0.21	1.74
Lairs/km^2	0.60	0.74
Total structures/km^2	0.81	2.48

In 1983, approximately 81 km of survey lines were searched (some repeatedly) within 13 km of Reindeer Island (Figure 2). Twenty breathing holes, including 5 basking holes, and 37 lairs were located (Table 1). The average number of structures per linear kilometer searched was 0.70.

In 1984, a total of 173 km of trails were searched in three areas of Kotzebue Sound. Overall, those searches yielded 157 structures or 0.91/km (Table 1). Approximately 25 of the 173 km were searched near the shore of the Choris Peninsula, where only 9 structures (0.36/km) were located. In the south-central part of the Sound, approximately 84 km of line were searched (a few repeatedly) and 115 structures (1.36/km) were located. About 64 km of trails were searched in northern Kotzebue Sound, within 30 km to the west and southwest of Cape Blossom, and these yielded 33 structures (0.51/km).

The number of breathing holes and lairs per square kilometer was estimated for areas where search efforts were most intensive in 1983 and 1984 (Table 2). We believe that virtually all seal holes were located in these areas which were searched two or more times by the same dog, under optimal scenting conditions.

Many of the breathing holes (13/31) located in northern Kotzebue Sound between 18 and 21 March 1984 were either open basking holes or showed evidence of having recently been used as basking holes. In the southern part of the Sound, only 6 of 77 breathing holes were open basking holes or showed evidence of recent use as basking holes when found. Two of those, as with the basking holes in the northern Sound, were located during an unusually warm spell in the second week of March, when air temperatures varied from -1.5 to -15.0°C. Basking holes were not found after that time until air temperatures consistently remained above -10°C (starting on 7 May).

Only two of the structures located by us in northern Kotzebue Sound between 18 and 21 March were ringed seal lairs. Another ringed seal lair and a bearded seal lair were located by J. J. Burns (*in litt.*) in the same vicinity (66°41.1'N, 162°55.9'W) on 29 March. The bearded seal lair and one of the ringed seal lairs consisted of natural cavities in ice piles, rather than excavations in snow drifts.

The relatively low ratio of lairs to breathing holes in Kotzebue Sound (Table 1) corresponded to an extremely low accumulation of snow, especially pronounced in the northern portion (Table 3). Snow depths at breathing holes in the northern Sound were significantly lower than in the southern Sound ($t_s = 1.76$, $p < 0.05$). The one active ringed seal lair we located in northern Kotzebue Sound was excavated in a snow drift 38 cm deep, barely deeper than the minimal depth of lairs located in southern Kotzebue Sound. Snow depths in southern Kotzebue Sound were significantly lower than in the Beaufort Sea at both breathing holes ($t_s = 3.17$, $p < 0.0025$) and resting and complex lairs ($t_s = 5.03$, $p < 0.0005$). Only at pupping lairs were the snow depths equivalent for both study areas ($t_s = 0.11$).

Lairs occurred disproportionately more often in snow drifts on the leeward sides (relative to the prevailing wind direction) of ice deformities than on the windward side. Generally, both sides of deformities accumulate similar snow depths. In the Beaufort Sea study area, drifts predominately were oriented northeast and southwest as the result of prevailing northeasterly winds. In a sample of 30 lairs investigated there in 1983, 28 were in drifts on the southwest side and 2 on the northeast side of deformities ($X^2 = 11.87$, $p < 0.005$). In southern Kotzebue Sound, the winds were very consistently out of the west and virtually all snow drifts trended to the east or west. Of 33 lairs in southern Kotzebue Sound, 28 were on the east side while 5 were on the west side of deformities ($X^2 = 16.04$, $p < 0.005$).

The relative proportions of open, frozen, partially frozen, and obstructed seal holes for each year of the study are given in Table 4. There were no significant differences in the

Table 3. Snow depths (mm) at three types of seal structures.

Structure type		Beaufort Sea 1982	Beaufort Sea 1983	Kotzebue Sound North 1984	Kotzebue Sound South 1984
Breathing holes	$\overline{X}$	378	379	169	243
	S.D.	217	236	103	209
	Min.	0	50	20	0
	Max.	1160	700	320	1100
	N	66	7	29	41
Resting & Complex lairs	$\overline{X}$	782	787	210	554
	S.D.	256	214	170	135
	Min.	290	450	40[1]	300
	Max.	1500	1300	380	850
	N	66	28	2	37
Pupping lairs	$\overline{X}$	962	610	--	945
	S.D.	171	--	--	386
	Min.	660	--	--	650
	Max.	1190	--	--	1600
	N	9	1	0	4

[1] Lair in ice cavity.

Table 4. Percentages of ringed seal breathing holes and lair access holes that were fully open, partially frozen or obstructed, and completely frozen when found.

	Beaufort Sea		Kotzebue Sound
Condition of hole	1982	1983	1984
Open	81	77	88
Partially frozen or obstructed	7	21	7
Completely frozen	12	2	5
Sample size	145	57	157

proportions of open structures between 1982 and 1983 in the Beaufort Sea, but those proportions were significantly lower than in the 1984 sample from Kotzebue Sound ($Z = 2.05$, $p < 0.05$), indicating higher rates of abandonment of structures by seals in the Beaufort Sea study area.

We saw no evidence of polar bear (*Ursus maritimus*) predation on ringed seals in our study areas. Arctic foxes (*Alopex lagopus*) were not present in Kotzebue Sound but became increasingly common in the Beaufort Sea study area after the onset of the seal pupping season. Arctic foxes entered 14 of 73 lairs examined in 1982 and one of 37 lairs in 1983. Ringed seal pups were killed by arctic foxes in three of nine pupping lairs in 1982 but at neither of two pupping lairs in 1983. Evidence of red foxes (*Vulpes vulpes*) and wolves (*Canis lupus*) was seen on the ice in Kotzebue Sound but with no signs of attempts to prey upon ringed seals.

Radio Tagging

Radio tags were placed on 9 ringed seals in the Beaufort Sea and on 5 seals in Kotzebue Sound (Table 5). Capture sites and haul-out sites located by radio tracking are shown in Figures 2 and 3. Two females, BA-82 and BE-82, and possibly one male, HU-84, were sexually immature; all others were sexually mature. Based on age, size, and haul-out patterns, we surmised that SA-82 and LR-83 were nursing pups before and after they were tagged. That LR-83 was nursing a pup was confirmed by tracking her signal to a birth lair. The age and weight of LK-84 and LU-84 suggested that they were both pregnant when captured in early March. LK-84 was tracked to a pupping lair in which long and regular haul-out bouts suggested that she was nursing a pup. Conversely, the haul-out patterns of LU-84 indicated that she may have abandoned her pup before weaning.

Haul-out site fidelity

Most of the radio-tagged seals were found to occupy more than one lair. The known number of lairs per seal ranged from 1 to 4 (mean = 2.85, S.D. = 2.51) and was based on variable numbers of attempts to ground-truth each seal's haul-out locations. Those cases in which only one lair per seal was located corresponded to relatively few attempts to ground-truth the haul-out locations. All structures known to be maintained by an individual seal were within 4.5 km of one another.

Only one (BA-82) of the three seals radio-tagged in 1982 was known to have used more than one lair. During 6 out of 45 recorded haul-out bouts between 19 and 24 April, she was found in lair 82H160, 650 m north of her capture site, 82B040 (Figure 2). On the seventh attempt (5 May) to locate her, the signal seemed to come from a position more than two kilometers to the northwest of lair 82H160, but she left that position before it could be positively located.

Four of SA-82's 26 recorded haul-out bouts were ground-truthed successfully between 30 April and 28 May. She was in lair 82H161, 900 m northeast of her capture site (82B045), each time (Figure 2). Thirty-six haul-out bouts were recorded from BE-82, but we ground-truthed the signal only once, on 7 May, when she was located in lair 82H162, 1000 m northwest of 82B036, her capture site (Figure 2).

Radio signals from each seal tagged in 1982 were consistent in strength and direction during April and the first weeks of May. In the last week of May, however, signal reception from two of the seal transmitters (SA-82 and BE-82) became erratic at Reindeer Island. On 28 May 1982, strong signals from those transmitters were detected from a helicoptor (457 m altitude) but not from the monitoring camp on Reindeer Island. The locations of SA-82 and

Table 5. Ringed seals radio-tagged in the Beaufort Sea (1982 & 1983) and Kotzebue Sound (1984).

Seal no.	Sex	Age (yrs) indicated by claws	Weight (kg)	Date tagged	First signal received	Last signal received	Known minimal no. of lairs
BA-82	F	2	~46	4/17/82	4/19/82	6/04/82	2
SA-82	F	5	~68	4/22/82	4/23/82	6/03/82	1
BE-82	F	1	~40	4/25/82	4/26/82	6/04/82	1
TI-83	M	8	~135	3/22/83	4/09/83	6/02/83	3
GI-83	M	8	~110	3/23/83	3/24/83	4/26/83	2
DQ-83	M	8	68	3/30/83	4/11/83	5/19/83	2
BR-83	M	7	68	3/31/83	--	--	--
JO-83	M	8	73	3/31/83	4/23/83	5/20/83	1
LR-83	F	7	60	5/08/83	5/09/83	6/04/83	4
LK-84	F	5	77	3/04/84	3/07/84	5/11/84	3
LU-84	F	5	73	3/04/84	3/07/84	4/24/84	2
HU-84	M	5	68	3/05/84	3/06/84	4/19/84	3
ZO-84	M	7	72	3/13/84	3/15/84	5/14/84	1
NA-84	M	7	~77	3/26/84	3/27/84	5/15/84	2

BE-82 at that time were not determined precisely, but apparently, based on the changes in the received signal strength, both seals were hauled out in locations (lairs or basking sites) other than the ones previously detected. The decreased strength of signals received at Reindeer Island may have been due to these new haul-out locations being further away from the camp or in areas of rougher ice.

Radio signals were received from five of the six seals tagged in 1983. No signals were received from BR-83, the only seal not captured at a breathing hole or a partially frozen access hole. His capture site (83H014) was a hole above which an incipient lair, not yet large enough to hold a seal, was being excavated. At least four of the five seals from which signals were received, utilized more than one lair (Figure 2).

TI-83, a very large (approximately 135 kg) male, smelling strongly of rut, was captured in the partially frozen access hole of a lair (83H001). We were unable to determine whether the lair had once been occupied by TI-83 or he only used it as a breathing hole. The access hole already was partially frozen when located by the dogs on 17 March.

Thirty-three haul-out bouts by TI-83 were monitored and his haul-out sites were ground-truthed 16 times between 16 April and 31 May. In that time, he used three lairs (83H060, 83H061, 83H062) and one basking site next to an uncovered basking hole, 83A052 (Figure 2). The greatest distance between any two of those haul-out sites (83H060 and 83H062) was approximately 3 km; the closest two (83H062 and 83H061) were separated by about 1 km. The hole in which TI-83 was captured (83H001) was approximately midway between his northernmost and southernmost lairs.

TI-83 was located in 83H060 during seven ground-truthings between 19 April and 20 May and in 83H061 during six ground-truthings between 16 April and 23 May, suggesting that he used those two lairs about equally. He was first located in 83H062 on 26 May and again on 29 May. On 31 May he was seen basking on the ice in the vicinity of 83H062, next to a basking hole (83A052) in a refrozen lead.

GI-83, also an odoriferous male, was captured and tagged at a breathing hole (83B002) and subsequently monitored during 25 haul-out bouts. In at least five of seven attempts to ground-truth his signal between 26 March and 24 April, he was located in lair 83H024, approximately 600 m from his capture site (Figure 2). Results of an attempt to locate him on 24 March were ambiguous, but indicated that he was in either that same lair or another 600 m to the northwest. On 23 April, we received a weak signal from him from southwest of lair 83H024, but its source was not further defined. The last signal from GI-83 was received on 26 April from an undetermined location.

Lair 83H024 was opened and examined on 17 May. The single chambered lair was excavated in a 55-65 cm deep snow drift on the southwestern side of a 0.55 to 1.0 m high ice hummock. The lair measured 2.04 by 1.05 m, with a maximal depth of 47 cm. The access hole measured 53 by 37 cm and was located in a refrozen lead. The lair showed signs of recent occupation by a seal.

A third adult male, DQ-83, was captured at breathing hole 83B015 (Figure 2) on 30 March. He too had the tigak odor but noticably less strongly than TI-83 or GI-83. We monitored 27 haul-out bouts by DQ-83 and located his haul-out site 11 times between 11 April and 18 May. On 11 April, DQ-83 was located in lair 83H016, a lair that had been located and investigated on 29 March. The lair was situated in an 85 cm deep snow drift on the southwestern side of a 1.5 m tall ice hummock. The single chamber measured 1.62 by 0.77 m with a maximal depth of 32 cm. The access hole was situated in the northeastern end of the chamber and was 57 cm in diameter.

On 6 May, a signal from DQ-83 was traced to a lair 100-200 m north of 83H016, but the exact location of this northern lair was not determined. On 7 and 8 May, this seal was seen lying next to a basking hole (83A054) 500 m north of 83H016. He was again in lair 83H016 on 12 May. That location was determined not by ground-truthing but by the exact match between the times at which his signal was received and marked temperature changes were recorded by a thermistor in lair 83H016 (see Lair Temperatures). On 13, 14, and 15 May, DQ-83 was seen lying at basking hole 83A054. On 16 May, his haul-out signal again coincided exactly with a marked temperature increase and subsequent decrease within lair 83H016, indicating that he hauled out there. He again lay at basking hole 83A054 on 17 and 18 May. Poor visibility prevented our locating him on 19 May, the last day his radio signal was received. A seal, possibly DQ-83 without his transmitter, was seen at basking hole 83A054 on 21, 26, and 27 May.

Temperature changes characteristic of a haul-out bout only occurred in lair 83H016 when signals simultaneously were received from DQ-83, suggesting that no other seal used the site during the study period.

JO-83, an adult male also with a strong tigak odor, was captured and tagged at breathing hole 83B018 and monitored during 12 subsequent haul-out bouts. On two attempts to locate his haul-out site, on 7 and 18 May, he occupied lair 83H047 (Figure 2). That lair was opened on 30 May and found to be 1.92 by 0.86 m with the access hole near the center of the long axis. Access to one side of the lair was blocked, however, by a wall of splash ice that extended from floor to ceiling along half of the perimeter of the access hole, which measured 38 cm in diameter. The lair thus was divided into a 0.85 m long accessible chamber and a 1.07 m long inaccessible chamber. The maximal depths of the two chambers were 43 and 52 cm, respectively. The lair was in a 0.77 m deep snow drift on the southwestern side of a 1.0 m tall ice hummock.

An adult female seal, LR-83, was captured and radio-tagged on 8 May at obstructed lair 83H022 and subsequently monitored during 20 haul-out bouts. Dilation and reddening of the vulva suggested that she was at or near estrus. In five ground-truthing sessions, we tracked her to four different lairs, all within a 750 m radius of her capture site (Figure 2). On 9 May, she was located in lair 83H063, approximately 370 m northeast of 83H022. She was found in lair 83H064, approximately 700 m southwest of 83H022, on 23 May. Lair 83H065, approximately 400 m southeast of 83H022, was her haul-out site on 27 and 28 May. She was located about 600 m east of 83H022 on 4 June, when we uncovered a melting complex lair (83P057), one chamber of which had a blood-stained floor, indicative of a birth site. Two chambers, 3.83 m and 1.80 m in length, formed a right angle with the access hole at the intersection. The lair was situated on the southwest side of a 1.0 m high ice ridge. The snow drift measured 0.61 m deep, but much melting had already taken place, and the access hole was accomodating a rapid flow of melt water.

Four of the five seals radio-tagged in Kotzebue Sound in 1984 were tracked to more than one lair. LK-84, a female caring for a pup, was ground-truthed 13 times during 69 recorded haul-out bouts. Her signal was tracked 11 times to 84P034, a small, single-chambered lair that had a frozen access hole when first located by the dogs on 9 March. That lair was 900 m southwest of the hole (84B016) in which she had been captured. She was tracked to lair 84P034 on 25, 26, 27, and 31 March and on 1, 2, 3, 4, 8, 10, and 11 April. An attempt to locate a weak and erratic signal from her on 9 April indicated that she was hauled out in a different lair, but we could not locate the site, despite searching an area in excess of 65 km^2.

On 12 April, we opened her lair (84P034) a second time and found that its access hole was clear of ice, and that the lair had been expanded into two chambers, 2.01 m and 4.30 m long. We inserted a transmitting thermistor and a highly sensitive transmitting microphone into the lair. Neither instrument detected activity at the lair until 17 April, when splashing, scratching of ice, and seal vocalizations were transmitted via the microphone. Early on 18 April, similar sounds were heard from the lair, and later that day, a signal from LK-84 was traced to the immediate vicinity of that lair. Nonetheless, neither the thermistor nor the microphone indicated the presence of a seal in lair 84P034. Although LK-84 must have been in another lair within a few meters of 84P034, our attempts with a dog to locate that other lair were unsuccessful.

On 25 April, we again opened lair 84P034 and discovered that its entire depth (30 to 40 cm) had flooded with sea water. Only a small area at one end of a chamber, including a pup tunnel, was not submerged. The water had seeped up through a crack in the ice and submerged the lair chambers, apparently because the ice along the crack had subsided under the weight of the snow drift. That drift, on the east side of a 3.5 m high ice hummock, measured 0.85 m deep on 9 March, 1.20 m on 4 April, and 1.60 m on 25 April.

LU-84, also an adult female, was captured at 84B022 and monitored during 15 haul-out bouts between 7 March and 24 April 1984. She was successfully traced to lairs in seven of nine attempts. On 7 March she was traced to a large and complex lair (84C024), 450 m north of breathing hole 84B022 where she had been captured (Figure 3). She was traced to single-chambered lair 84H023 on 25, 26, and 31 March, as well as on 11, 16, and 18 April. Both lairs were in snow drifts on the eastern side of the same 1.0 to 1.5 m high ice ridge and were approximately 300 m apart. LU-84's transmitter signal was last received on 24 April, but a thermistor and microphone in lair 84H023 indicated that it was still utilized by her or some other seal(s) after that date. Sounds of a seal breathing, splashing, and scratching the ice (but apparently not hauling out) were heard from that lair from 27 April to 3 May, at which time the microphone was removed. Subsequently, the thermistor registered temperature changes indicative of haul-out bouts in that lair on 9 and 13 May. A thermistor in lair 84C024 from 8 March to 15 May, however, indicated no haul-out bouts.

Lair 84C024 was opened and examined on 8 and 20 March and on 15 May. The access hole was fully open each time and the lair appeared to be in continuing use except on the final visit when a low roof over the hole indicated that a seal had not hauled out recently. The lair consisted of three chambers, the longest of which exceeded 3.00 m. Its access hole was over 50 cm in diameter. Maximal snow depth over the lair was 65 cm and the snow roof generally measured 40 cm thick.

Lair 84H023 was examined four times. On 29 February, it was opened and found to have a partially frozen access hole. On 26 March, the access hole was fully open and measured 62 cm in diameter. The greatest length of the lair was 1.98 m; its depth was 55 cm and the roof thickness was 15 cm. At that time, a thermistor and microphone were placed in the lair. The access hole was slightly smaller in diameter when examined on 15 May, and a small build-up of ice around its rim confirmed that a seal had used it for a breathing hole but not recently for a haul-out.

HU-84, a small male without the tigak odor, was captured and tagged on 5 March and was monitored during 17 haul-out bouts between 6 March and 19 April. His haul-out site was located successfully six times between 8 March and 26 March. On 8 March he was found in a lair (84H160) approximately 1.75 km northwest of the breathing hole (84B017) at which he was captured (Figure 3). He hauled out in another lair (84H049), 500 m south of that first lair, on 10 March. His signal was traced to a large, complex lair (84C095), 4.5 km north-northwest of his capture site on 12, 17, 21, and 26 March. Furthermore, a transmitting thermistor placed in lair 84C095 on 22 March confirmed that each of HU-84's haul-out bouts recorded (by radio-transmitter) after that date were inside of that lair. Those haul-out bouts were recorded on 26 March, 1, 3, 7, 13-14, 14-15, and 18-19 April. The thermistor additionally indicated 6 haul-out bouts when no signals were received from HU-84; 24-25 March, 11, 23-24, 27-28 April, 30 April-1 May, and 4 May (Figures 32-39), indicating that at least one other seal occasionally occupied the same lair.

Two of HU-84's lairs were opened and examined. Lair 84H049 was in a 0.62 m deep snow drift on the west side of an ice hummock that was less than 1.0 m in height. On 14 March the access hole of that lair was fully open to 82 cm diameter and the lair was measured at 1.28 m long and 43 cm deep. The roof of the lair consisted of 7 cm of hard, metamorphosed snow. The access hole was partially frozen and, apparently, only used as a breathing hole through 24 April. The odor of a rutting male was detected at the hole on 23 and 24 April. On 25 April, the access hole was completely frozen, but it was fully open again on 11 May with signs of a recent haul-out. A small opening had been scratched through the roof from the inside.

Lair 84C095 (Figure 3) was first examined on 22 March. It consisted of two chambers at right angles to one another, 1.56 and 1.92 m in length. The smaller chamber was in a snow drift on the east side of a 1.5 m tall ice hummock, the larger one was in snow that had drifted under a 20 cm thick slab of ice. The maximal depth of the lair was 37 cm. The lair was examined again on 15 May and showed evidence of recent occupation, including large clumps of molted, adult hair and stratum corneum.

A rutting male, ZO-84, was captured and tagged on 13 March and monitored during 10 haul-out bouts from 15 March to 14 May. His haul-out site was located during 5 haul-out bouts between 3 and 18 April. On 3 and 9 April, he was located in a lair (84H110) approximately 2.3 km west-southwest of breathing hole 84B039, his capture site (Figure 3). That lair was not present in early March and, therefore, must have been excavated in late March or the first days of April. On 15, 17, and 18 April, he was seen lying next to an open basking hole (84A046), approximately 1.8 km south-southwest of his capture site. On 27 April, he hauled out at an undetermined site but not at 84A046 where another seal was basking. There were no further signals received from him at the monitoring camp, but a haul-out bout beyond the range of the camp was detected from a helicopter (915 m altitude) on 14 May. The actual location of that haul-out was not determined. A seal other than ZO-84 was seen basking next to the hole where ZO-84 had been captured (84B039) on 12, 13, 15, and 16 May.

Lair 84H110 was situated in a snow drift on the east side of a 0.50 m high ice ridge and approximately 80 m west of another resting lair (Figure 3). On 4 April, the snow drift was 45 cm deep, the lair was 42 cm deep, leaving a roof thickness of only 3 cm. The access hole was fully open. When the lair was next examined on 26 April, both ends of it had been expanded, giving a total length of 1.73 m. The access hole remained fully open and measured 60 cm in diameter. The lair depth was 45 cm, and the snow drift had deepened to 56 cm, but much of the ceiling remained as thin as 15 mm. On 15 May, the access hole remained open, but the roof of the lair had collapsed to a few centimeters above the floor, indicating that the lair was no longer used as a haul-out site.

NA-84, a mature male with no detectable tigak odor, was captured and tagged on 26 March and monitored during 21 haul-out bouts. On 17 and 19 April, he was traced to a complex lair approximately 1.0 km north of his capture site (84B099). That lair (84C133) was opened on 23 April and again on 5 May, and both times the access hole was found to be partially frozen to a diameter too small for a seal to transit. Thus, a haul-out bout by NA-84 on 24 April probably was in some other lair. The last radio signal received from him was on 15 May, during a helicopter survey, but that signal was not detectable from the Ninemile Point camp. This suggests that NA-84 may have had yet another lair, out of range of the camp.

Lair 84C133 was complex and peculiar in having two access holes, one of which was frozen and the other partially frozen when we investigated it. The lair was located in snow filling a large crack in the ice and it consisted of two parallel chambers 1.22 m and 1.69 m long, each with its own access hole. The chambers appeared to have been excavated originally as separate lairs that were later joined by excavating a short tunnel between them. The maximal depths of the chambers were 32 and 35 cm, each with a snow roof thickness of 15 cm.

Structures (breathing holes, basking holes, and lairs) used by individual female seals generally were much closer together than were structures used by individual males. The distances between structures used by an individual female ranged from 125 to 1100 m, while distances between structures used by an individual male ranged from 450 to 4438 m. The mean distance between structures used by individuals was 638 m for females and 1738 m for males. The difference was highly significant ($t_s = 5.25$, $p < 0.0001$).

Frequency and duration of haul-out bouts

The radio-tagged seals were out of the water from 3.5 to 30.8% of the time (Table 6). Three seals began hauling out outside of lairs (basking) before we ceased monitoring. Each of those seals showed slight increases in the percentage of time hauled out after the onset of the basking period, but the differences were not significant ($p > 0.05$). Greater differences might have been observed if we had monitored haul-outs later in the basking period. The length of haul-out bouts varied from less than 1 to 20 hours, with a mean bout length of 5.4 hours (Table 7).

Periods when radio signals were not received from the tagged seals ranged from less than one hour to over 160 hours (mean = 18.9). The absence of signals indicated that the seals were either in the water or out of range of the monitoring camps. Monitoring from aircraft, we found no evidence of radio-tagged seals hauling out beyond radio range of the camp during the main study periods. Exceptions occurred during the last days of the study periods in 1982 and 1984 when some signals were detected beyond the range of the monitoring camps. Data from those periods were excluded for comparisons of "in-water periods." The lengths of those in-water periods for seals in the Beaufort Sea were very similar in 1982 and 1983; the in-water periods for seals in Kotzebue Sound, however, tended to be considerably longer (Table 8).

Sampling bias may account for some of the disparity among seals in percentages of time spent out of the water. In each of the three years of the study, the seals that were most frequently recorded as hauled-out (SA-82, GI-83, and LK-84) were those whose known lair sites were closest to the monitoring camps (Table 6). This suggested that the low percentages of out of water time recorded for some of the other seals may have been due to their occasional occupation of lairs beyond radio range of our camps. A slight negative correlation ($r = -0.30$) between percentage of time hauled out and distance to farthest known lair site, however, was not significantly different from $r = 0$.

Monthly increases in the percentage of time seals hauled out were observed in 11 out of 16 cases (Table 9). In many cases, the number of monitoring periods sampled was quite small and it was necessary to combine data to test the significance of monthly changes. Combining data from all seals (Table 9), the percentage of time hauled out more than doubled from March to June ($X^2 = 85.0$, $p < .005$). Deviations in that pattern were evident in the cases of SA-82, BE-82, GI-83, HU-84, and LK-84.

Based on large samples, HU-84 showed a decrease in the proportion of time out of water between March and April. Furthermore, the number of consecutive days on which he did not haul out increased from a mean of 0.43 in March to 2.00 in April ($t_s = 2.897$, $p < 0.05$). No signals were received from HU-84 after 19 April. As noted earlier, at least one other seal

Table 6. Percentages of monitoring periods in which radio-tagged ringed seals were out of the water and the distances from the monitoring camps to the farthest known lair of each seal.

Seal no.	Percentage time out of water[1]		Number of monitoring periods	Distance between camp & farthest known lair (km)
	Pre-basking	Basking		
BA-82	21.6	--	1104	3.0
SA-82	29.2	--	914	0.8
BE-82	20.7	--	917	4.0
TI-83	16.6	17.8	1499	4.5
GI-83	30.8	--	504	2.2
DQ-83	26.2	28.6	946	3.9
JO-83	9.7	--	958	3.6
LR-83	15.7	--	752	3.3
LK-84	19.9	--	1546	0.7
LU-84	8.7	--	1142	3.5
HU-84	17.9	--	1023	5.4
ZO-84	3.5	6.6	1026	2.2
NA-84	12.9	--	641	6.0

[1] Time out of water is shown for the "pre-basking" period when seals hauled out only in lairs and the "basking" period when seals hauled out in the open as well as in lairs. The basking period began on 31 May for TI-83, 7 May for DQ-83, and on 15 April for ZO-84.

Table 7. Duration of haul-out bouts of radio-tagged ringed seals.

	Length of haul-out bouts (hours)				
Seal no.	Mean	S.D.	Minimum	Maximum	N
BA-82	3.22	3.78	0.33	14.00	34
SA-82	9.70	5.99	0.50	18.50	12
BE-82	4.34	4.19	0.50	15.00	19
TI-83	4.87	3.21	0.25	12.00	25
GI-83	5.21	5.99	0.50	19.52	9
DQ-83	6.91	4.10	0.33	16.72	20
JO-83	4.03	2.91	0.50	7.83	11
LR-83	3.24	3.09	0.75	11.00	14
LK-84	4.12	4.15	0.50	17.00	68
LU-84	6.03	2.87	0.77	9.00	13
HU-84	10.24	4.69	2.50	20.00	16
ZO-84	4.61	3.11	1.32	11.00	9
NA-84	3.76	2.16	0.50	8.00	19

Table 8. Length of periods when radio-tagged ringed seals were believed to be in the water between haul-out bouts. Data from late spring, when some radio-tagged seals were known to haul-out beyond range of the camps, were excluded.

	Time in the water (hours)				
Seal no.	Mean	S.D.	Minimum	Maximum	N
BA-82	8.20	9.95	0.42	43.50	32
SA-82	18.14	13.28	2.50	39.00	10
BE-82	14.41	13.99	0.50	44.50	16
TI-83	8.51	9.16	0.50	36.00	22
GI-83	5.90	4.51	0.57	14.65	9
DQ-83	16.22	11.93	2.17	42.70	20
JO-83	22.38	21.76	1.92	71.42	9
LR-83	11.99	7.33	2.00	27.50	15
LK-84	13.69	25.98	0.65	156.50	70
LU-84	39.45	47.48	3.00	160.50	15
HU-84	32.85	34.54	3.83	123.33	16
ZO-84	30.00	26.48	1.50	81.00	8
NA-84	23.51	29.65	2.00	134.00	21

Table 9. Monthly percentages of monitoring periods when radio-tagged ringed seals were out of the water.

	March		April		May		June	
Seal	% Out	N	% Out	N	% Out	N	% Out	N
BA-82	--	--	16.5	200	22.7	904	--	--
SA-82	--	--	61.8	34	28.0	880	--	--
BE-82	--	--	61.3	31	19.3	715	--	--
TI-83	0	12	14.5	539	19.2	770	41.0	61
GI-83	75.0	20	28.3	495	--	--	--	--
DQ-83	--	--	26.3	297	27.2	649	--	--
JO-83	--	--	9.5	294	9.8	664	--	--
LR-83	--	--	--	--	15.9	573	20.8	130
LK-84	11.5	616	30.4	677	11.9	253	--	--
LU-84	8.3	617	9.1	525	--	--	--	--
HU-84	19.4	612	5.6	411	--	--	--	--
ZO-84	1.9	429	6.2	597	--	--	--	--
NA-84	11.8	119	13.2	522	--	--	--	--
Combined	11.5	2425	17.8	4622	20.4	5579	27.2	191

began hauling out in HU-84's primary lair (84C094) on 24 March and did so increasingly throughout April and into May.

LK-84 spent almost three times as much time hauled out in April than in March or May ($X^2 = 66.32$, $p < 0.005$). We believe that she was nursing a pup during late March and most of April and, as a consequence of that, spent almost one third of that period in a lair. She hauled out for part of every day from 24 March to 23 April, with the possible exceptions of 6 and 7 April when monitoring was incomplete due to strong winds (45 to 50 km/hour). She did not haul out on 24 or 25 April, and on the evening of 25 April, we found her primary lair (84P034) to be flooded and abandoned.

LU-84 also was believed to be pregnant when radio-tagged in early March. Like LK-84, she hauled out at least once every day, beginning on 24 March, but that ended abruptly after 31 March. In the first ten days of April, no signals were received from her transmitter, and from 11 April to 24 April, the date of her last recorded haul-out bout, she was recorded as out of the water on an average of every third day. If she was nursing a pup in late March, she must have lost or abandoned it early in April.

Two other females were believed to be nursing pups when they were radio-tagged in late April (SA-82) and early May (LR-83). SA-82 was recorded as out of the water more than twice as often in April than in May, but the number of monitoring periods sampled in April was small.

The overall trend of increase, from March to June, in time seals spent out of the water may be attributed in part to a tendency toward longer haul-out bouts (Table 10). Increases in haul-out bout lengths mostly were slight for individual seals, and none was statistically significant (t-tests). Conceivably, some of the apparent increase in duration of haul-outs might have been due to more frequent haul-outs, which should have been evident in decreased length of periods in the water between haul-out bouts. The high variances observed for the latter, however, do not indicate such an effect (Tables 8 and 11).

Haul-out behavior relative to the 24-hour cycle was investigated for periods of continuous monitoring (Table 12). Continuous monitoring was defined as listening for the seal's transmitter signal hourly or at least once every two hours throughout the 24-hour period. On average, the seals spent one-fourth or less of each 24-hour period hauled out. The lone exception was GI-83, whose daily mean (11.5 hours) was calculated from only 5 days of continuous monitoring within one week.

In 1984, sample sizes were sufficient to permit monthly comparisons of the amount of time that the seals spent out of the water within the 24-hour period. Only LK-84 showed significant monthly changes in that parameter. In April her mean time hauled out per 24-hour period was 7.06 hours versus 2.58 hours in March ($t_s = 3.356$, $p < 0.01$) and 1.89 hours in May ($t_s = 2.551$, $p < 0.05$).

In contrast to the three males, females LK-84 and LU-84, went through extended periods in which they hauled out for part of every day. For LK-84 that period extended from 24 March to 23 April and for LU-84 it was from 24 March to 31 March. We think that those were nursing periods. The mean haul-out time within the 24-hour cycle during those assumed nursing periods for both seals was significantly longer than during the periods before and after (Table 13).

Figures 4 through 16 show the percentage of monitoring periods per hour in which a radio signal was received from each seal during the 24 hour cycle. In essence, therefore, each figure shows the percentage of time per hour during which the seal was hauled out. Various periods from early March to early June were sampled, depending on the dates each seal was radio-tagged and when their last signals were received (Table 5). Overall, there was a trend toward

Table 10. Duration of haul-outs of twelve radio-tagged ringed seals in March, April, and May.

	Durations of haul-outs (hours)								
	March			April			May		
Seal no.	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
BA-82	--	--	--	2.7	3.7	18	3.8	3.9	16
SA-82	--	--	--	11.9	7.4	4	8.6	5.4	8
BE-82	--	--	--	2.4	2.1	7	5.6	4.9	11
TI-83	--	--	--	4.1	1.8	9	5.3	3.8	16
GI-83	--	--	--	5.2	6.0	9	--	--	--
DQ-83	--	--	--	6.3	3.3	8	7.2	4.6	12
JO-83	--	--	--	3.4	2.9	4	4.4	3.1	7
LK-84	3.8	4.1	19	4.1	3.9	46	6.3	9.2	3
LU-84	6.3	2.8	8	5.6	3.2	5	--	--	--
HU-84	10.2	5.4	11	10.4	3.2	5	--	--	--
ZO-84	8.0	0	1	4.2	3.0	8	--	--	--
NA-84	4.7	1.2	3	3.6	2.2	16	--	--	--

Table 11. Length of time when radio-tagged seals were believed to have remained in the water between haul-out bouts in March, April, and May. Data from late spring, when some radio-tagged seals were known to haul-out beyond range of the camps, were excluded.

	Time between haul-out bouts (hours)								
	March			April			May		
Seal no.	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
BA-82	--	--	--	32.4	7.5	3	12.7	10.8	6
SA-82	--	--	--	7.0	8.9	17	9.9	11.5	14
BE-82	--	--	--	25.2	15.5	5	9.5	10.6	11
TI-83	--	--	--	5.9	7.4	8	10.0	10.0	14
GI-83	--	--	--	5.9	4.5	9	--	--	--
DQ-83	--	--	--	12.3	11.1	5	16.0	11.2	14
JO-83	--	--	--	13.9	15.6	4	29.2	25.2	5
LR-83	--	--	--	--	--	--	12.0	7.3	15
LK-84	24.8	38.4	19	6.8	5.2	47	33.0	9.9	2
LU-84	36.8	48.0	9	43.4	50.9	6	--	--	--
HU-84	36.8	26.1	10	6.9	3.5	5	--	--	--
ZO-84	--	--	--	30.0	26.5	8	--	--	--
NA-84	3.5	2.1	2	19.6	15.9	18	--	--	--

Table 12. Number of hours spent hauled out per 24 hour cycle by radio-tagged ringed seals.

	Hours of haul-out / 24 hour cycle					
Seal no.	Mean	S.D.	Min.	Max.	N	Sampling period
BA-82	4.9	4.1	0	13.5	19	4/22 - 5/26
SA-82	6.3	4.8	0	15.0	17	5/01 - 5/26
BE-82	5.3	5.1	0	14.5	17	5/01 - 5/26
TI-83	3.6	3.6	0	11.0	14	4/18 - 6/05
GI-83	11.5	8.4	0	21.5	5	4/13 - 4/26
DQ-83	6.2	4.7	0	16.0	19	4/18 - 5/19
JO-83	1.7	2.8	0	8.0	21	4/18 - 5/20
LR-83	4.0	3.6	0	8.0	7	5/11 - 6/05
LK-84	4.4	6.8	0	16.0	57	3/06 - 5/09
LU-84	1.7	3.0	0	12.0	43	3/06 - 4/23
HU-84	4.2	5.2	0	17.0	39	3/06 - 4/19
ZO-84	0.8	1.5	0	5.0	39	3/14 - 4/27
NA-84	2.2	2.2	0	8.0	24	3/27 - 4/23

Table 13. Hours spent hauled out per 24 hour cycle by two female ringed seals before, during, and after periods of daily haul-outs.

Seal no.		Period: Pre-daily haul-outs	Daily[1] haul-outs	Post-daily haul-outs
LK-84	Mean	0.3	8.4	1.2
	S.D.	0.3	17.6	16.9
	Min.	0.0	1.0	0.0
	Max.	2.0	16.0	16.0
	N	16	27	14
			$t_s = 7.62$ ($p < 0.001$)	$t_s = 5.24$ ($p < 0.001$)
LU-84	Mean	0.8	4.2	1.4
	S.D.	7.1	4.2	8.6
	Min.	0	1.5	0
	Max.	11.0	8.0	12.0
	N	16	8	19
			$t_s = 3.19$ ($p < 0.01$)	$t_s = 2.45$ ($p < 0.01$)

[1]Period of daily haul-outs included 24 March to 23 April for LK-84 and 24 to 31 March for LU-84.

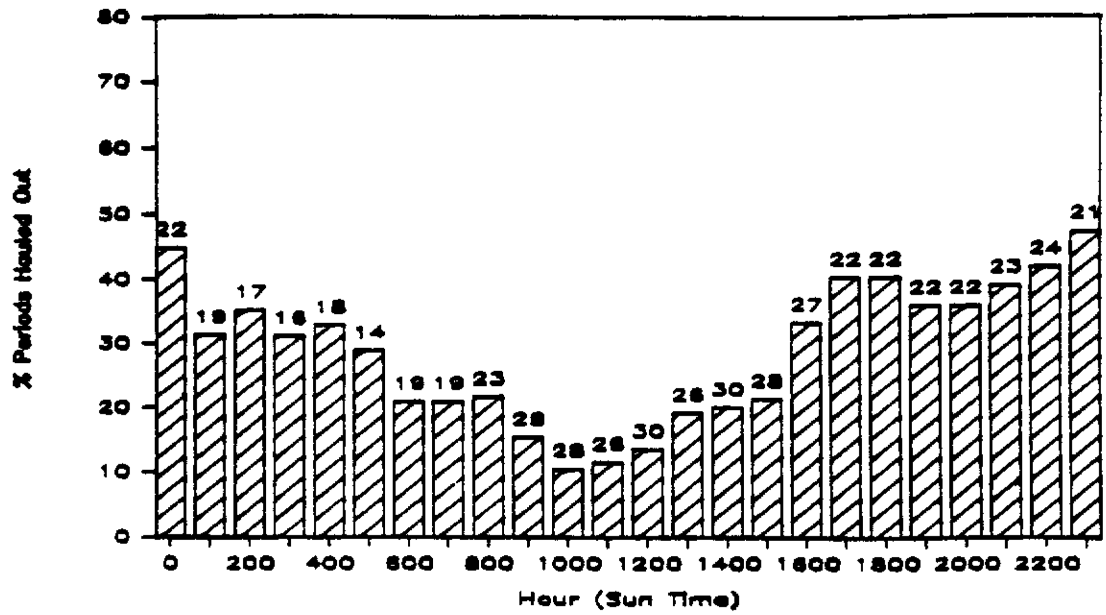

Figure 4a. Diel haul-out of radio-tagged seal SA-82 from 23 April to 11 May 1982. The number of times each hour was sampled is given above the percentage bar.

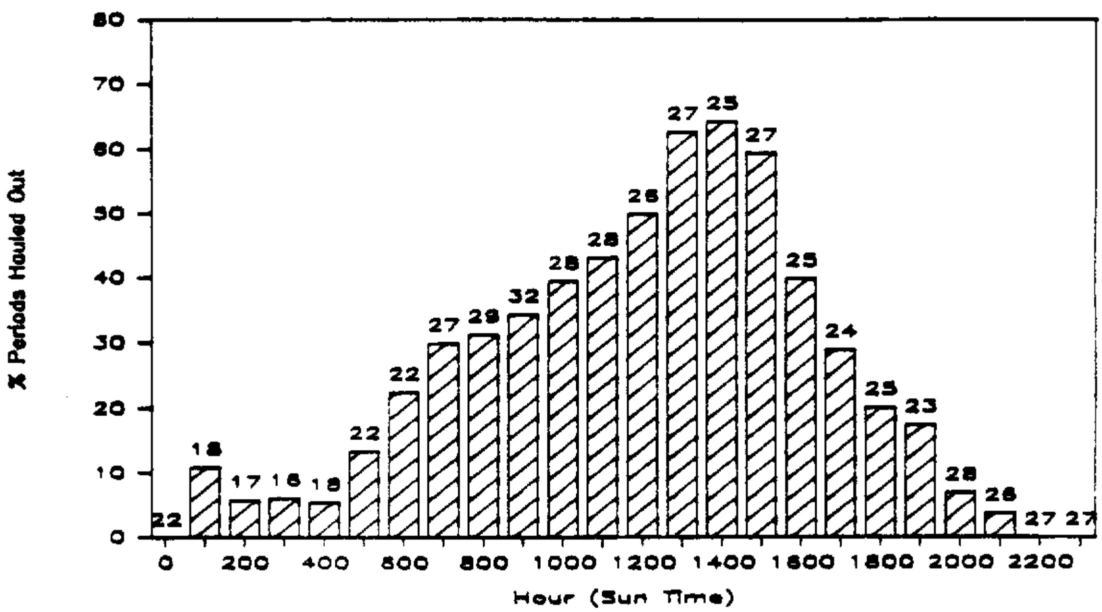

Figure 4b. Diel haul-out of radio-tagged seal SA-82 from 12 May to 3 June 1982. The number of times each hour was sampled is given above the percentage bar.

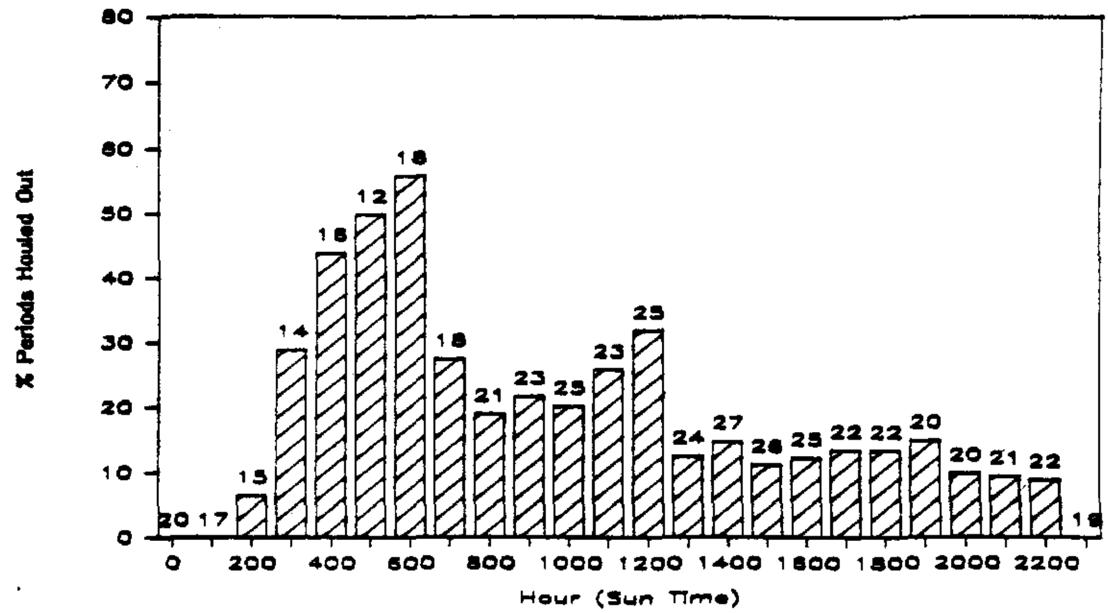

Figure 5a. Diel haul-out of radio-tagged seal BE-82 from 26 April to 11 May 1982. The number of times each hour was sampled is given above the percentage bar.

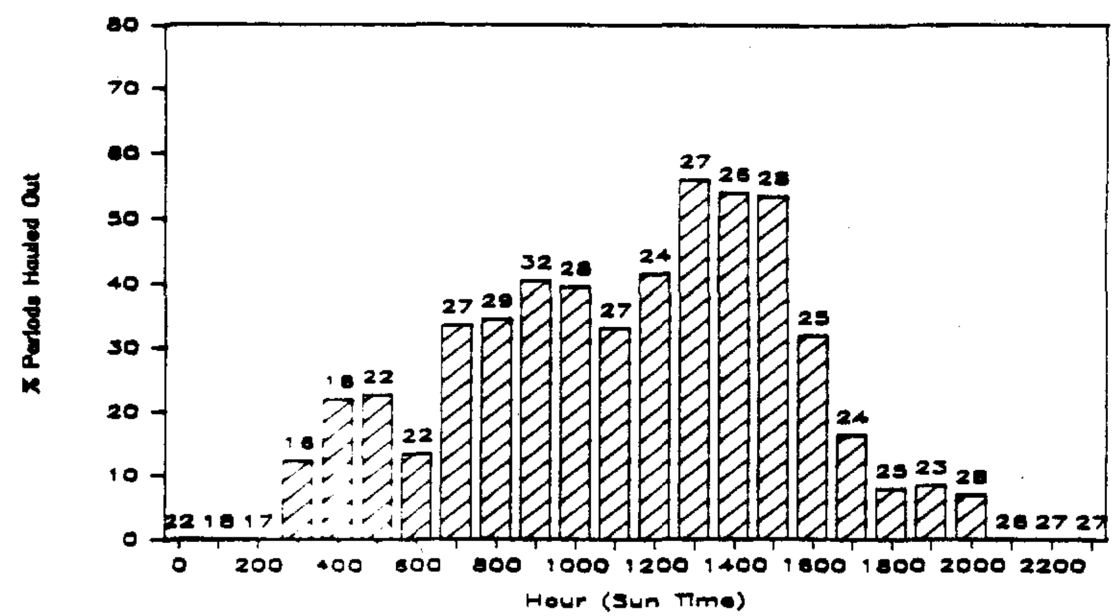

Figure 5b. Diel haul-out of radio-tagged seal BE-82 from 12 May to 4 June 1982. The number of times each hour was sampled is given above the percentage bar.

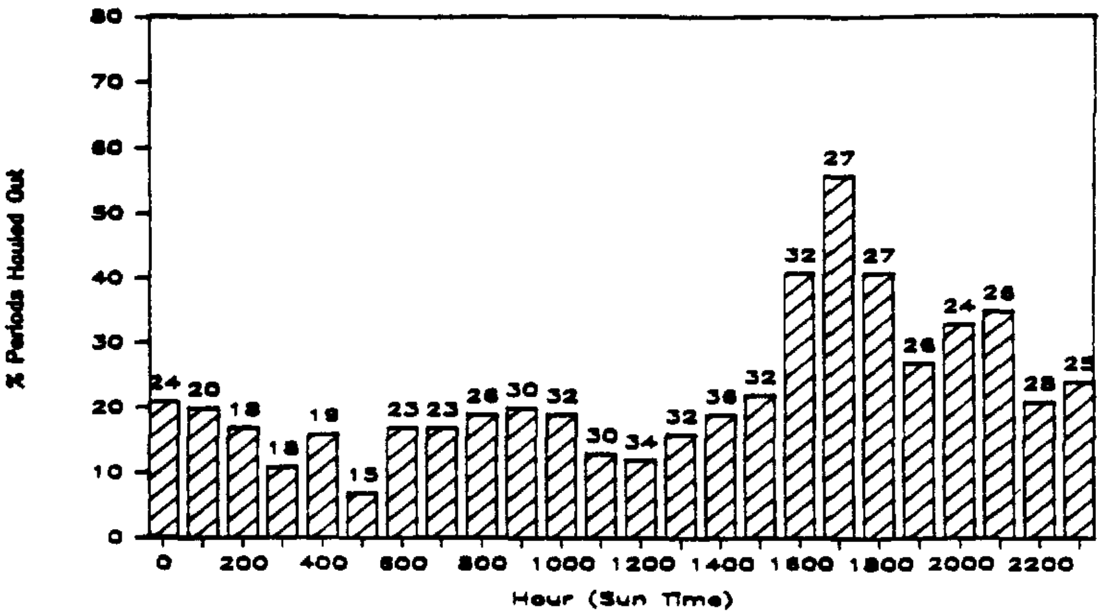

Figure 6a. Diel haul-out of radio-tagged seal BA-82 from 19 April to 11 May 1982. The number of times each hour was sampled is given above the percentage bar.

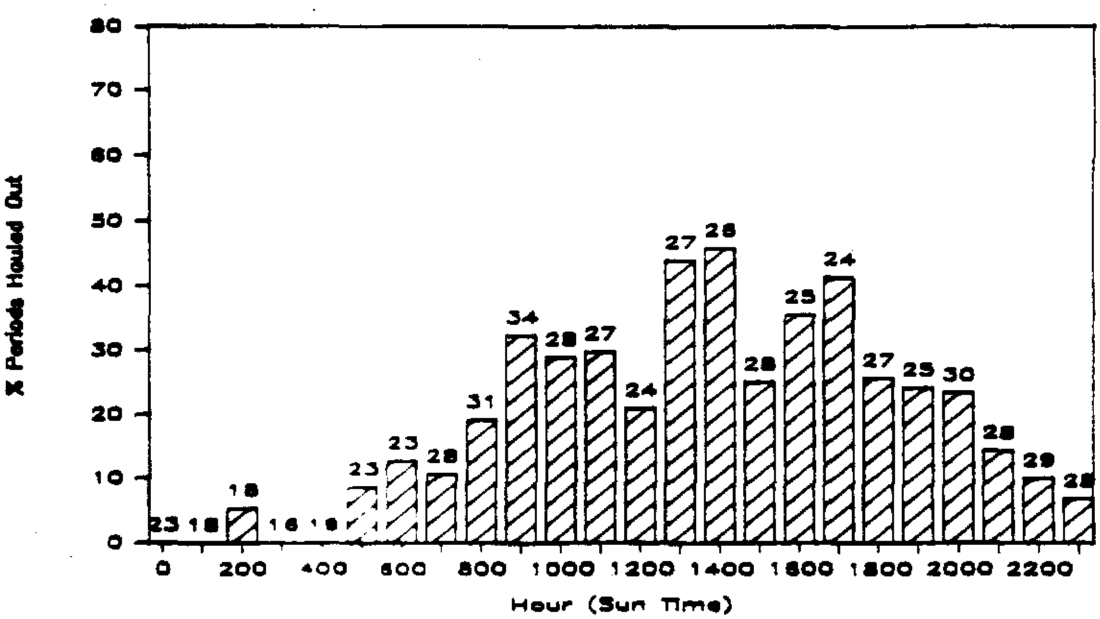

Figure 6b. Diel haul-out of radio-tagged seal BA-82 from 12 May to 2 June 1982. The number of times each hour was sampled is given above the percentage bar

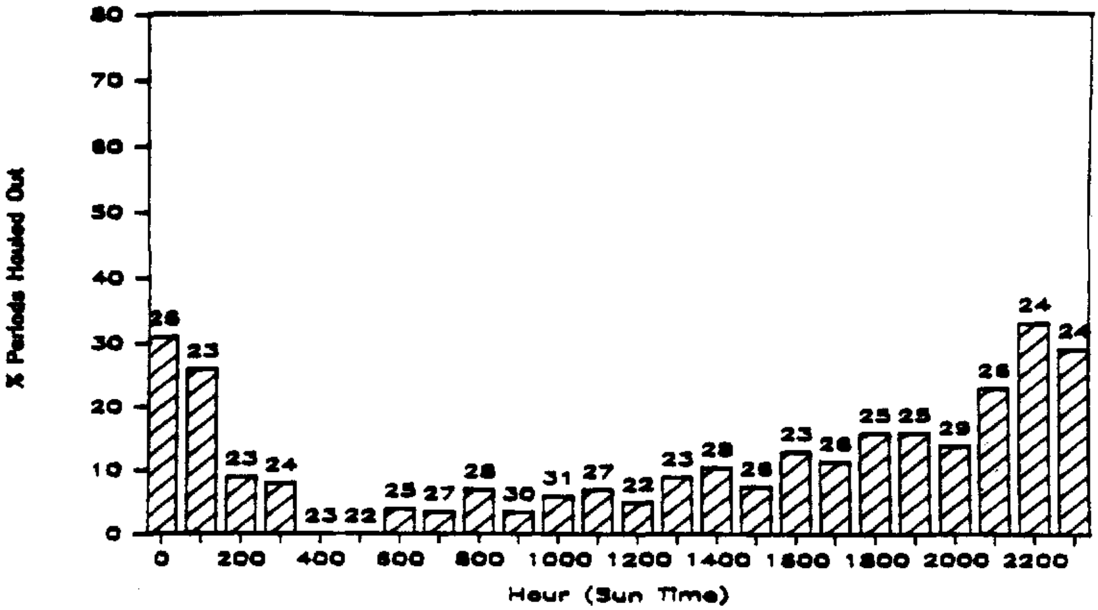

Figure 7a. Diel haul-out of radio-tagged seal TI-83 from 1 April to 11 May 1983. The number of times each hour was sampled is given above the percentage bar.

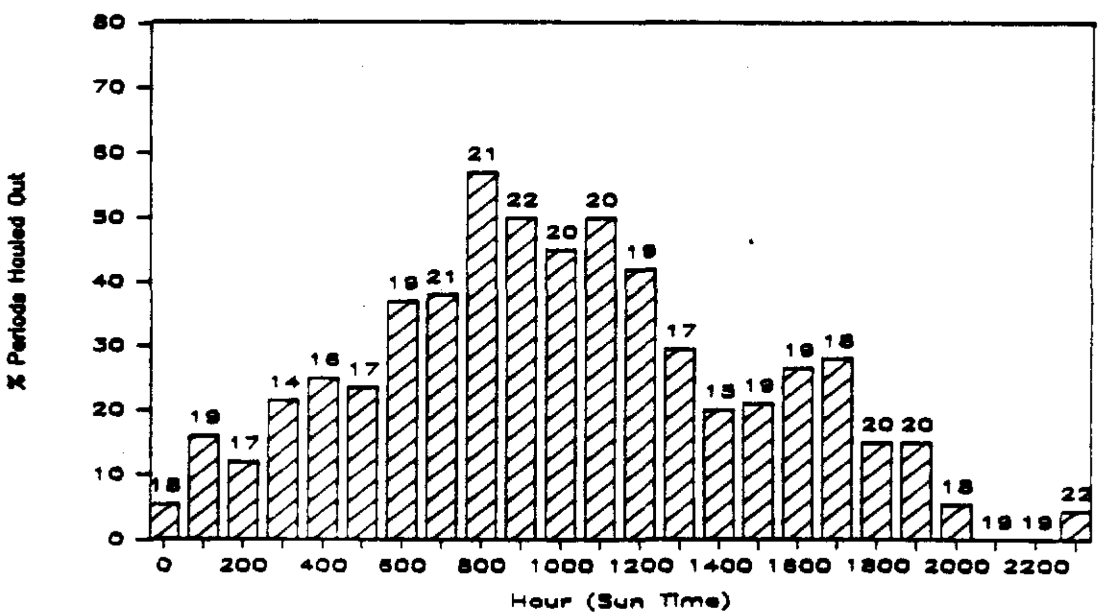

Figure 7b. Diel haul-out of radio-tagged seal TI-83 from 12 May to 2 June 1983. The number of times each hour was sampled is given above the percentage bar.

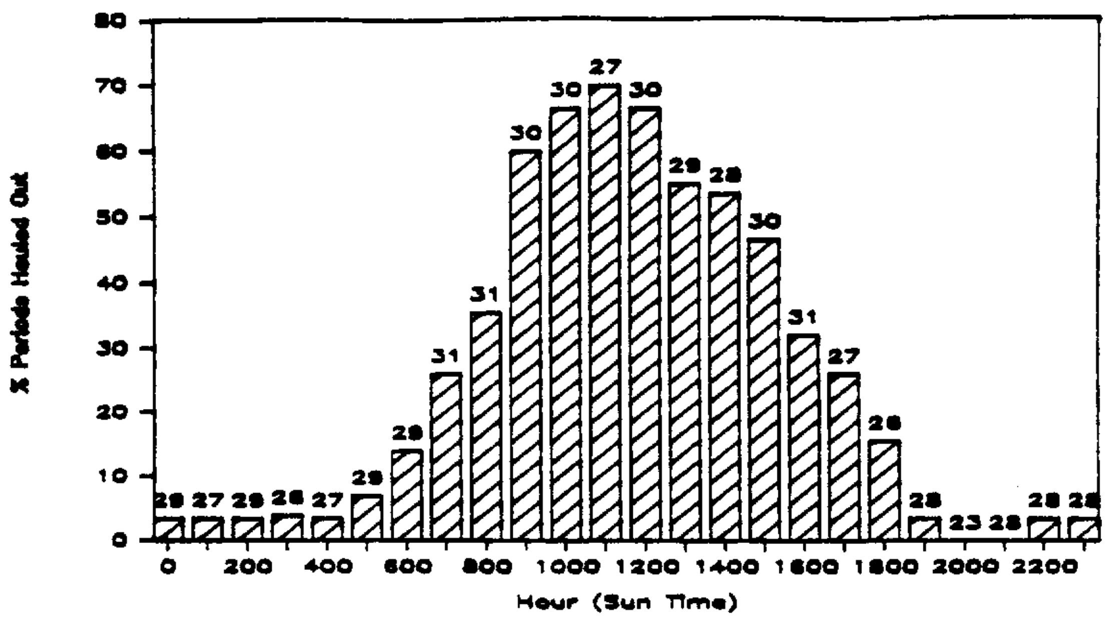

Figure 8. Diel haul-out of radio-tagged seal DQ-83 from 14 April to 19 May 1983. The number of times each hour was sampled is given above the percentage bar.

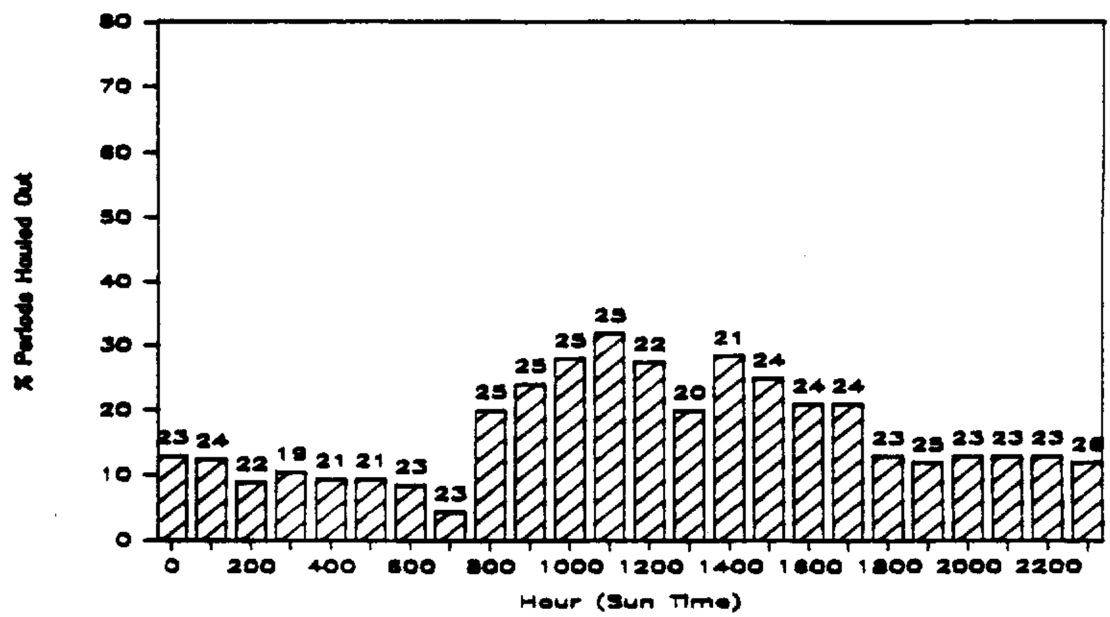

Figure 9. Diel haul-out of radio-tagged seal LR-83 from 8 May to 4 June 1983. The number of times each hour was sampled is given above the percentage bar.

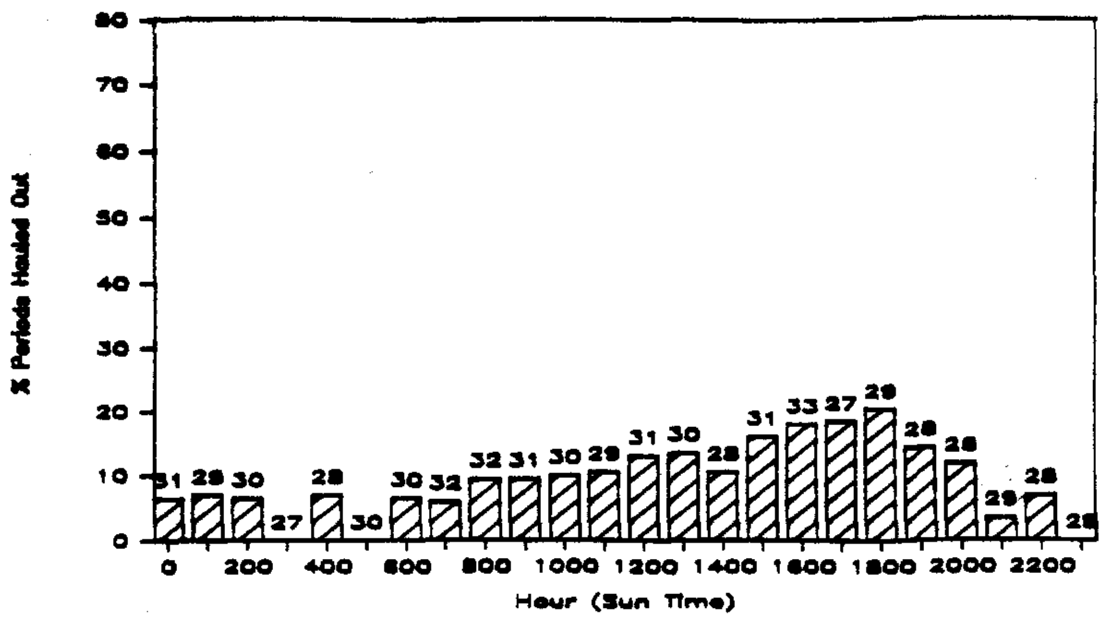

Figure 10. Diel haul-out of radio-tagged seal JO-83 from 14 April to 20 May 1983. The number of times each hour was sampled is given above the percentage bar.

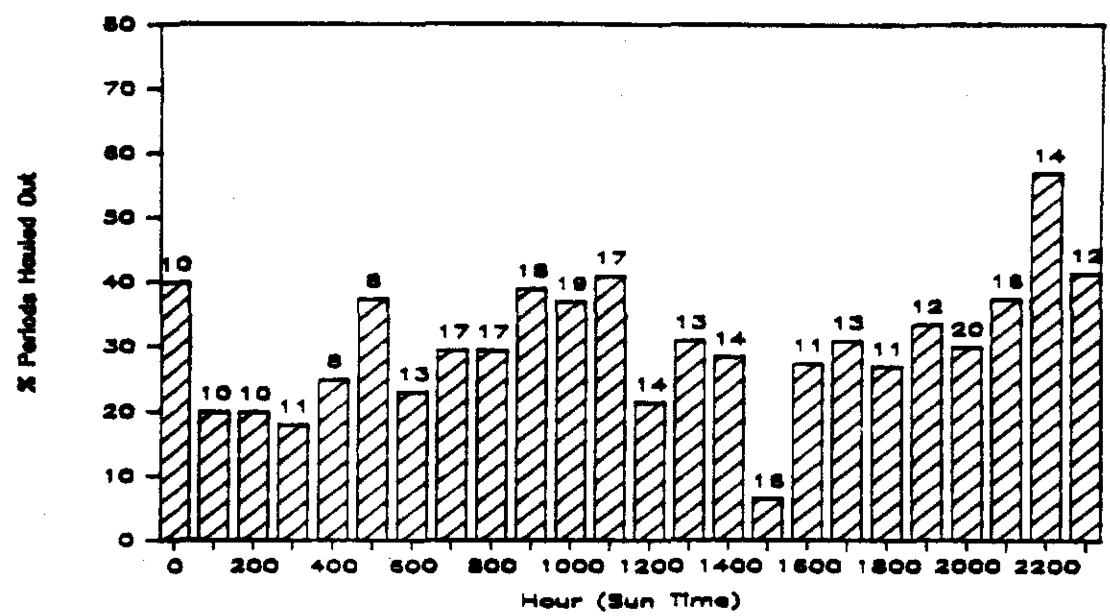

Figure 11. Diel haul-out of radio-tagged seal GI-83 from 24 March to 26 April. The number of times each hour was sampled is given above the percentage bar.

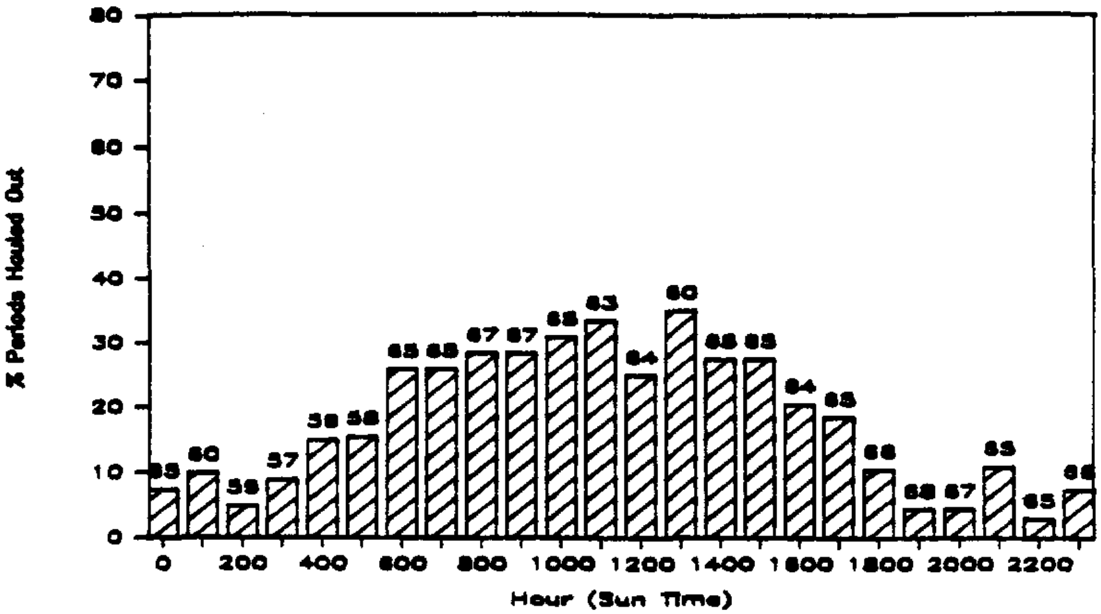

Figure 12. Diel haul-out of radio-tagged seal LK-84 from 4 March to 11 May 1984. The number of times each hour was sampled is given above the percentage bar.

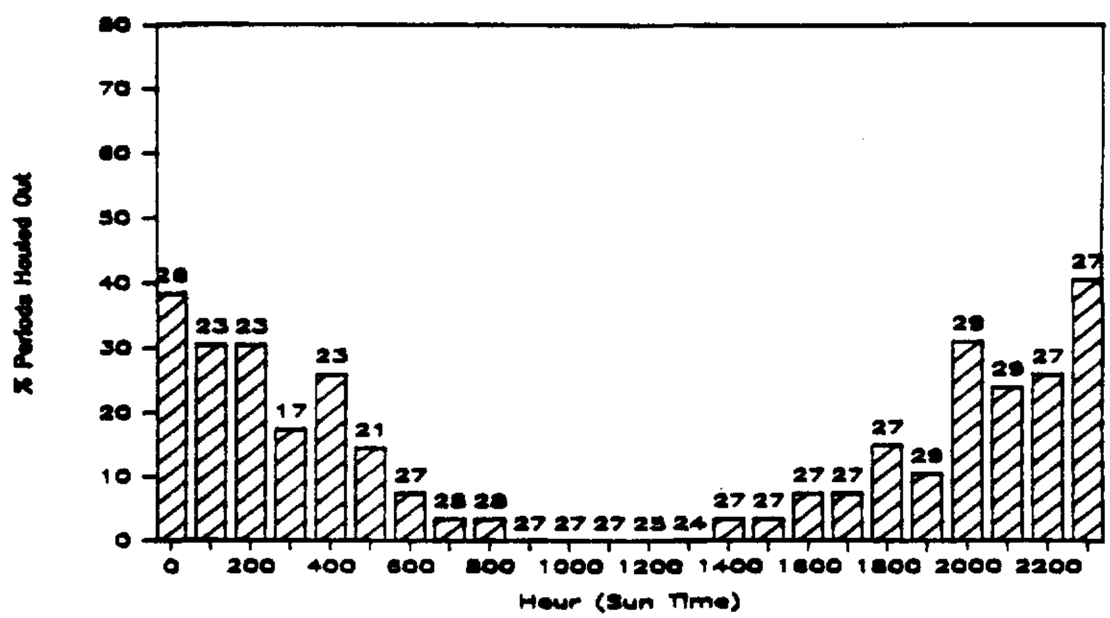

Figure 13. Diel haul-out of radio-tagged seal NA-84 from 26 March to 24 April 1984. The number of times each hour was sampled is given above the percentage bar.

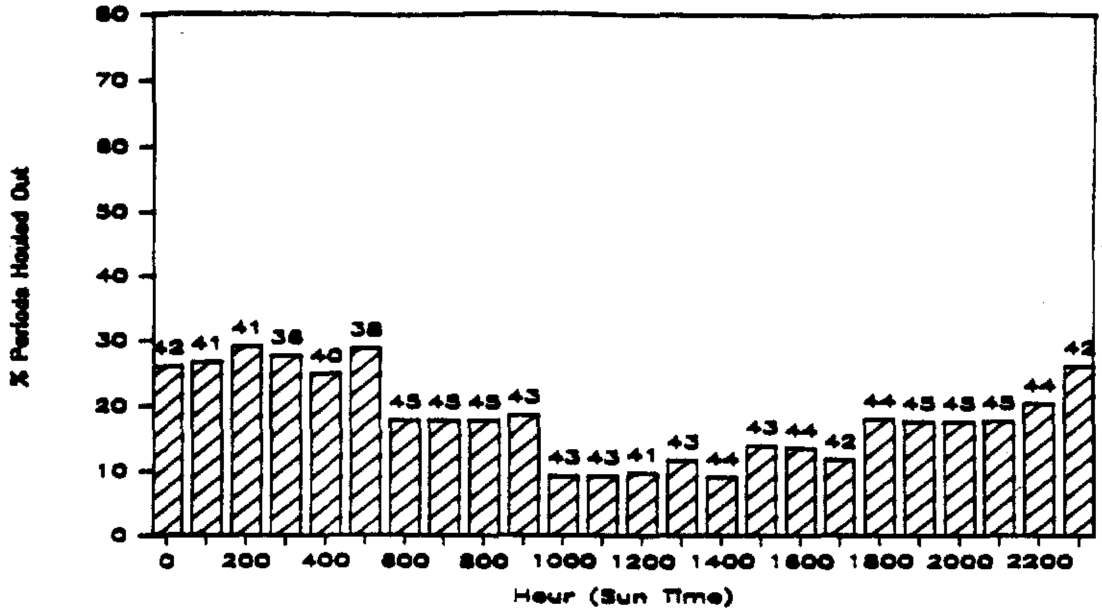

Figure 14. Diel haul-out of radio-tagged seal HU-84 from 5 March to 19 April 1984. The number of times each hour was sampled is given above the percentage bar.

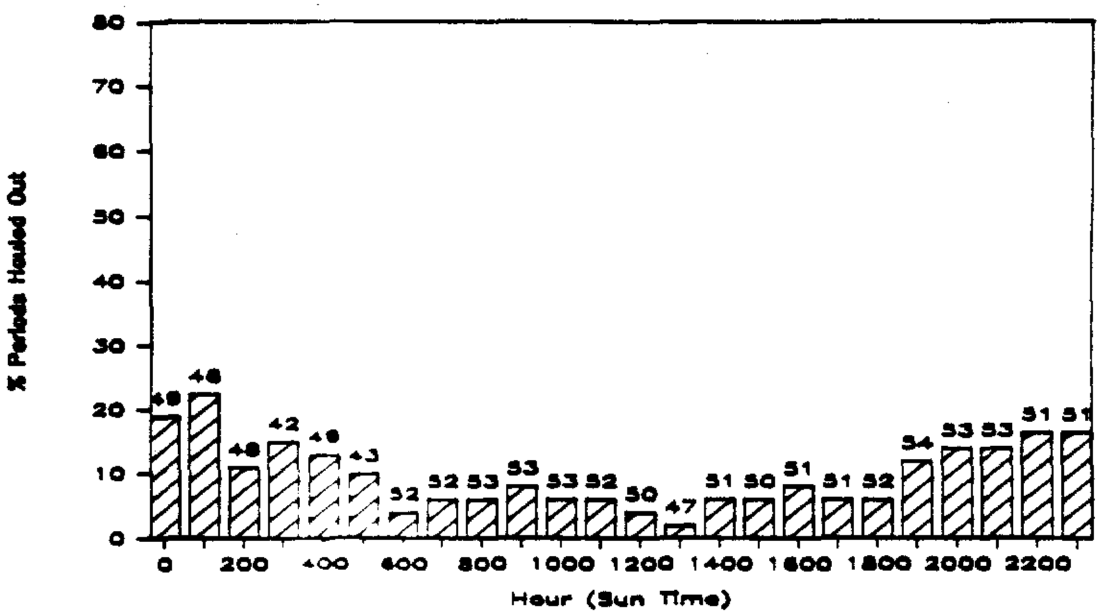

Figure 15. Diel haul-out of radio tagged seal LU-84 from 4 March to 24 April 1984. The number of times each hour was sampled is given above the percentage bar

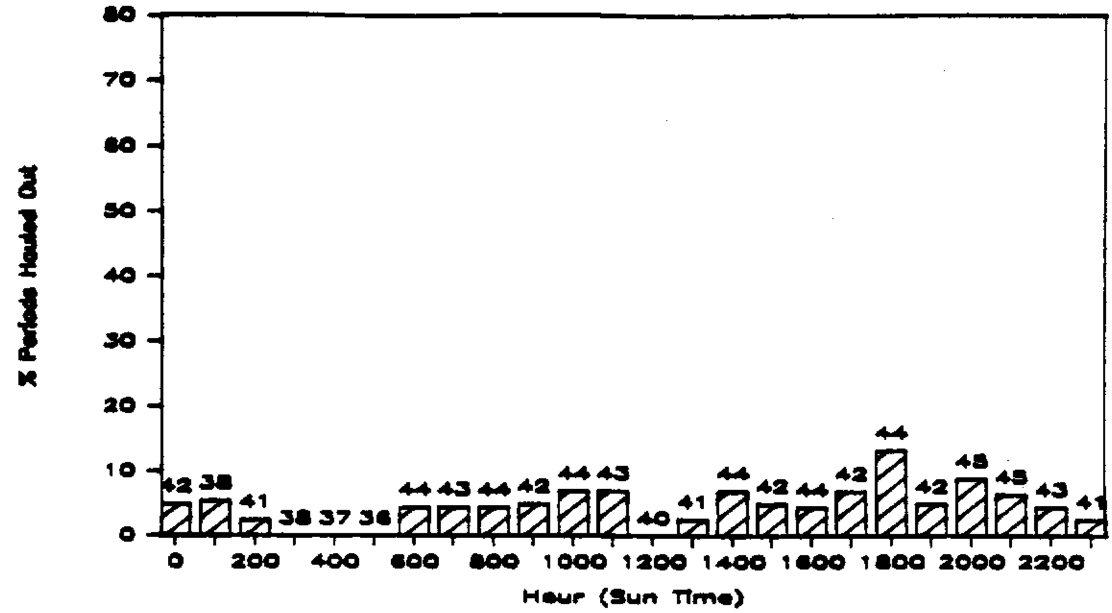

Figure 16. Diel haul-out of radio-tagged seal ZO-84 from 13 March to 27 April 1984. The number of times each hour was sampled is given above the percentage bar.

nocturnal or arhythmic haul-outs until early to mid May when the trend shifted to midday haul-outs. Four seals (BA-82, SA-82, BE-82, and TI-83) were monitored for sufficient lengths of time before and after 11 May to permit comparisons of diel haul-out trends through and after that date. The probability that the observed trends were random was tested in each case via a runs test for trend data (Sokal and Rohlf 1969).

In late April and early May, the hourly percentages of SA-82 (Figure 4) and BE-82 (Figure 5) were significantly different from random (t_s = -3.52 and -3.18 respectively, $p < 0.05$), but those of BA-82 (Figure 6) were not different from random (t_s = -0.353). SA-82 was hauled out more than 30% of the time from 1600 to 0400, with a peak at 2300. BE-82 was hauled out in more than 30% of the samples from 0400 to 0700 and between 1200 and 1300 with the peak at 0600. In mid May to early June, a tendency to haul-out mostly in the afternoon hours was observed in BA-82 (t_s = -2.470, $p < 0.05$), SA-82 (t_s = -2.823, $p < 0.05$), and BE-82 (t_s = -2.823, $p < 0.05$). Both SA-82 and BE-82 generally were out greater than 30% of the time between 0700 and 1600 (peaks at 1300-1400) during that period. BA-82, during that period, mostly hauled out from 0900 through 1800 with the peak at 1400.

Only two of five seals radio-tagged in 1983 showed diel haul-out trends significantly differing from random. TI-83 showed a significant trend toward midday haul-outs from mid-May to early June and DQ-83 showed a trend toward midday haul-outs in mid-April to mid-May. Trends appeared to be similar among the other three seals tagged in 1983 but sample sizes and dates of monitoring were limited in those cases. In April and early May, TI-83 (Figure 7) hauled out mainly late at night, exceeding 30% of the time only between 2200 and 0000 hours, but that trend was not significant (t_s = 0.354). During mid-May to early June, however, he showed a strong peak in late morning to midday (t_s = -7.566, $p < 0.05$). In that period he was out of the water more than 30% of the time from 0600 to 1200 (peak at 0800). DQ-83 (Figure 8) showed a strong preference for midday haul-outs during the period from mid-April to mid-May (t_s = -2.816, $p < 0.05$). He was hauled out more than 25% of the time from 0700 to 1600 (peak at 1100) in that period. LR-83 was out 20% or more of the time from 0800 to 1700 in early May to early June (Figure 9), but the trend was not significant (t_s = -1.760). JO-83 showed a weak tendency for late afternoon haul-outs in mid-April to mid-May (Figure 10), but these did not differ significantly from random. GI-83's haul-outs in late March to late April (Figure 11) also did not differ significantly from random.

Monitoring of seals radio-tagged in 1984 ceased in mid-May, and only two showed haul-out trends that differed significantly from random. LK-84 showed a strong tendency to haul-out mostly in early to midday in March, April, and early May (t_s = -3.872, $p < 0.05$). She was in her lair more than 25% of the time from 0600 to 1500 hours, with a peak at 1300 hours (Figure 12). In contrast, NA-84 (Figure 13) occupied a lair 25% or more of the time from 2000 to 0200 hours and not at all during 0900 to 1300 hours (t_s = -2.816, $p < 0.05$). HU-84 and LU-84 also showed a tendency to haul out mainly during the night and early morning (Figures 14, 15), but neither those nor ZO-84's haul-outs (Figure 16) differed significantly from random.

Lair Temperatures

Air temperature was recorded inside of four lairs in 1983 and nine lairs in 1984 (Table 14). Only one of the lairs (83H016) monitored in 1983 appeared to be utilized for haul-outs after insertion of a thermistor. Lair 83H016 showed signs of being actively used when it was first examined on 29 March and again on 30 May, and it appeared to be in use throughout the study period. Air temperatures inside the lair were compared with outside air temperatures (Figures 17-19) without correction for wind chill effect. Reliable wind speed measurements were not obtained at times that the lair temperature was sampled. Before the thermistor was

Table 14. Ringed seal lairs in which air temperature was monitored.

Lair	Maximal lair dimensions (m)			Drift Depth[1] (m)	Roof Thickness[2] (m)	Dates Monitored
	Length	Width	Depth			
83H022	1.55	1.00	--	1.05	--	4/12 - 4/29/83
83C023	1.72	1.70	--	1.00	--	4/15 - 4/29/83 5/07 - 5/12/83
83H016	1.62	0.77	0.32	0.88	0.40	5/05 - 5/29/84
83H047	1.92	0.87	0.52	0.77	0.36	5/21 - 5/29/84
84H018	1.90	0.70	0.37	0.50	0.15	3/06 - 3/22/84
84H021	1.30	--	0.30	0.55	0.23	3/06 - 3/20/84
84H020	1.75	0.85	0.30	0.53	0.23	3/06 - 3/15/84
84H024	3.00	--	0.22	0.80	0.42	3/08 - 4/12/84
84C044	3.28	2.20	0.47	0.68	0.21	3/20 - 4/11/84
84C095 (2 chambers)	1.56 1.92	-- --	0.37 --	-- --	-- --	3/22 - 5/15/84
84H113	--	--	--	0. 78	--	4/11 - 5/14/84
84P034 (2 chambers)	4.30 2.01	-- --	0.40 0.30	1.60 --	1.20 --	4/12 - 4/25/84
84H023	1.98	--	0.55	0.70	0.15	4/26 - 5/14/84

[1] Snow depth at deepest portion of lair.
[2] Measured as thickest portion of lair roof.

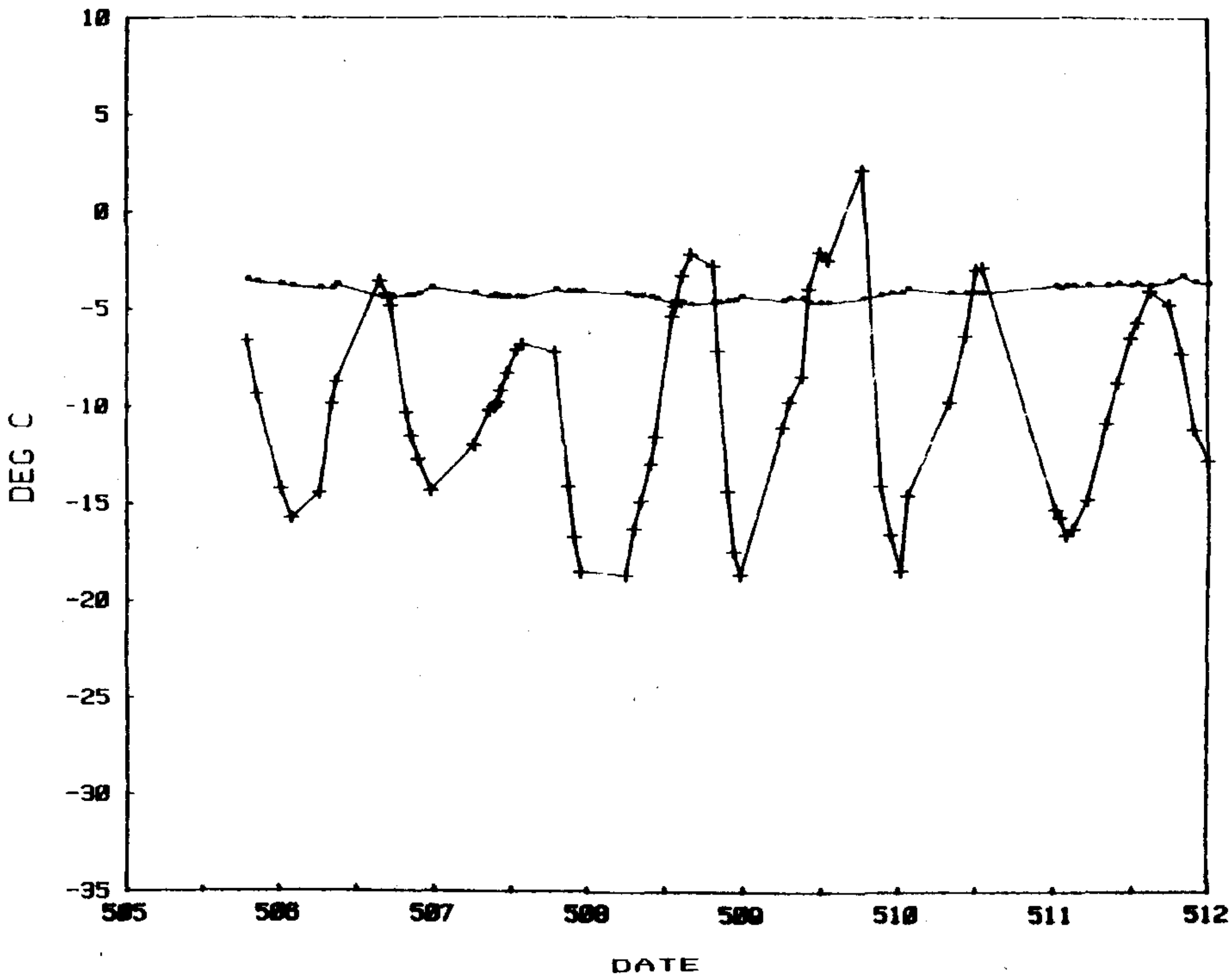

Figure 17. Internal (line with dots) and outside (line with crosses) air temperature at lair 83H016 between 5 and 11 May 1983. No correction was made for wind chill effect.

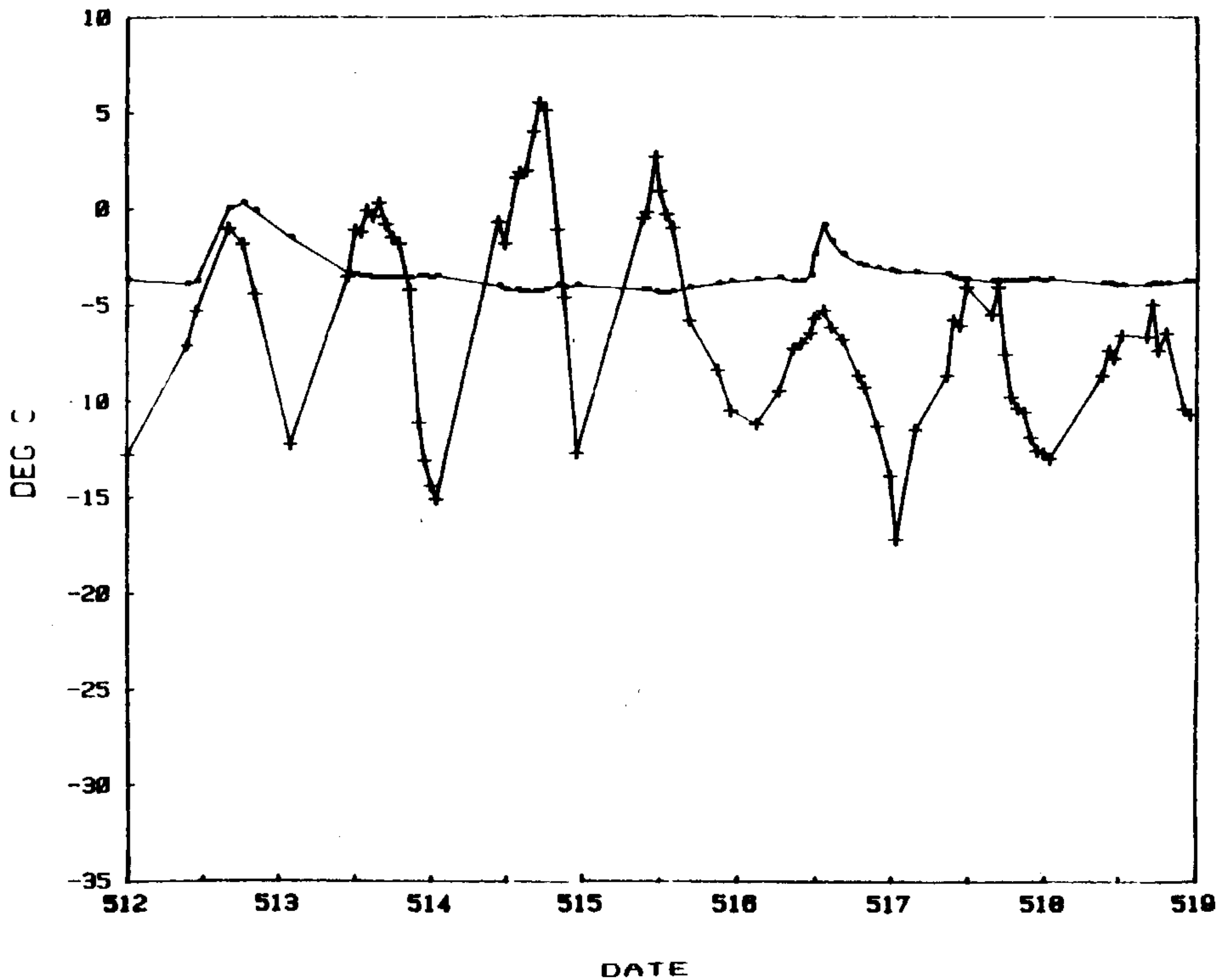

Figure 18. Internal (line with dots) and outside (line with crosses) air temperature at lair 83H016 between 12 and 18 May 1983. No correction was made for wind chill effect.

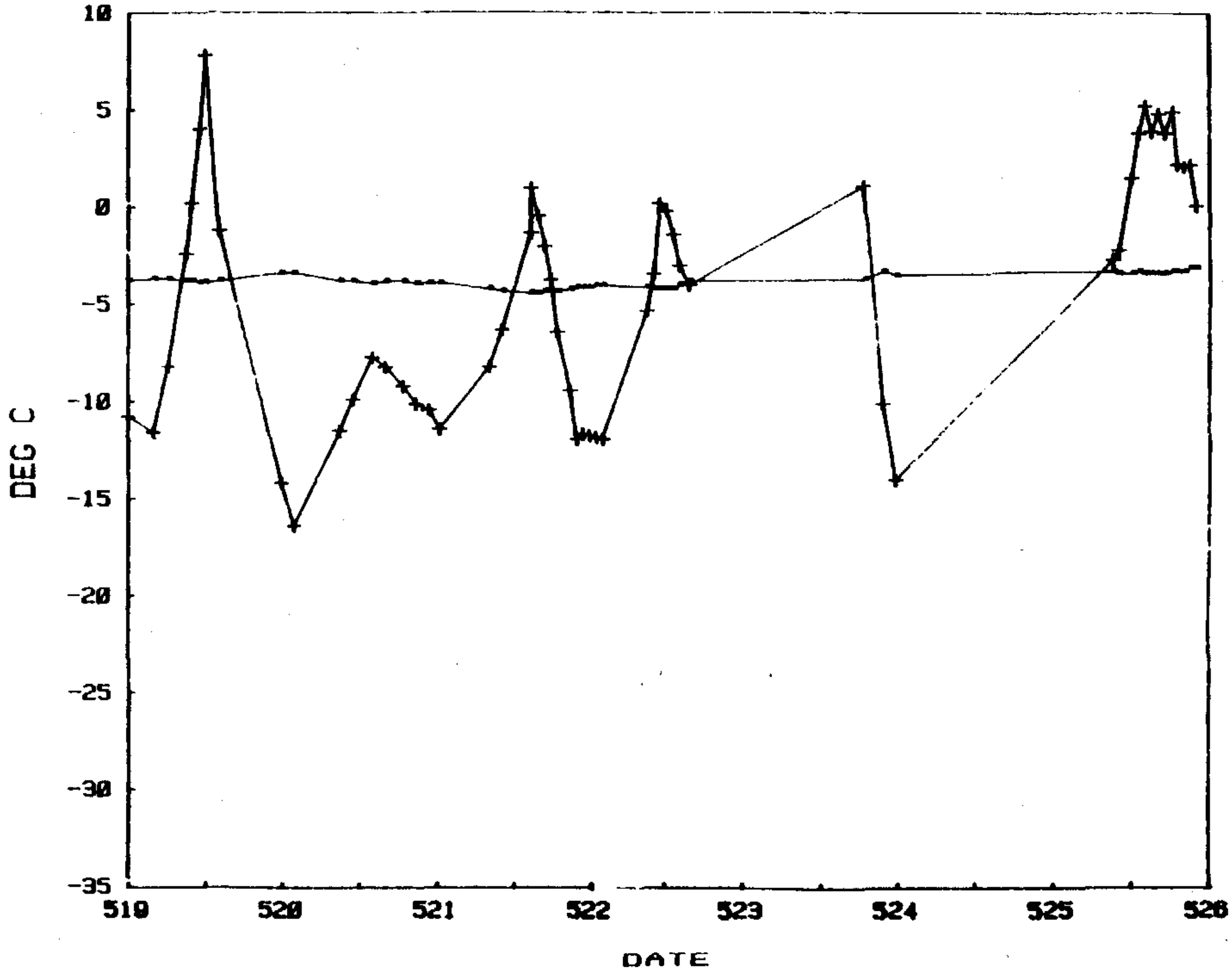

Figure 19. Internal (line with dots) and outside (line with crosses) air temperature at lair 83H016 between 19 and 25 May 1983. No correction was made for wind chill effect.

inserted in the lair, it was known to be used, at least occasionally, by a radio-tagged seal (DQ-83). On two occasions abrupt temperature increases and subsequent decreases in the lair corresponded with haul-out bouts recorded via the transmitter attached to DQ-83. On 12 May the seal's haul-out was followed by a 4.2°C increase in lair temperature and on 16 May by a 2.9°C increase (Figure 18).

Even without a seal's presence, internal temperatures of all lairs tended to remain higher than ambient as a result of heat dissipated from the underlying sea water. Internal lair temperatures in 1983 ranged from -9.1°C to +0.3°C, while ambient temperatures (exclusive of wind chill effect) ranged from -34.6 to +7.8°C (Table 15).

Table 16 gives internal and ambient temperatures for 83H016, the one temperature-monitored lair in 1983 which remained in active use, over a four week period. Through the first three weeks the internal temperature averaged higher than ambient. In the fourth week, however, ambient temperatures tended to be higher than those inside of the lair.

Lair temperatures were monitored in nine lairs in 1984 (Table 14), four of which were used by seals for haul-out bouts while being monitored. Wind speed was measured with each sampling of outside air temperature, and the air temperature within lairs was compared with outside temperatures corrected for wind chill effect (Figures 20-38).

Air temperature in lair 84H018 increased from -5 to +6°C within two hours on 14 March and within three hours on 15 March (Figures 20 - 22). Those temperature increases did not correspond with signals received from any of the radio-tagged seals and must have resulted from haul-out bouts by some other seal(s).

Lair 84C095 experienced 13 such abrupt temperature increases (Figure 23 - 30) with a mean increase per incident of 7.8°C (S.D. = 1.70). Seven of those warming events coincided exactly with haul-out bouts by HU-84 who was traced by his radio signal to this lair. At least two of the warmings (24 - 25 March and 23 - 24 April) were not caused by HU-84 but by another seal, as evidenced by the lack of transmitter signal from HU-84 during those events. Four warmings of the lair after the last signal was received from HU-84 (19 April) may have been caused by him (if he had lost his transmitter) or by another seal. Abrupt temperature increases averaging 5.8°C (S.D. = 1.98) also were recorded on 8 occasions in lair 84H113. Figures 31 - 35 show the temperature records for lair 84H113 and the corresponding ambient temperature (corrected for wind chill effect).

The temperature in lair 84H023 increased 7.2°C in 3 hours on 9 - 10 May and 6.0°C in 3 hours on 13 May (Figures 36 - 38). No signals were received from radio-tagged seals during those warming events. LU-84 used lair 84H023 before the last signal from her transmitter was recorded on 24 April, and she may have continued to use it in May without a transmitter or with a failed transmitter. On the other hand, another seal might have been using the lair in the absence of LU-84.

The longest, most continuous record of internal air temperature was obtained from lair 84C095 (Table 15). Air temperature in that lair averaged 27.0°C warmer than outside wind chill temperatures in March, 26.2°C warmer in April, and 16.4°C warmer in May. By the second week of May, ambient wind chill temperatures frequently were higher than internal air temperature (Figure 30).

Reactions of Seals to Noise Disturbances

The three seals radio-tagged in 1982 were captured at breathing holes and maintained lairs within an extensive grid of seismic lines (Figure 2). Those seals were tagged after the seismic surveys had been completed, so we do not know whether they changed their haul-out behavior

Table 15. Internal and ambient air temperatures (°C) at four ringed seal lairs in 1983.

Lair (Dates)	83H022 (12-29 April)		83C023 (15-29 April)		83H016 (5-29 May)		83H047 (21-29 May)	
	Lair	Ambient	Lair	Ambient	Lair	Ambient	Lair	Ambient
N	92	92	80	80	232	232	80	80
Mean	-6.4	-13.5	-5.3	-8.9	-3.6	-6.2	-3.9	-2.7
S.D.	1.5	9.3	1.5	6.7	0.9	5.9	0.6	4.5
Min.	-8.2	-34.6	-9.1	-26.8	-4.8	-18.7	-5.0	-14.0
Max.	-3.3	5.0	-3.2	3.6	0.3	7.8	-2.8	5.2

Table 16. Internal and ambient air temperatures (°C) at lair 83H016 between 5 May and 29 May.

Dates	5 - 11 May		12 - 18 May		19 - 25 May		26 - 30 May	
	Lair	Ambient	Lair	Ambient	Lair	Ambient	Lair	Ambient
N	69	69	80	80	55	55	29	29
Mean	-4.2	-10.1	-3.5	-5.9	-3.8	-4.3	-2.2	-1.3
S.D.	0.4	5.1	0.9	5.2	0.4	6.2	0.9	2.8
Min.	-4.8	-18.7	-4.4	-17.2	-4.4	-16.4	-3.0	-5.5
Max.	-3.3	2.1	0.3	5.5	-3.1	7.8	-0.3	3.7

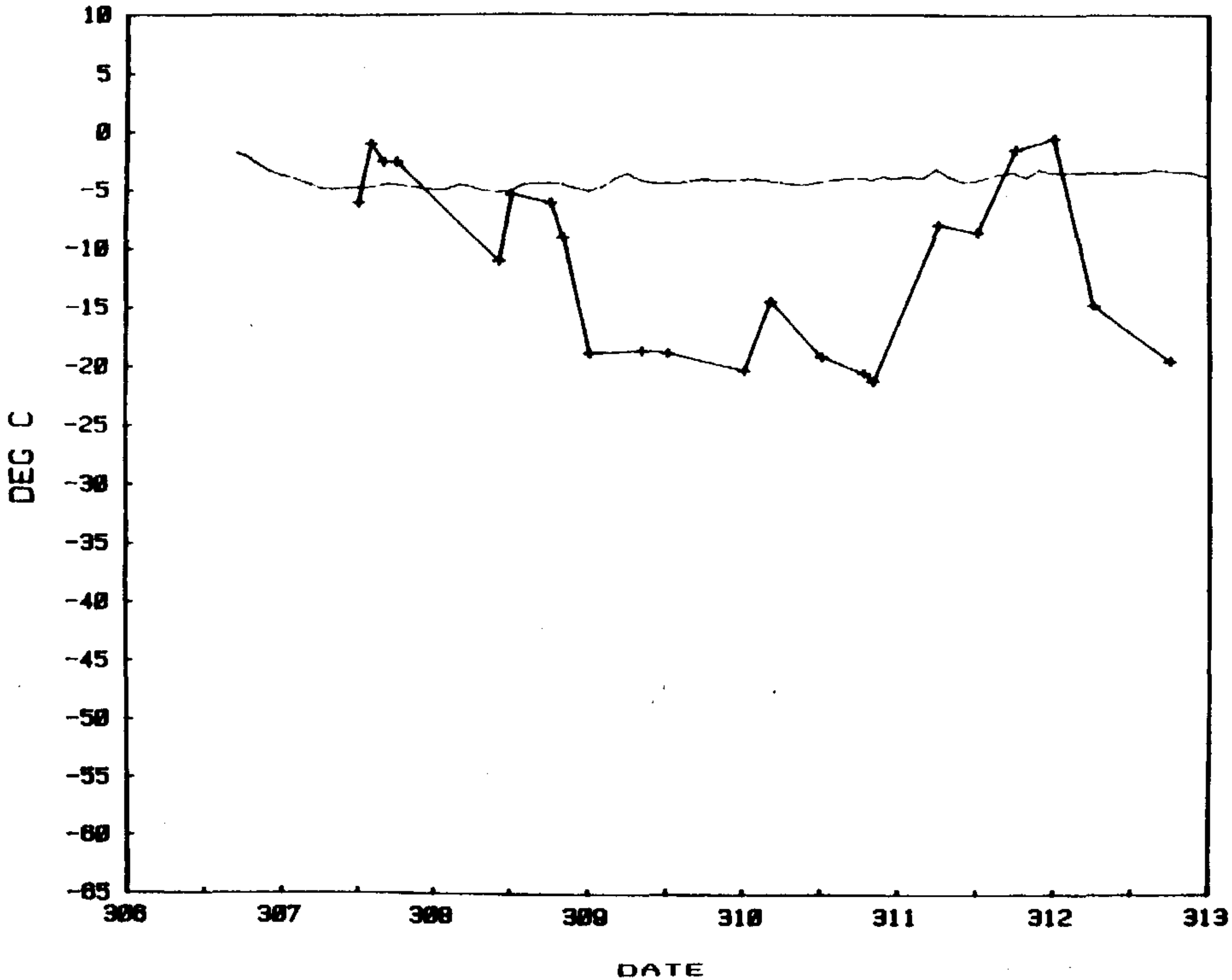

Figure 20. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H018 between 6 and 13 March 1984.

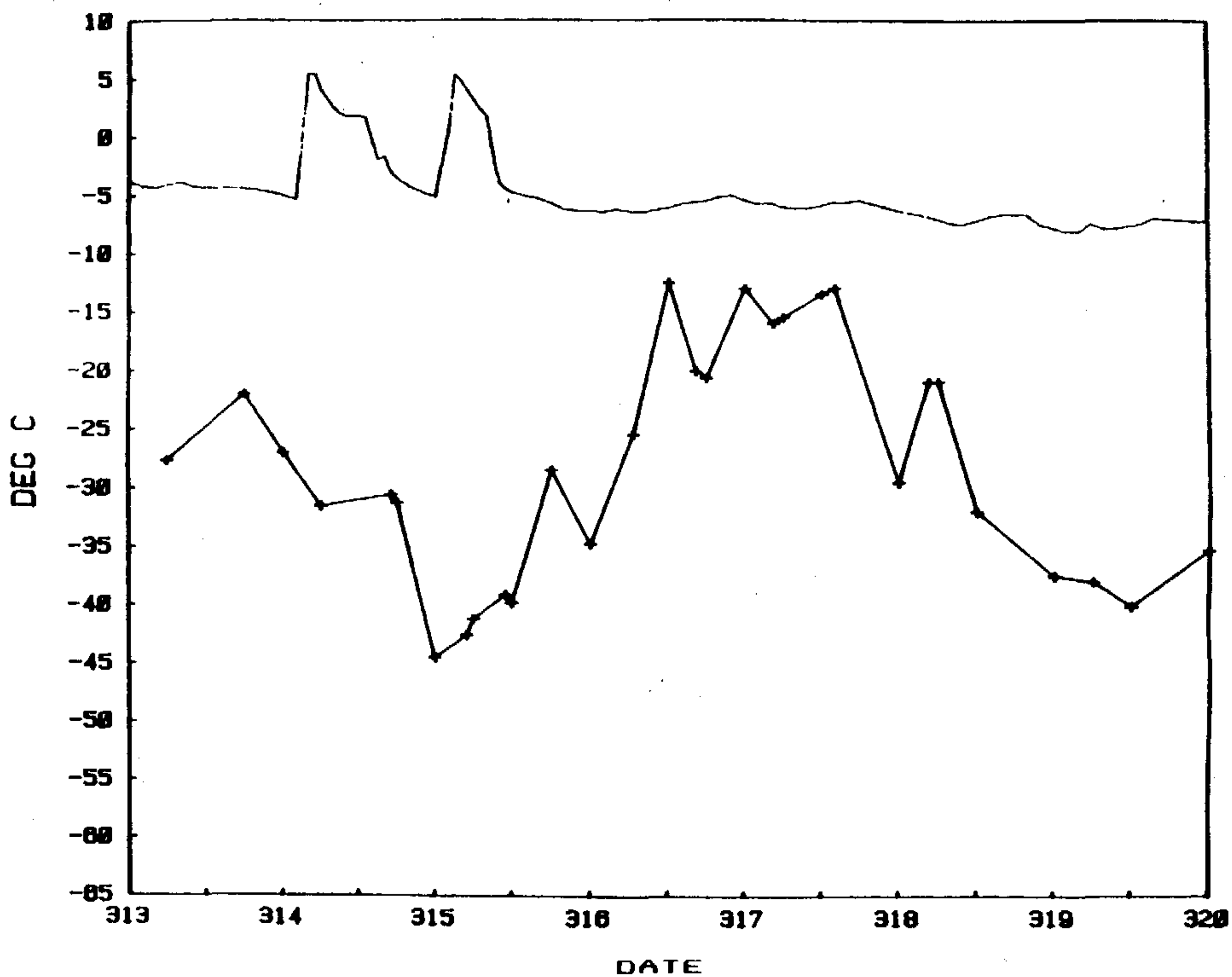

Figure 21. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H018 between 13 and 20 March 1984.

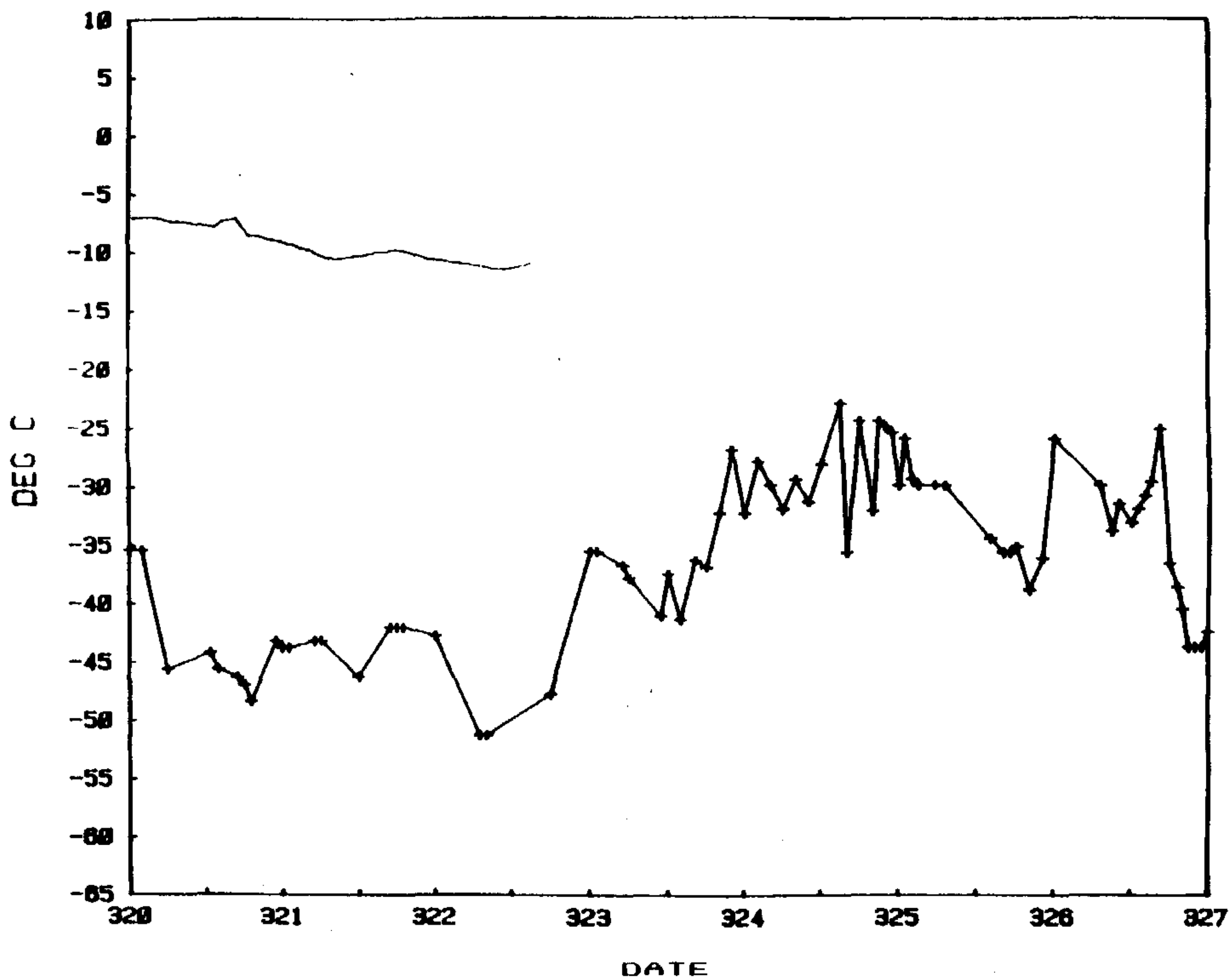

Figure 22. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H018 between 20 and 27 March 1984.

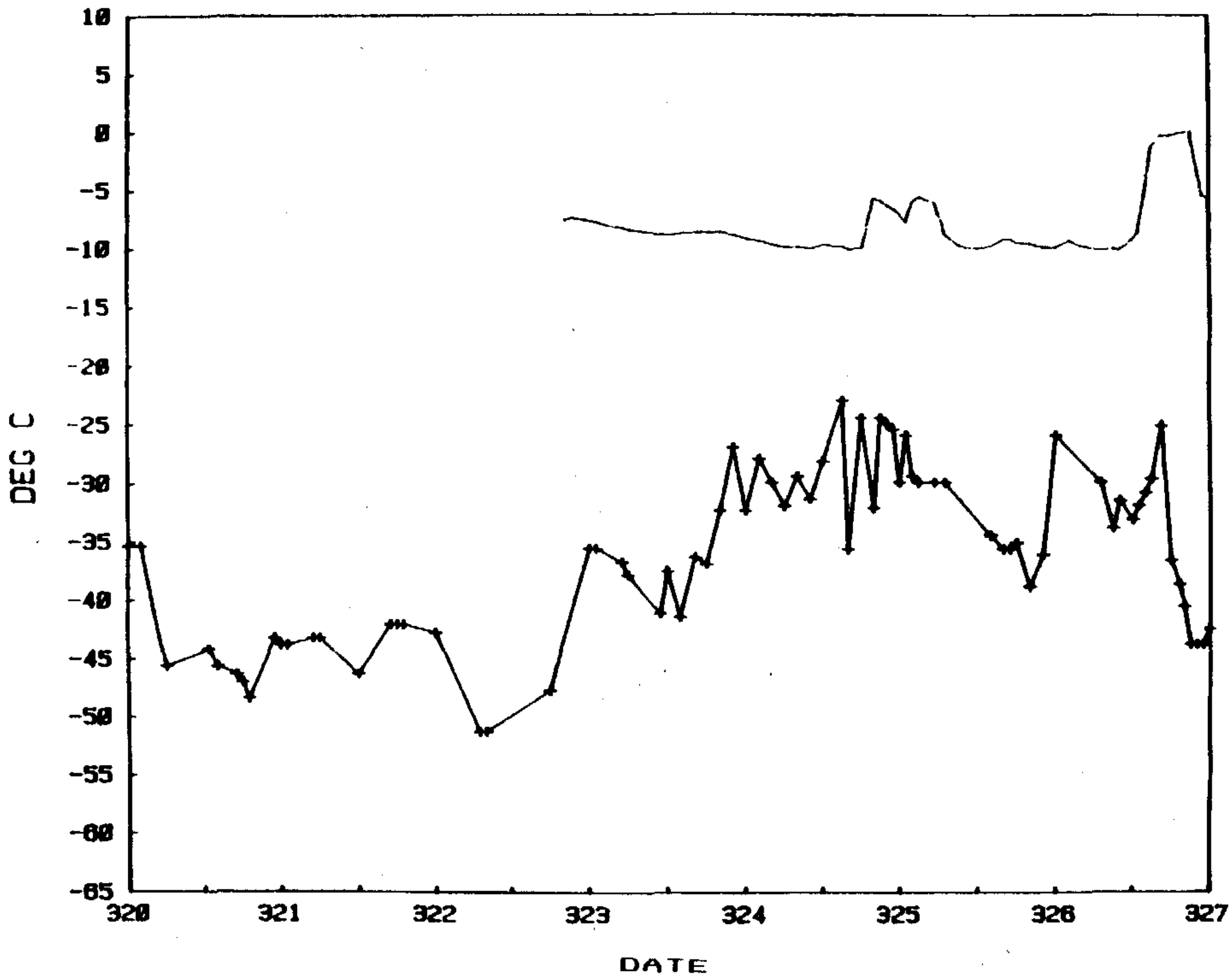

Figure 23. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84C095 between 20 and 27 March 1984.

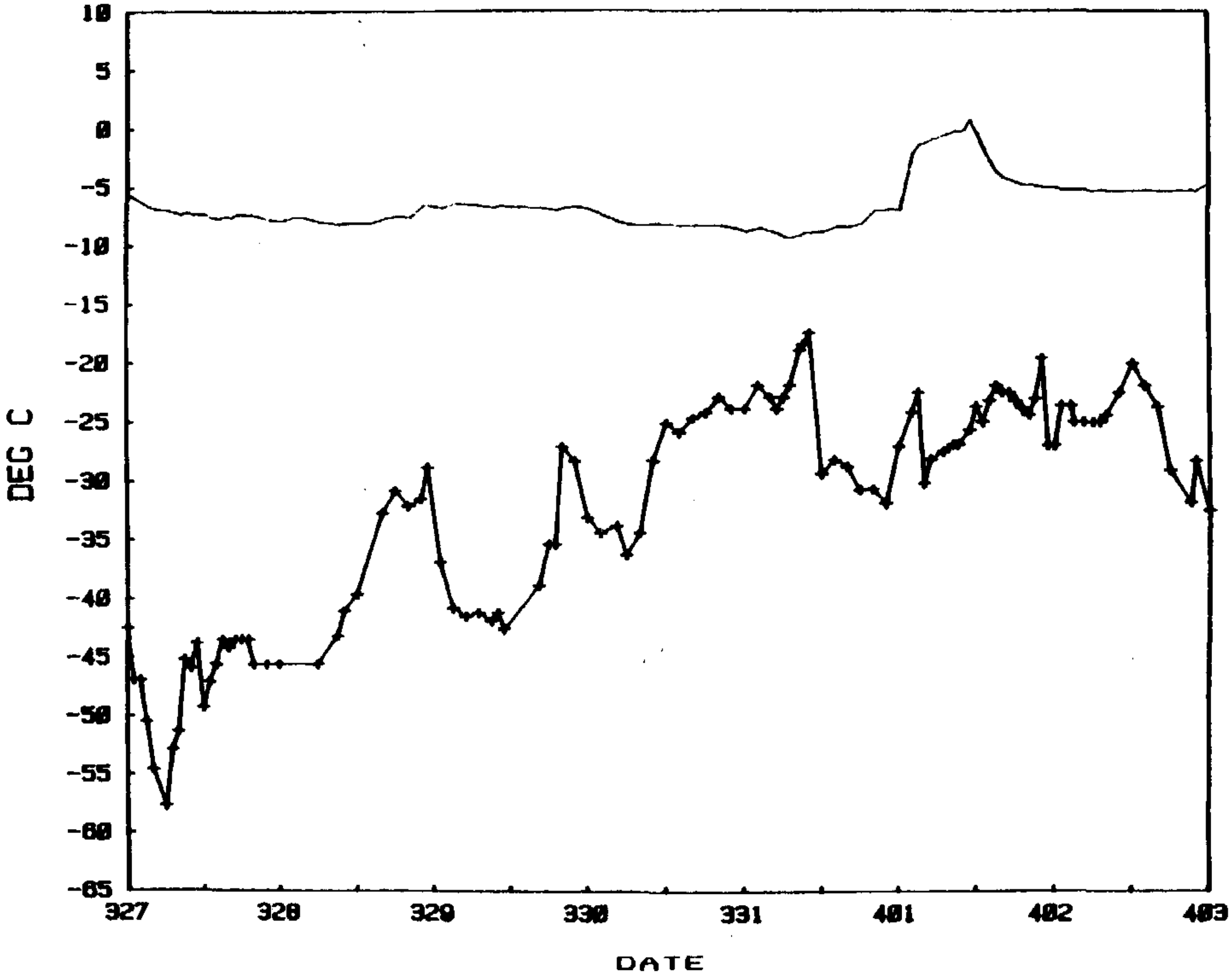

Figure 24. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84C095 between 27 March and 3 April 1984.

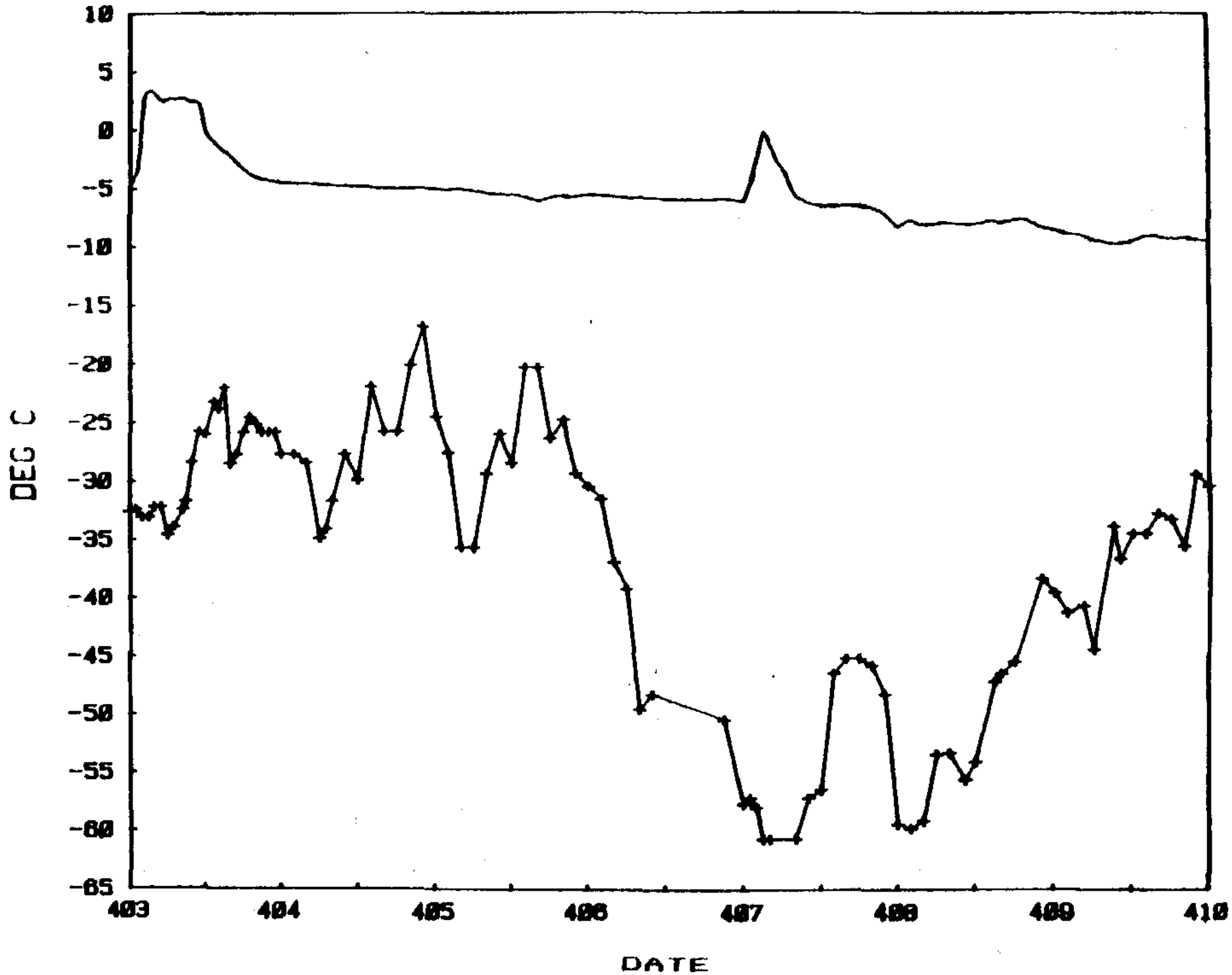

Figure 25. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84C095 between 3 and 10 April 1984.

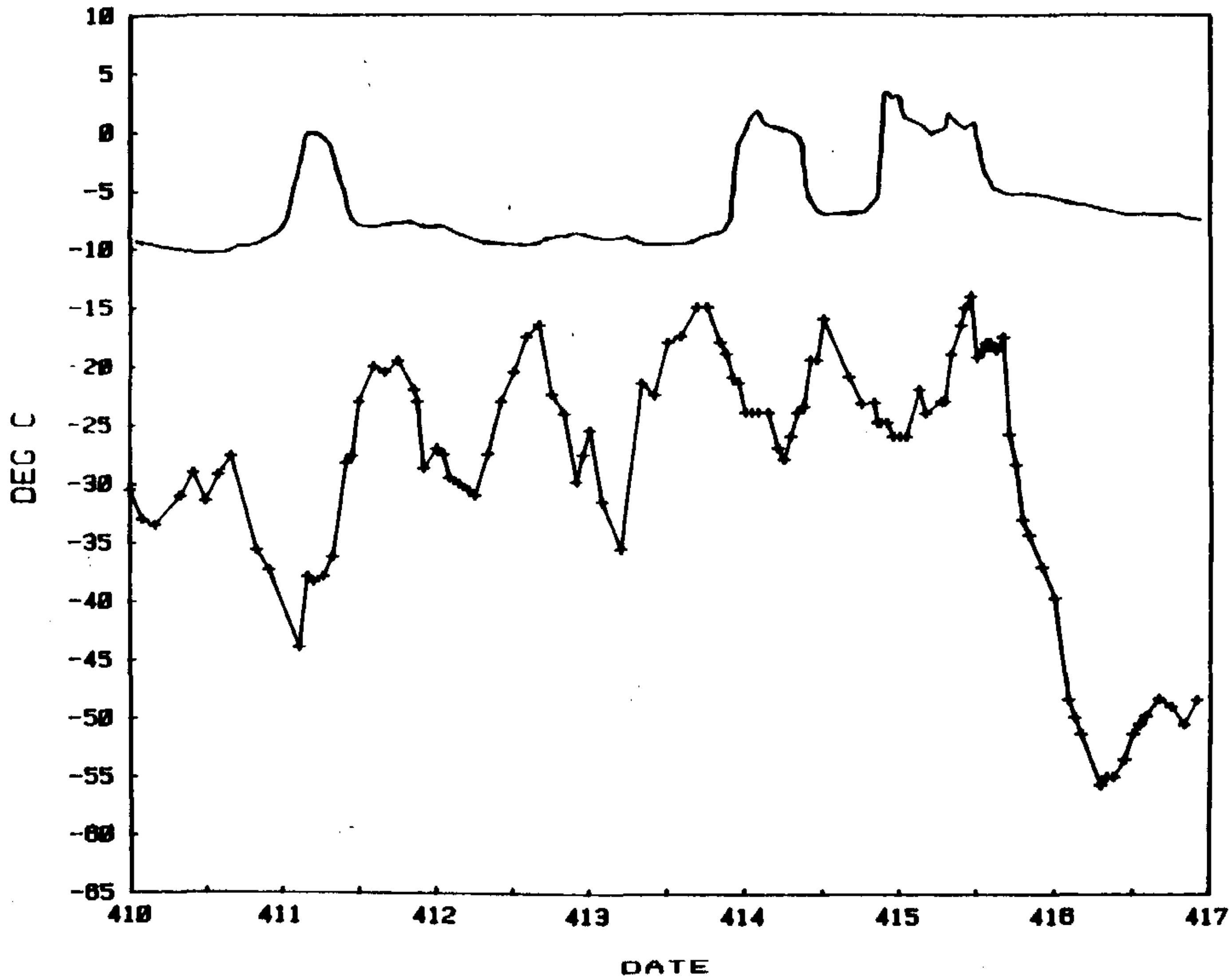

Figure 26. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84C095 between 10 and 17 April 1984.

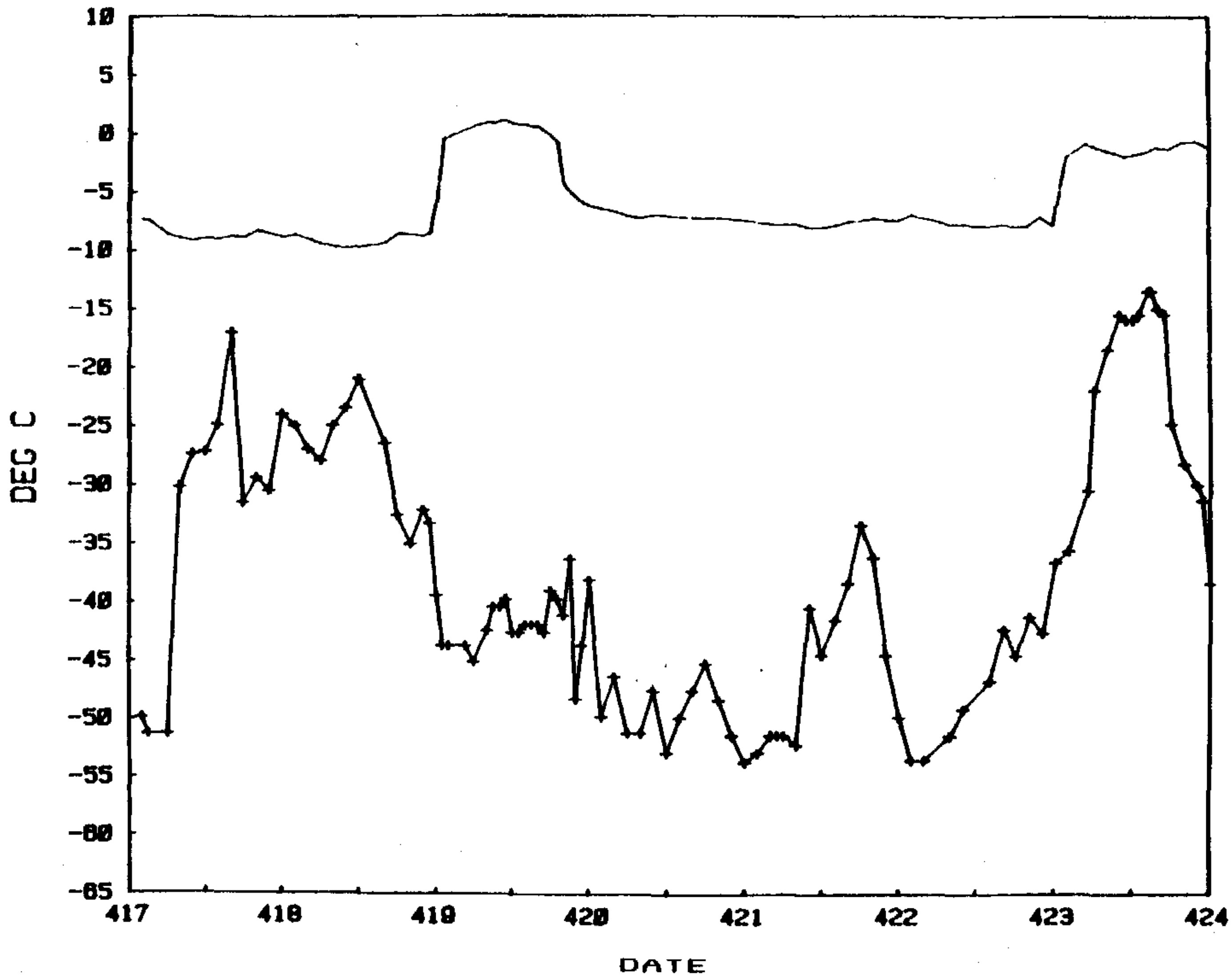

Figure 27. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84C095 between 17 and 24 April 1984.

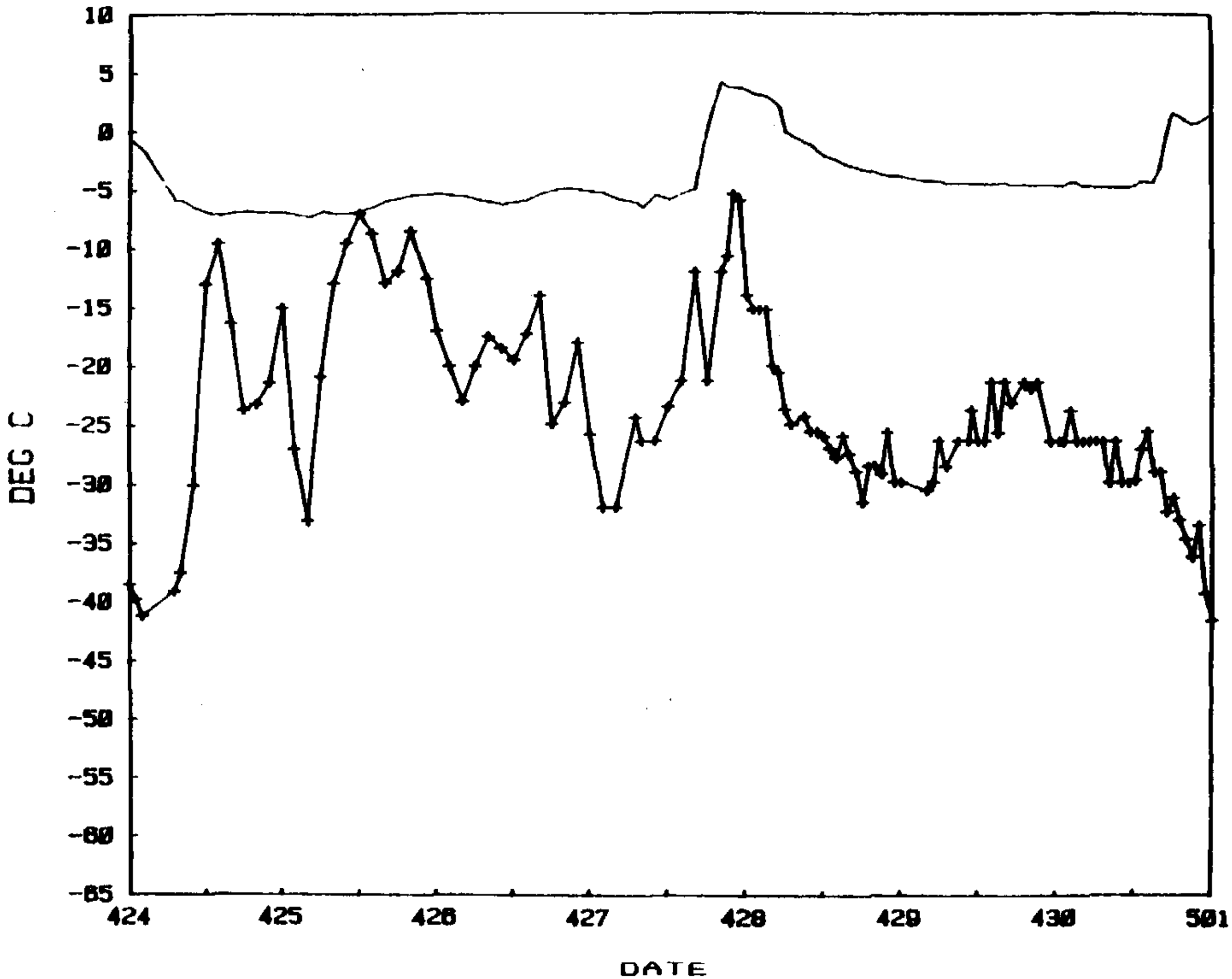

Figure 28. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84C095 between 24 April and 1 May 1984.

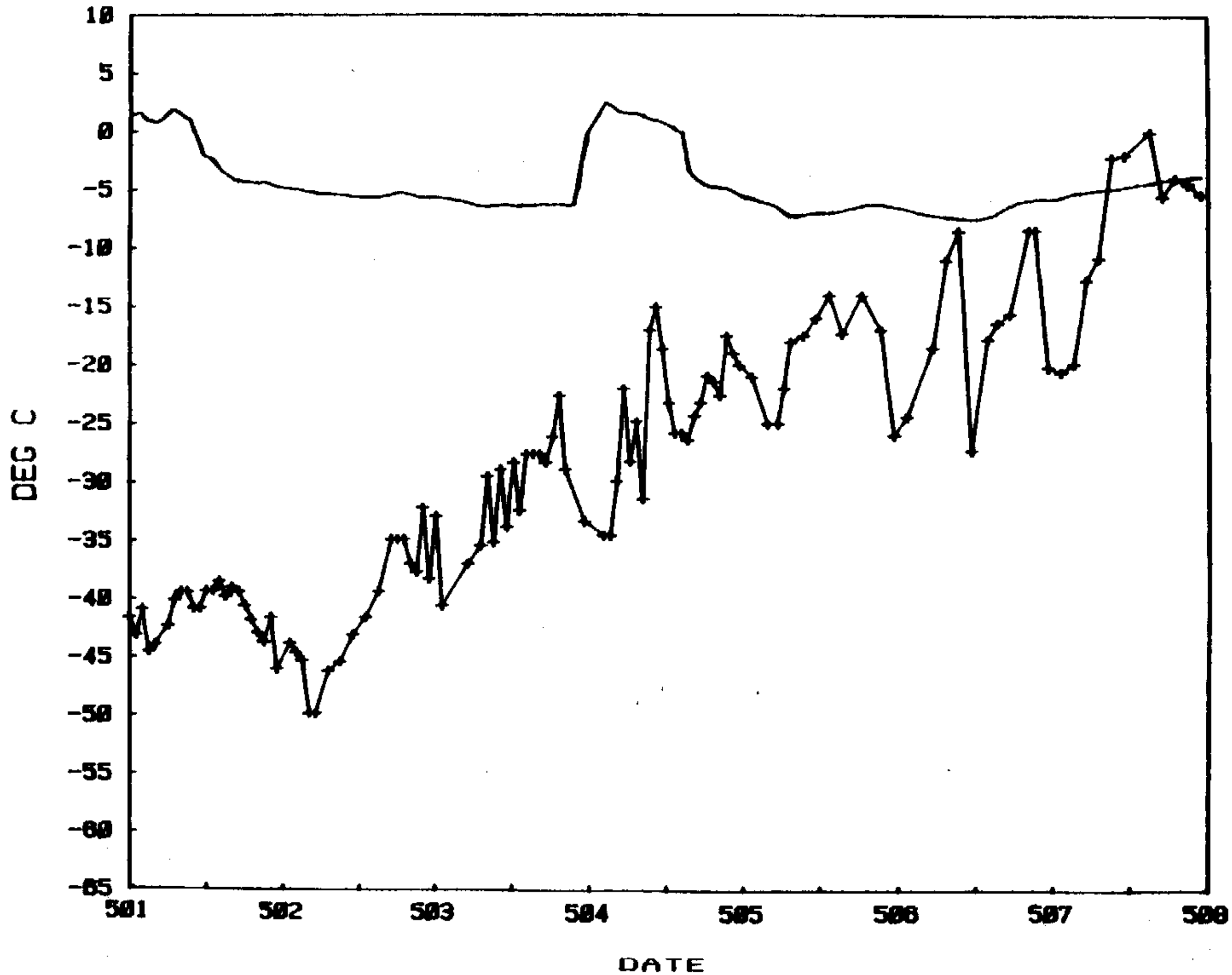

Figure 29. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84C095 between 1 and 8 May 1984.

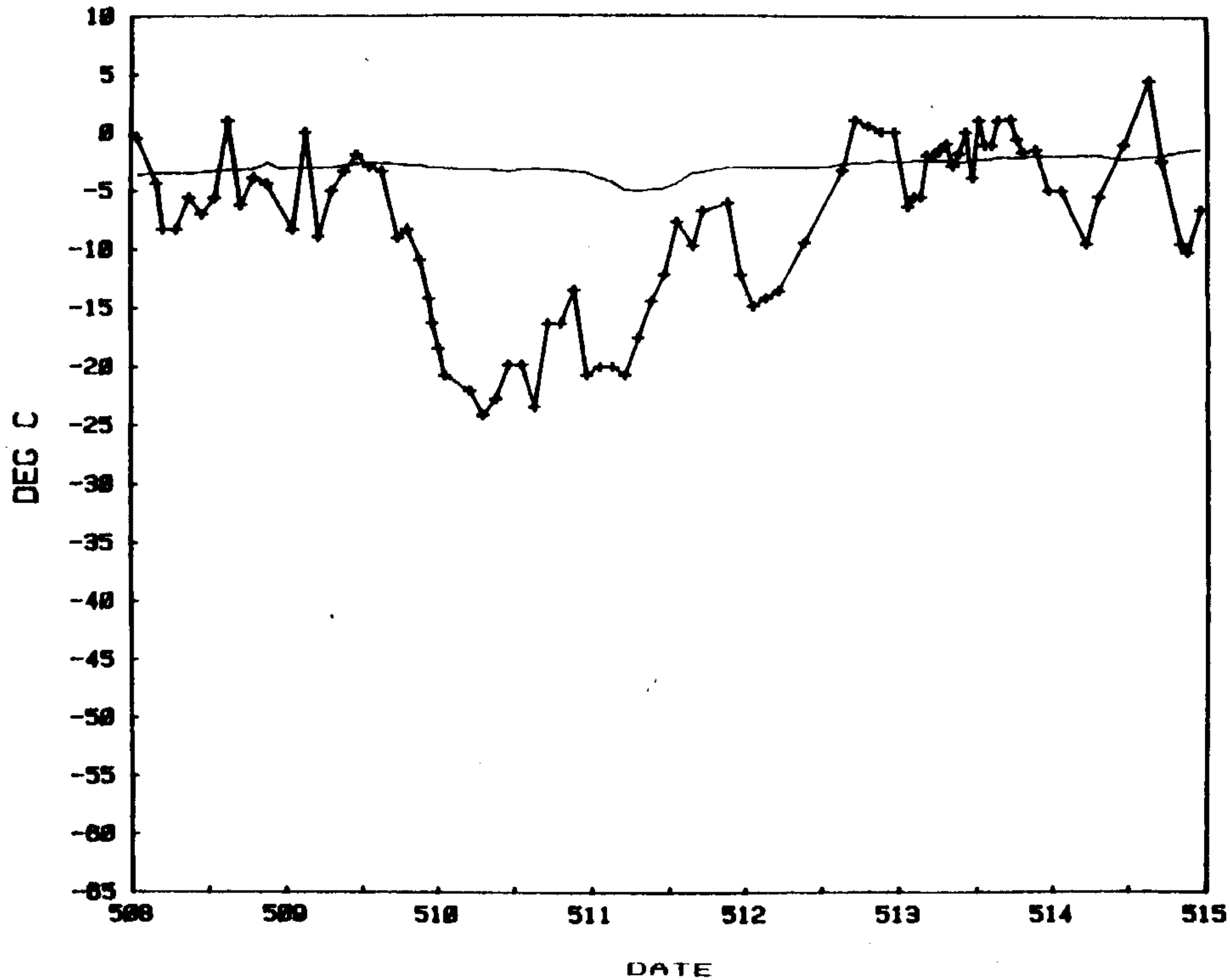

Figure 30. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84C095 between 8 and 15 May 1984.

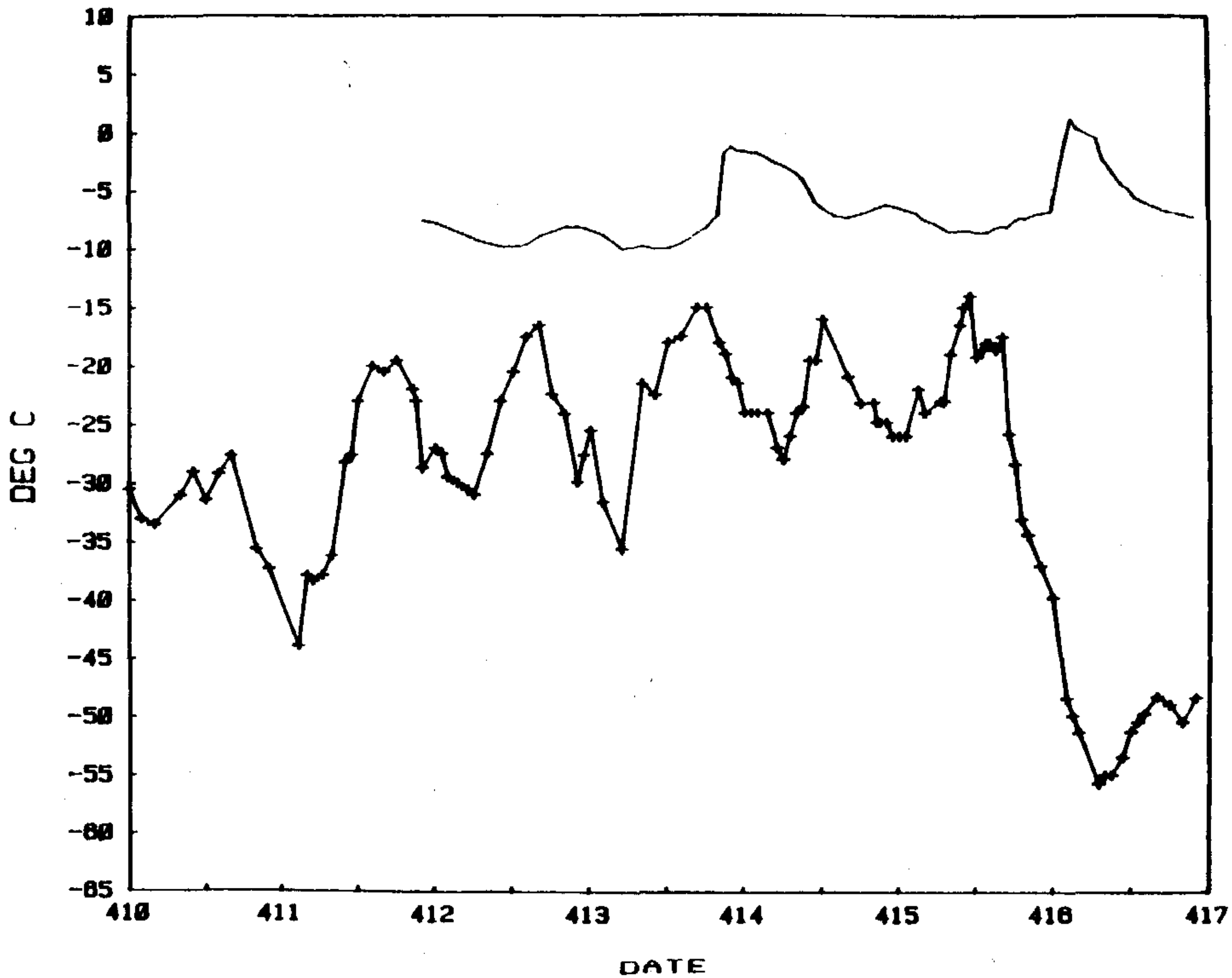

Figure 31. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H113 between 10 and 17 April 1984.

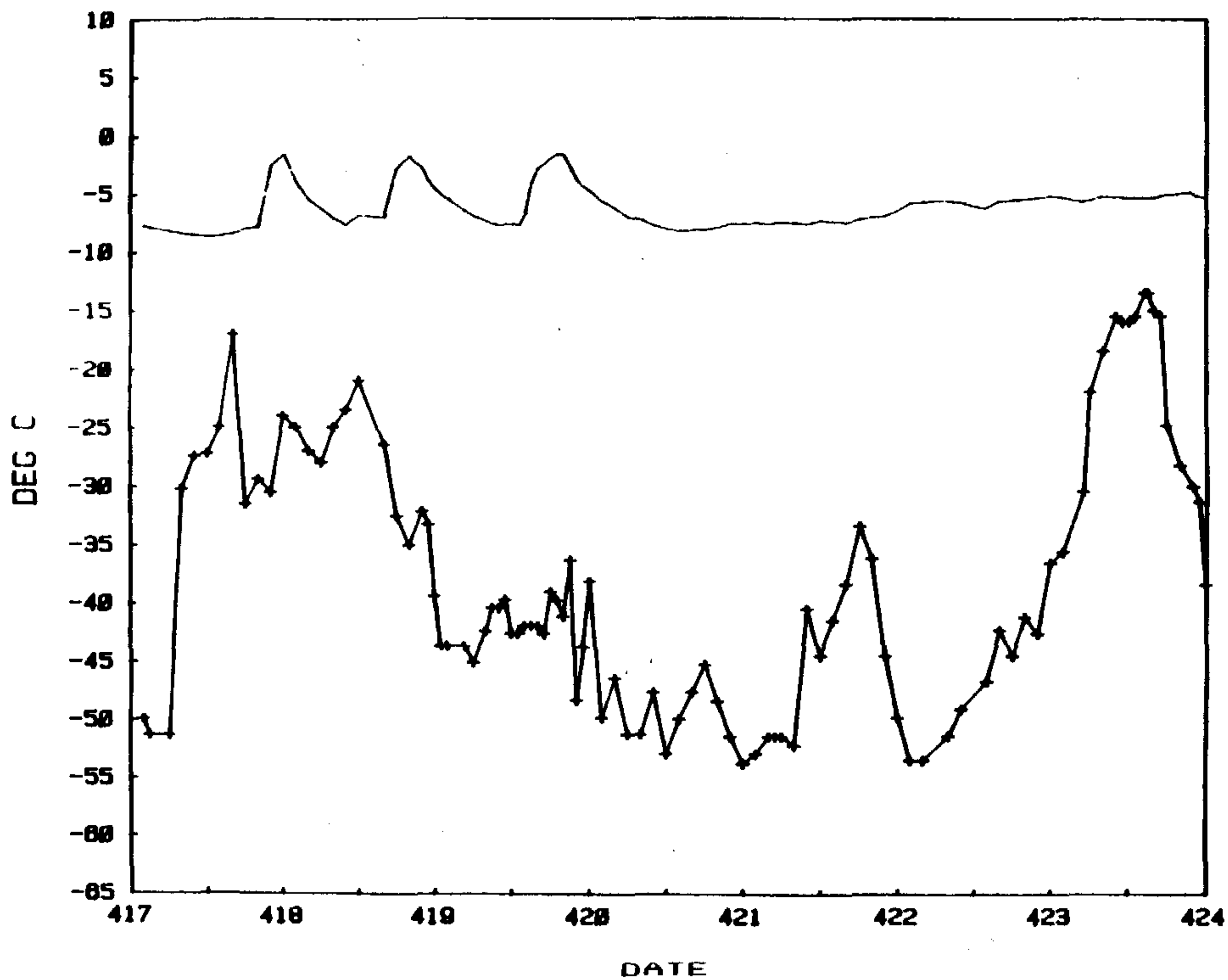

Figure 32. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H113 between 17 and 24 April 1984.

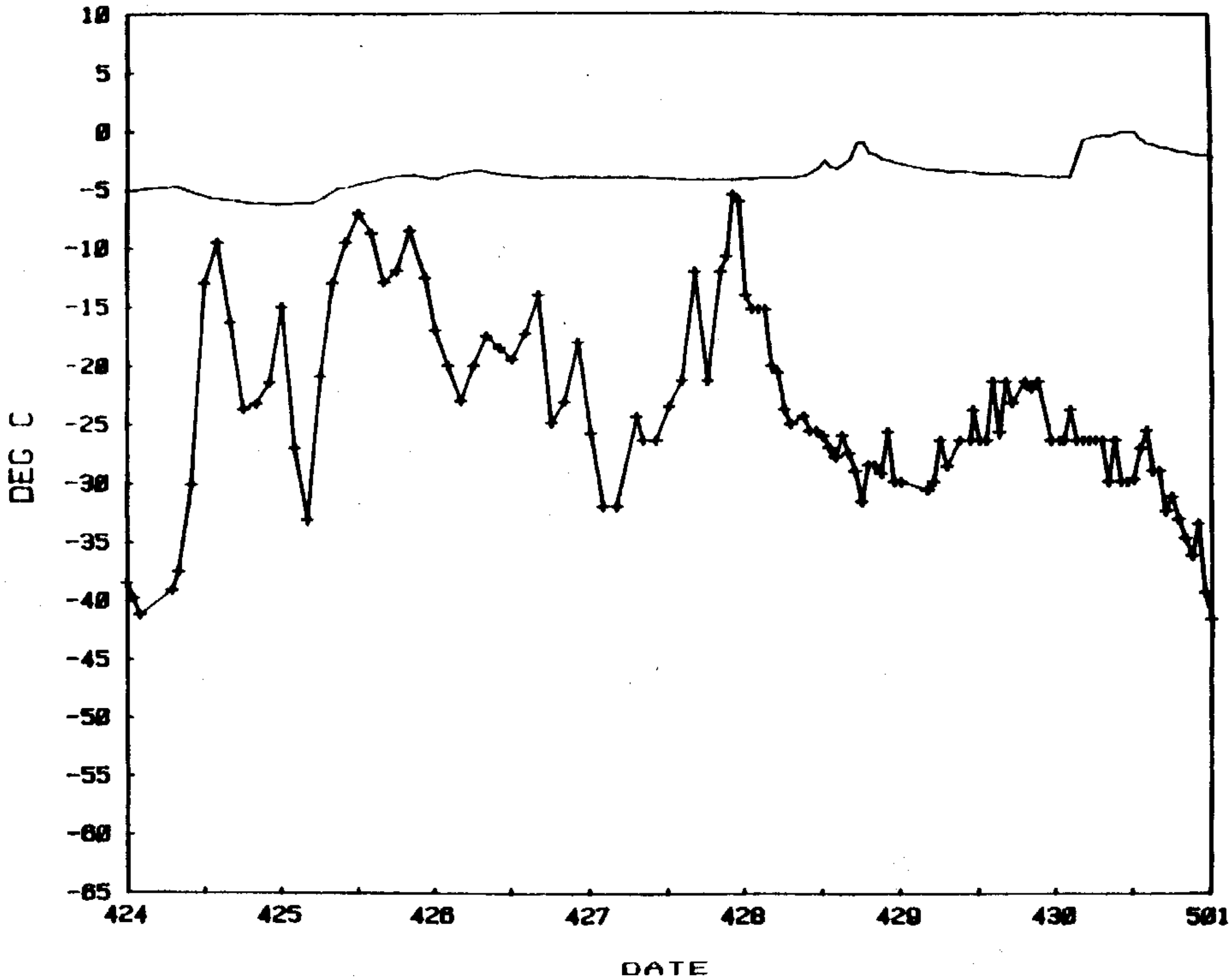

Figure 33. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H113 between 24 April and 1 May 1984.

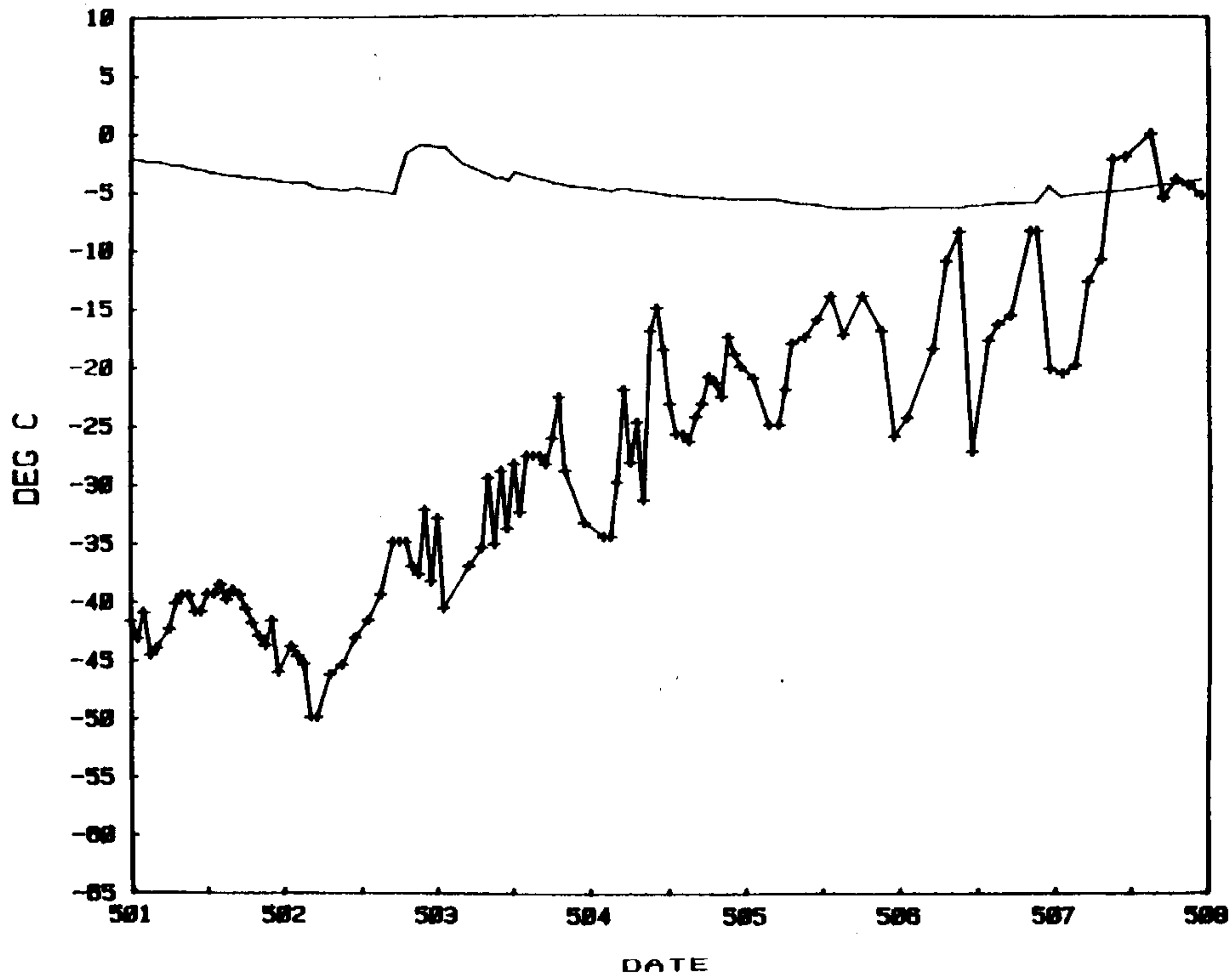

Figure 34. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H113 between 1 and 8 May 1984.

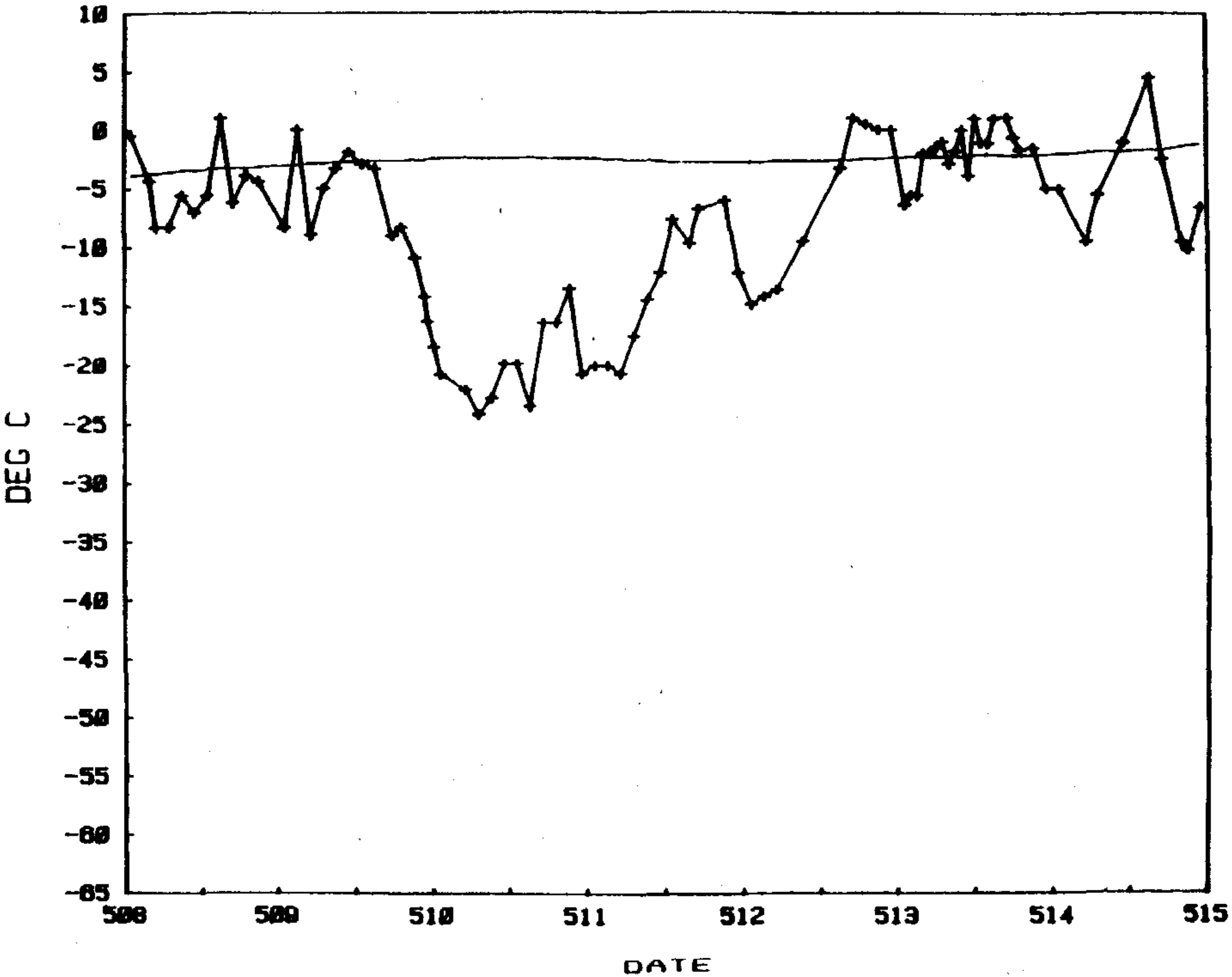

Figure 35. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H113 between 8 and 15 May 1984.

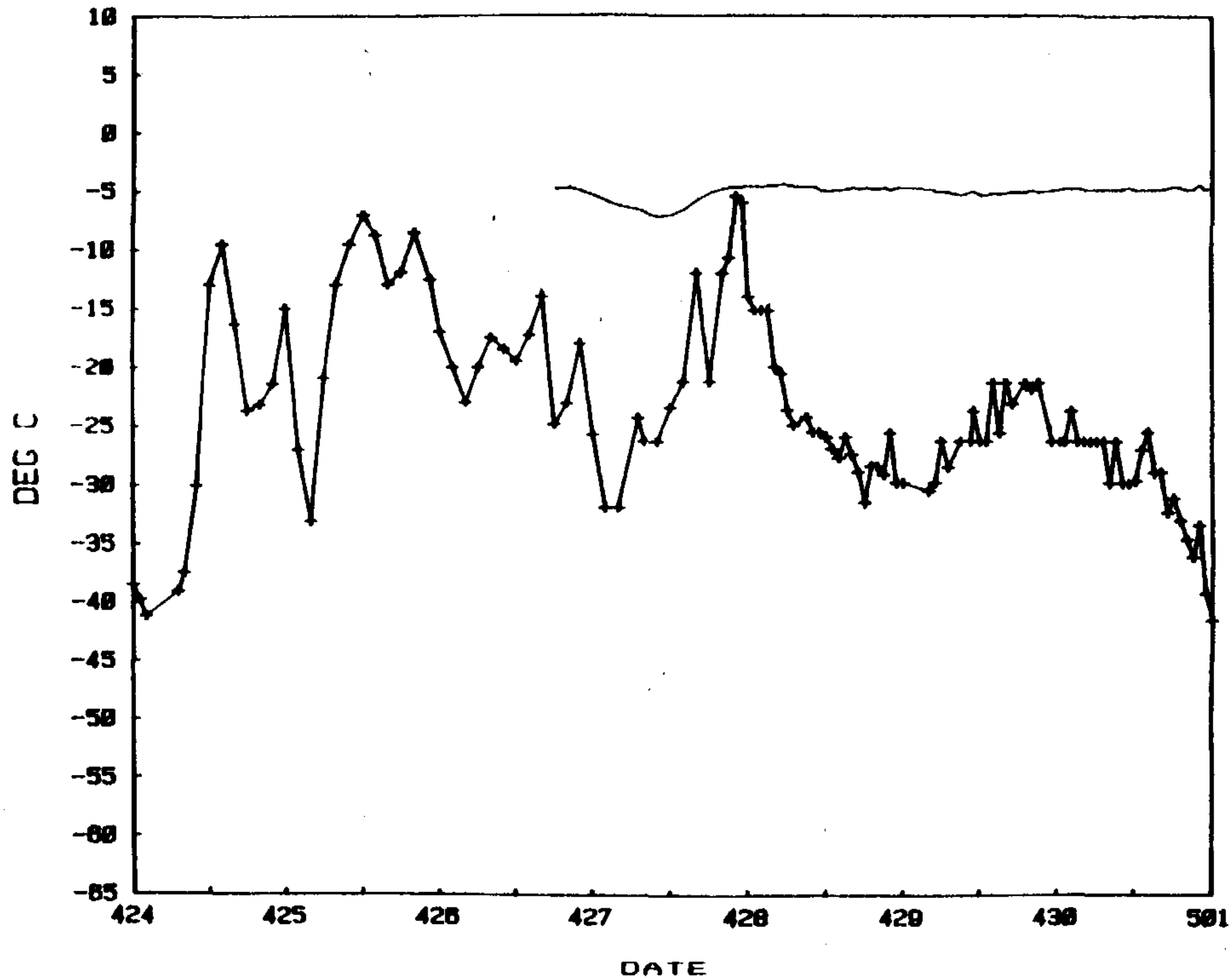

Figure 36. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H023 between 24 April and 1 May 1984.

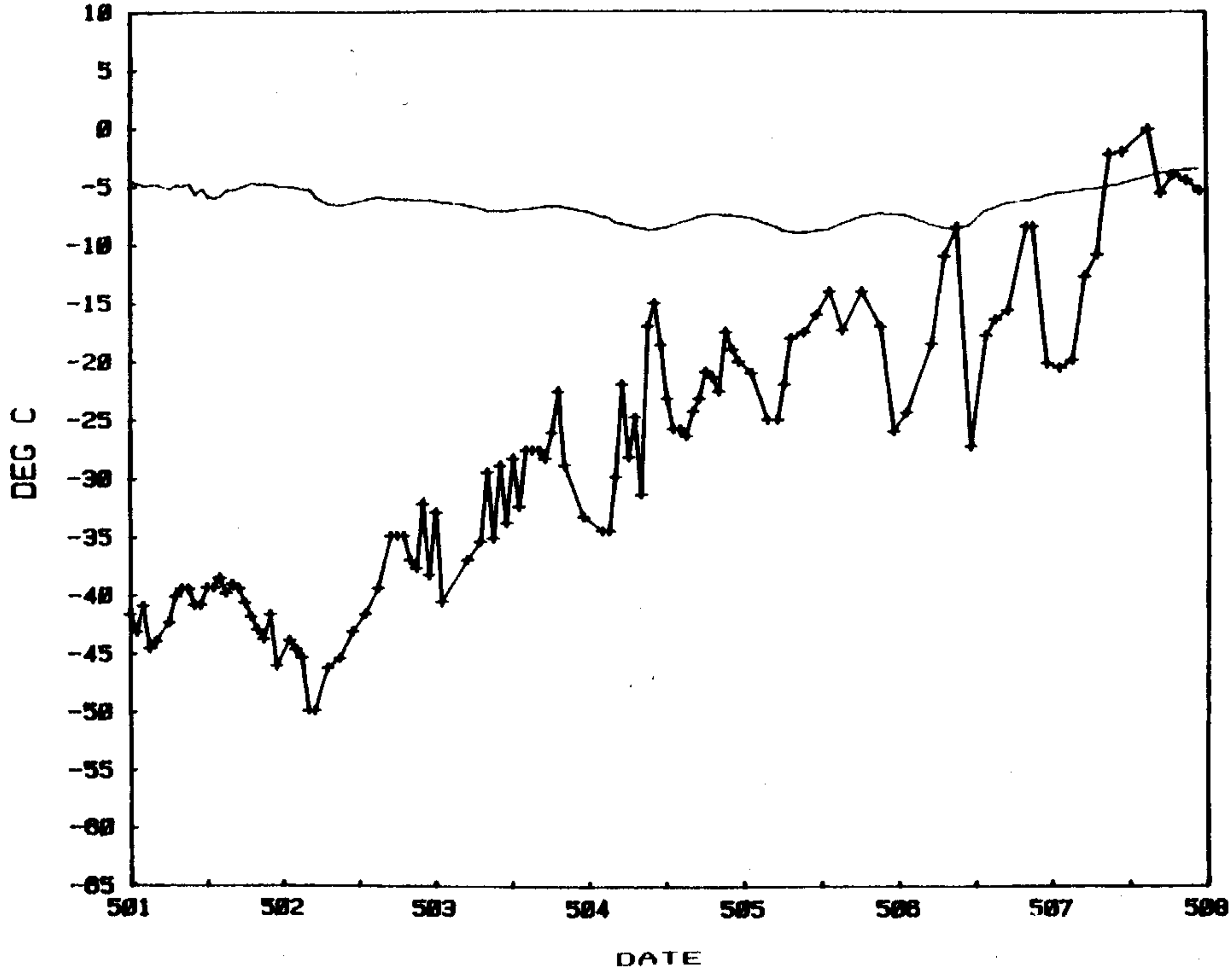

Figure 37. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H023 between 1 and 8 May 1984.

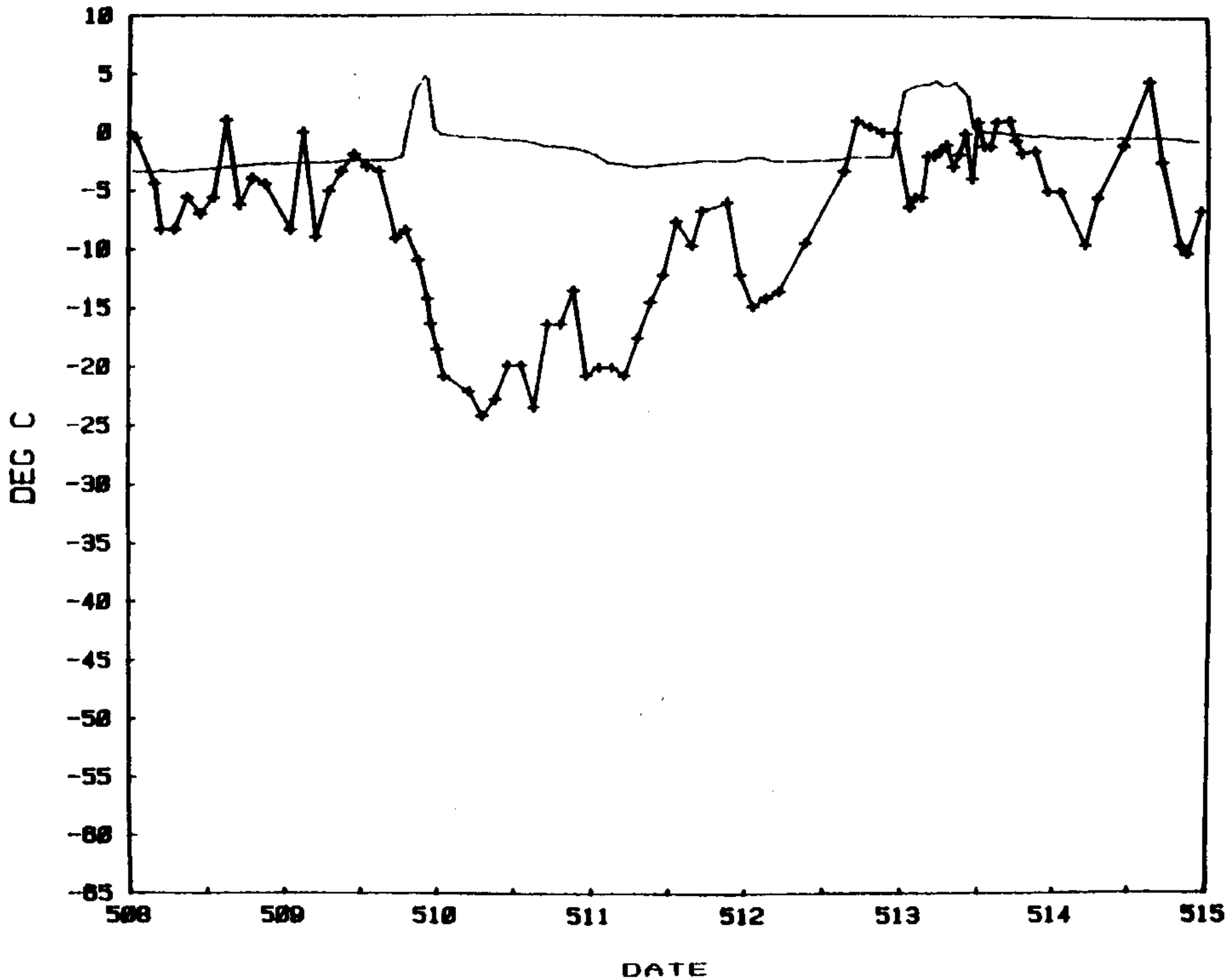

Figure 38. Internal (solid line) and outside (line with crosses) air temperature (corrected for wind chill effect) at lair 84H023 between 8 and 15 May 1984.

in response to the seismic surveys. It is clear, however, that they did not permanently abandon their established lairs. Table 17 details the structures used by those seals and the distance to the nearest seismic survey line.

Three of the five seals radio-tagged in 1983 occupied lairs in the vicinity of seismic survey lines (Figure 2). TI-83 and GI-83 were tagged before the simulated seismic surveys; LR-83 was tagged afterward.

Not only during the seismic surveying, but throughout April, TI-83 tended to haul out mostly at night (Figure 7a). His signal was never received during the daytime when the seismic convoy was operating, but he did haul out most evenings during that period. Two exceptions were 26 and 27 April (third and final days of seismic convoy operations), when he did not haul out at all during the 24 hour cycle. A typical evening haul-out was recorded again on 28 April.

GI-83 tended to haul out in the midday more than did TI-83 (Figure 11). During late March and early April, he commonly spent periods as long or longer than 20 hours in his lair. On 21 April, he began a haul-out at 0550 hours, approximately 1.5 hours before the seismic convoy entered the study area. That haul-out ended at 1701 hours when the advancing convoy was 644 m from his lair (83H024). The Vibroseis was idling between sweeps when GI-83 dove. Holliday *et al.* (1984) estimated noise levels received at GI-83's lair at that time as: 136 dB re 1 micro Pa (underwater); 69 dB re 20 micro Pa (airborne); 40 dB re 10^{-8} m/s (vertical vibration). No signal was received from GI-83 the next day and only a brief, weak signal, (not from lair 83H024) was received on 23 April. Five additional haul-outs by GI-83 were recorded thereafter, at least two of them from lair 83H024. The last was a brief bout (1555 to 1645 hours) on 26 April. On 17 May, we excavated lair 83H024 and found signs of its continuing use as a haul-out site. We were unable to ascertain whether GI-83 or some other seal was using the lair at that time.

LR-83 was radio-tagged after the simulated seismic survey was completed. Her haul-out sites were between seismic lines A and C (Figure 2), and her birth lair probably was in use prior to the seismic survey. She continued to use that lair as late as 4 June, more than one month after the seismic survey.

In addition to the seals' responses to the seismic survey convoy and related activities, we recorded responses to noise generated by helicopters (Table 18), snow machines and other equipment operating on the ice (Table 19), and people walking and skiing on the ice (Table 20). In those cases where the seals' response is shown as "departed," we judged that they did so in response to human activity. In some cases their departures may have been coincidental with, but not in response to human activities.

Responses to helicopter noise tended to vary with altitude of the machine and its lateral distance from the haul-out site. Seals did not leave their haul-out sites in response to helicopter flights at or above an altitude of 457 m. Departures were observed in 8 of 15 (53%) instances when helicopters were at altitudes of 305 m or less. Seals departed in 6 of 9 (67%) instances at that altitude when helicopters were within 2 km (lateral distance) of the haul-out site. At distances greater than 2 km, helicopters at or below 305 m caused 2 of 6 (33%) seals to depart their haul-out sites.

The responses to machinery operating on the ice also varied considerably. Snow machines operating as far as 2.8 km from a haul-out site, at times caused a seal to depart (Table 19). At other times, snow machines within 0.5 km did not cause a departure.

People moving on the ice caused seals to depart haul-out sites from as far as 600 m but generally not until within 200 m (Table 20). Seals departed in 8 of 17 (47%) episodes of people walking at distances of 0.2 to 1.0 km from the lairs. Skiers at the same ranges resulted in 4

Table 17. Subnivean seal structures utilized by radio-tagged ringed seals in 1982 and their distances from seismic survey lines.

Seal no.	Subnivean structure	Nearest seismic line (m)
BA-82	82B040	129
BA-82	82H160	400
SA-82	82B045	37
SA-82	82H161	700
BE-82	82B036	19
BE-82	82H162	250

Table 18. Responses of hauled out seals to helicopter noise. Durations given are of haul-out bouts during which seals were exposed to helicopter noise and of subsequent nonhaul-out bouts in those cases when seals departed (went into the water) when exposed to helicopter noise.

Date	Time	Seal no.	Helicopter altitude (m)	Approximate distance to lair (km)	Seal's response	Bout durations (hours) Haul-out/Nonhaul-out
4/24/82	1020	BA-82	Landing	1.0	Departed	? / ?
4/29/82	1140	BA-82	Landing	3.0	Departed	1 / ?
4/30/82	1800	SA-82	Landing	2.5	Remained	12 / --
5/23/82	1030	BA-82	Landing	3.0	Remained	? / --
5/23/82	1036	BE-82	Landing	4.0	Remained	? / --
5/23/82	1430	BA-82	Takeoff	3.0	Remained	? / --
4/24/83	1349	GI-83	61	1.9	Remained	23 / --
5/17/83	1300	DQ-83	122	0.6	Remained	10 / --
5/17/83	1300	TI-83	122	1.9	Remained	10 / --
5/18/83	1930	JO-83	122	1.0	Departed	10 / 36
4/26/82	1330	BE-82	152	0	Departed	1 / 2
3/30/83	1151	GI-83	152	5.0	Departed	4 / 4
4/18/83	1205	GI-83	198	0.8	Departed	13 / 2
4/30/82	0945	SA-82	305	0	Departed	? / 3
4/12/84	1315	LK-84	305	0.6	Remained	12 / --
5/28/82	1045	SA-82	457	4.0	Remained	? / --
5/28/82	1045	BE-82	457	4.5	Remained	? / --
4/11/83	1640	DQ-83	762	0	Remained	? / --
5/04/83	1345	JO-83	914	0	Remained	7 / --
5/04/83	1345	DQ-83	914	0	Remained	16 / --

Table 19. Responses of hauled out seals to machinery on the ice. Durations given are of haul-out bouts during which seals were exposed to machinery noise and of subsequent nonhaul-out bouts in those cases when seals departed (went into the water) when exposed to machinery noise.

Date	Time	Seal no.	Machinery	Approximate distance to lair (km)	Seal's response	Bout durations (hours) Haul-out/Nonhaul-out
4/21/83	1701	GI-83	Vibroseis convoy	0.6	Departed	11 / 42
4/30/82	1500	SA-82	Hovercraft	2.5	Remained	12 / --
4/30/82	1700	SA-82	Two snow machines	0.5	Remained	12 / --
5/18/82	1530	SA-82	Snow machine	0.5	Remained	10 / --
3/29/83	1015	GI-83	Snow machine	0.5	Departed	1 / 22
3/25/84	1437	LK-84	Snow machine	0.5	Departed	10 / 2
4/01/85	1530	LK-84	Snow machine	0.6	Departed	14 / 19
3/07/84	1457	? basking	Snow machine	1.2	Departed	? / ?
4/08/84	2030	LK-84	Snow machine	1.6	Departed	7 / 1
4/11/84	1830	LK-84	Snow machine	2.2	Departed	10 / 6
4/14/84	2146	LU-84	Snow machine	2.8	Departed	0.6 / 46

Table 20. Responses of hauled out seals to noises of people and dogs moving on the ice. Durations given are of haul-out bouts during which seals were exposed to noises of people or dogs moving on the ice and of subsequent nonhaul-out bouts in those cases when the seal departed (went into the water) when exposed to the noise.

Date	Time	Seal no.	Noise	Approximate distance to lair (km)	Seal's response	Bout durations (hours) Haul-out/Nonhaul-out
4/19/82	1530	BA-82	Two walkers	0.1	Departed	? / ?
5/06/82	1740	SA-82	One walker	0.1	Departed	0.6 / 0.3
5/07/82	0741	BE-82	One walker	0.1	Departed	3 / 8
5/09/83	1159	LR-83	One walker	0.1	Departed	3 / 35
4/21/82	0815	BA-82	One walker	0.2	Remained	4 / --
4/30/83	1750	TI-83	Two walkers	0.2	Remained	5 / --
5/04/83	1220	TI-83	Two walkers	0.2	Remained	5 / --
5/07/83	1540	DQ-83	One walker	0.2	Departed	7 / 18
3/21/84	2200	HU-84	One walker	0.2	Remained	11 / --
5/14/82	1823	SA-82	One walker	0.4	Departed	4 / 38
4/11/83	2030	DQ-83	Two walkers	0.4	Departed	4 / 46
5/06/83	1655	DQ-83	One walker	0.4	Departed	6 / 16
3/25/84	1100	LK-84	One walker	0.4	Remained	10 / --
3/27/84	1200	LK-84	One walker	0.4	Remained	8 / --
3/31/84	1200	LK-84	One walker	0.4	Remained	6 / --
5/28/82	1415	SA-82	Two walkers	0.5	Departed	2 / ?
3/24/83	1530	GI-83	Two walkers	>0.5	Departed	1 / 17
5/12/83	1600	DQ-83	One walker	0.5	Remained	6 / --
4/22/83	0034	TI-83	Two walkers	0.6	Departed	2 / 23

Table 20 (continued).

Date	Time	Seal no.	Noise	Approximate distance to lair (km)	Seal's response	Bout durations (hours) Haul-out/Nonhaul-out
3/26/84	2123	HU-84	One walker	0.6	Departed	6 / 124
4/18/84	1945	LU-84	One walker	1.0	Remained	17 / --
3/25/84	1830	LU-84	One walker	?	Remained	4 / --
3/26/84	2200	LU-84	One walker	?	Remained	7 / --
4/17/84	2253	NA-84	One walker	?	Departed	3 / 22
4/19/84	2200	NA-84	One walker	?	Remained	2 / 2
4/24/83	2000	TI-83	Skier	0.2	Remained	6 / --
5/27/83	0100	LR-83	Skier	0.2	Remained	9 / --
5/28/83	1300	LR-83	Skier	0.2	Remained	7 / --
3/08/84	1400	HU-84	Skier	0.2	Remained	11 / --
3/31/84	1926	LU-84	Skier	0.2	Departed	2 / 204
4/03/84	2130	ZO-84	Skier	0.2	Remained	9 / --
4/23/83	0000	TI-83	Skier	0.3	Remained	3 / --
5/29/83	1416	TI-83	Skier	0.3	Departed	7 / 19
4/24/83	1300	GI-83	Skier	0.4	Remained	23 / --
4/28/83	2000	TI-83	Skier	0.4	Remained	5 / --
5/18/83	1300	TI-83	Skier	0.4	Remained	12 / --
5/26/83	2000	TI-83	Skier	0.4	Remained	12 / --
3/26/84	1130	LK-84	Skier	0.4	Remained	12 / --
4/01/84	1300	LK-84	Skier	0.4	Remained	13 / --
4/02/84	1300	LK-84	Skier	0.4	Remained	7 / --
4/03/84	1300	LK-84	Two skiers	0.4	Remained	8 / --

Table 20 (continued).

Date	Time	Seal no.	Noise	Approximate distance to lair (km)	Seal's response	Bout durations (hours) Haul-out/Nonhaul-out
4/04/84	1400	LK-84	Skier	0.4	Remained	7 / --
4/08/84	1600	LK-84	Skier	0.4	Remained	7 / --
4/10/84	1200	LK-84	Skier	0.4	Remained	4 / --
4/11/84	1330	LK-84	Skier	0.4	Remained	10 / --
4/18/84	1130	LK-84	Skier	0.4	Remained	11 / --
5/23/83	1600	LR-83	Skier	0.4	Departed	6 / 24
4/09/84	2200	ZO-84	Skier	0.4	Departed	2 / 22
3/07/84	1630	LU-84	Skier	0.5	Remained	7 / --
3/17/84	2000	HU-84	Skier	0.6	Remained	13 / --
3/10/84	1300	HU-84	Skier	1.0	Remained	14 / --
4/15/84	1310	ZO-84 basking	Skier	1.5	Departed	5 / 50
4/15/83	1250	GI-83	Dog running	0.05	Departed	4 / 58

departures in 26 (15%) episodes. The difference in the frequency of departures in reponse to people walking versus skiing is significant ($Z = 2.27$, $p < 0.05$).

Of 30 haul-out bouts that were disrupted by human activities (helicopters, snow machines, heavy equipment, foot traffic) the mean length of the disturbed haul-out bouts was 5.0 hours (S.D. = 3.77), not significantly different from the mean length (5.4 hours) of nondisturbed haul-out bouts ($t_s = 0.512$, $df = 58$). Periods of nonhaul-out subsequent to those disturbances averaged longer (30.4 hours) than nonhaul-out episodes not preceded by disturbance (18.9 hours) but the difference was not statistically significant ($t_s = 1.51$, $df = 58$).

DISCUSSION

Ringed seals use thick claws on their pectoral limbs to create and maintain the breathing holes which allow them to survive in areas of complete ice cover. They also use their pectoral limbs to excavate subnivean lairs in which haul-out is confined during the coldest weather. The ability to occupy areas of unbroken ice allows ringed seals to take advantage of food sources denied to species that must seasonally migrate to areas of less extensive ice cover. Occupation of areas of unbroken ice and dependence on breathing holes and lairs also makes ringed seals more vulnerable to predation by polar bears, arctic foxes, and man. Increasingly, human activities on the ice (especially stable, unbroken ice), extend beyond hunting and include industrial development. Noise associated with that development may adversely affect ringed seals and assessment of such effects requires detailed information about ringed seal ecology. Ecological concerns relevant to potential noise impacts include: (1) the areal distribution of subnivean seal structures, (2) the temporal distribution of those structures, (3) the temporal patterns of haul-out on the ice, (4) the numbers of seals utilizing individual subnivean structures and the number of structures utilized by individual seals, and (5) the nature of the seals' dependency on subnivean structures.

Areal Distribution of Subnivean Seal Structures

The pupping habitat of ringed seals was believed to be confined generally to shore-fast ice (McLaren 1958; Burns 1970; Smith 1973a), areas important for seismic profiling and gravel island construction. Recent evidence suggests that the drifting pack ice also may be important pupping habitat for ringed seals (Lentfer 1972; Finley *et al.* 1983; Burns unpublished data), hence ice-breaking ships also may create additional sources of disturbance to ringed seals during the critical periods of pupping and nursing.

The distribution of ringed seal lairs is influenced by the depth of snow on the ice; a minimum of 20 cm is required for lair construction (McLaren 1958; Smith and Stirling 1975; Burns and Kelly 1982). Shallow drifts limit the amount of insulation to the lair. Insufficient insulation can result in the lair being abandoned, as we observed in central Kotzebue Sound in 1984, and/or freezing of the newborn pup (Lukin and Potelov 1978). We think that the relatively low ratio of lairs to breathing holes in Kotzebue Sound in 1984 resulted from minimal snow depth and that it probably contributed to the low productivity of seals. Ice deformation of sufficient relief to promote deep drifts also can limit lair distribution. Areas of flat ice often contain breathing holes but cannot accommodate lairs. Even given adequate snowfall and ice deformation, suitably deep snow drifts still may not form if wind direction is erratic. Frequent changes in wind direction result in small, unstable drifts with few lairs, as we saw in northern Kotzebue Sound in 1984.

Breathing holes do not have the same requirement for insulating snow cover as do lairs and can be found in areas of essentially no snow cover and no deformation. Our aerial surveys indicated reduced frequencies of seals in areas of greater than 40% ice deformation, perhaps because seals are less likely to be ambushed by polar bears on the flatter ice (Burns *et al.* 1981). Comparisons of seal densities in rough and flat ice are confounded, however, by the fact that seals are more difficult to see when they are hauled out in the rougher ice.

Water depth was comparatively uniform in both of our study areas, hence could not have influenced the distribution of seal holes there. Several breathing holes and lairs were found in locations where water depth under the ice was less than 2 m. Aerial surveys in the eastern Beaufort Sea have suggested a slight preference by basking seals (June) for water depths from 50 to 100 m (Stirling *et al.* 1982).

Smith and Stirling (1975) gave the mean distance between breathing holes in one area as 233 m (S.D. = 163) and between lairs as 124 m (S.D. = 105). Those distances probably exhibit great variation from place to place, depending on the density of seals in the area, the snow cover, and the ice conditions. They also described "lair complexes," which were clusters of lairs around pupping lairs and within 3 to 65 meters of one another. Such complexes were thought to provide alternative haul-out sites for pups and thus some protection from predators. We found adult males as well as females (including those with pups) using more than one lair, although generally separated by greater distances (up to 4 km) than described by Smith and Stirling (1975). Smith and Hammill (1981) suggested that female ringed seals maintain under-ice territories around birth lair complexes, and that several of those territories are contained within a larger territory maintained by a male. We found some support for that idea in the distribution of breathing holes and lairs used by radio-tagged seals. Distances between structures used by individual males averaged almost three times as great as distances between structures used by individual females. We have no direct evidence of territorial behavior, but the abandonment of lair 84C095 by a subadult male, HU-84, may have been the result of displacement by another seal. His occupation of that lair decreased in April, when another seal began occupying it more frequently.

Temporal Distribution of Subnivean Structures

Ringed seals begin to maintain breathing holes through the ice when it first forms in the autumn. Excavation of lairs must await the accumulation of sufficient snow depth which usually can be found by late February. Lairs with "pup tunnels" are first evident shortly after the onset of pupping in late March. By then, seal holes frequently are found in ice two or more meters thick, indicating that those holes must have been maintained for several months as the ice thickened. The distribution of seal holes, however, does not remain static throughout the winter. We have observed several instances in which seals opened new holes when cracks formed late in the winter, even in the relatively stable ice of southern Kotzebue Sound. Over the course of several days in April, a lair, eventually occupied by a female and pup, was excavated in the snow above a breathing hole that was opened in a new crack. Breathing holes remain important until ice break-up, but lairs are abandoned when the snow begins to soften, generally in late May or early June along the coast of Alaska.

Frequency and Duration of Haul-out Bouts

From March to early June, ringed seals tend to spend increasingly longer periods hauled out. At the same time, there is a shift from generally arhythmic to a rhythmic pattern, with a strong peak in the midday period. These longer periods out of the water may be necessitated by the onset of new hair growth, which can span three months (Ashwell-Erickson *et al.* 1986).

Growth of new hair apparently requires sustained epidermal temperatures above those which can be attained in the water (Feltz and Fay 1966). Molting (shedding) of the old hair begins while lairs are still being used and continues through the basking season (pers. obs.). During the molt, seals are more subject to stress (Ronald *et al.* 1970; Geraci and Smith 1976) and thus may be more sensitive to noise disturbances at that time.

Females caring for pups especially increased the frequency and length of haul-out bouts after parturition. Post-parturient females and their pups spent more time in lairs than did males or nonlactating females, confirming that they are especially vulnerable to disturbance during the nursing period. On-ice industrial activities thus are likely to have negative effects on ringed seals during midday from late March to late May.

The radio-tagged seals generally spent 80% or more of their time in the water, but we can do little more than speculate on their activities under the ice. The under-ice range of ringed seals remains unknown and probably varies with prey availability, breeding status, and access to air. Female seals may range beyond the vicinity of their lairs prior to pupping and after the pup is weaned, but care of the young may restrict them during the nursing period. Similarly, males may range more extensively outside of the breeding season than during that season when they presumably maintain under-ice territories. Prey distributions may be patchy in time and space which would favor extended underwater ranges, although little is known about the distribution and abundance of ringed seal prey in winter. Access to air may limit under-ice movements in areas of extensive, flat ice cover but may not be a problem where the ice is highly deformed or leads are numerous. The long periods of nonhaul-out by radio-tagged seals in Kotzebue Sound and the high density of breathing holes there suggested that those seals may have been unrestricted in under-ice range.

Relationship Between the Number of Seals and the Number of Holes

Our data have shown that, in most instances, each ringed seal maintains more than one lair and that two or more seals may share maintenance of several breathing holes. Preventing breathing holes from freezing over requires frequent abrading of the ice, and to share that cost with other seals is energetically efficient. We consider the average number of lairs (2.85) used by radio-tagged seals in this study to be conservative, since many haul-outs could not be ground-truthed to document the haul-out site. Seals that abandon lairs in response to the activities of predators, human beings, or other seals are likely to have one or more alternative haul-out sites, and may not be greatly disadvantaged. Alternative haul-out sites used by females (and their pups), however, are retricted to smaller areas than are those used by males. Local disturbances thus are more likely to drive females and dependent young from their normal home range. The fate of seals displaced from their home range and deprived of their regular alternate lairs is unknown.

Our data suggest that, generally, only one seal occupies a particular lair. Inuit hunters of the shore-fast ice recognize certain large lairs as being used by more than one seal (Smith and Stirling 1975) and at least one large lair (84C095) in our study was used by two or more seals. As stated previously, we think that seal may have been displaced by another, but we cannot discount the possibility that the two seals simply shared the lair. The extent to which more than one seal uses a lair remains unknown but could be investigated by further studies of radio-tagged seals and by equipping lairs with thermistors and/or microphones to detect the presence of seals. The ratio of lairs to seals would provide the basis for accurate estimates of seal numbers per unit area. The ratio could be applied to counts of lairs using trained dogs (Smith and Stirling 1978; Burns and Kelly 1982; Hammill *et al.* 1985) to yield an accurate estimate of seal density. Surveys of lairs are inexpensive relative to aerial surveys and can cover large areas. At present, however, lair surveys provide only relative indices of abundance, rather than accurate estimates of seal density.

Advantages of Subnivean Lair Occupation

The mean duration (5.4 hours) of haul-out bouts by ringed seals in lairs is close to the time required for clearance of the digestive tract (6 to 8 hours: Parsons 1977), suggesting that haul-out in lairs may be related, in part, to digestion between foraging bouts. Lair occupation also may provide protection from predators and from cold.

Predators of ringed seals other than man include gulls, ravens, wolverines, wolves, dogs, killer whales, walruses, red foxes, arctic foxes, and polar bears (Fay 1960; McLaren 1962; Burns 1970; Stirling and Calvert 1979), but only the last two are of real significance in the fast ice.

By giving birth to her pup inside of a lair, the female seal presumably protects the helpless pup to some degree from predators. Lairs help protect seals by making them invisible during haul-out and by offering a barrier through which the predator must penetrate to gain access to the prey. Nonetheless, they are not completely protected, as arctic foxes (*Alopex lagopus*) and polar bears (*Ursus maritimus*) can detect them in the lair by smell and then penetrate the lair by digging or, in the case of polar bears, sometimes by jumping on and collapsing the lair (Smith 1976, 1980).

Despite repeated examinations of many of the lairs in the Beaufort Sea study area, we found only 13.6% to have been entered by arctic foxes, in contrast to 30.5% found by Smith (1976) in eastern Amundsen Gulf. Smith found the average annual predation rate by foxes to vary from 4.4% to as much as 57.7% (26.1% overall) of pup production. We examined 11 pupping lairs and found that three (27.3%) pups had been taken by foxes. Fox predation clearly varies widely from year to year and with the status of local fox populations. Foxes and pupping lairs are less numerous in the western than eastern Beaufort Sea and foxes probably have less influence on ringed seal numbers there, as well.

Arctic foxes are not known to take ringed seals older than pups, but polar bears prey on all age classes and most heavily on those under 2 years of age (Stirling and Smith 1977; Stirling and Archibald 1977). In many regions, the bears are most successful preying on ringed seals in the moving pack ice (Stirling *et al.* 1975; Stirling and Archibald 1977). In some areas, however, bears are successful hunters of seals also in the stable shore-fast ice where they catch seals both at breathing holes and in lairs (Smith 1980). Bear depredation of lairs in the shore-fast ice of the Canadian Arctic varied regionally from 1.6% to 20.3% or more, with the success rate varying between 17% and 33% of the depredated lairs. Taugbøl (1982) reported that polar bears opened 62.2% of 193 lairs that he examined in Kongsfjorden, Svalbard, and that the bears were successful in 5.8% of the lairs, apparently obtaining just pups. Polar bears rarely are seen in Kotzebue Sound, and we saw no evidence of their presence in 1984. In the Beaufort Sea, however, we saw evidence of bears in our study area both in 1982 and 1983, but found no evidence of predation. A sow with two cubs passed through our study area in 1983 and, just outside of that area, opened 10 lairs, killing at least 4 seals (S. Amstrup pers. comm.). The use of multiple lairs by individual seals probably lessens the likelihood of successful bear predation, as suggested by Smith (1980). He also suggested that many lairs in close proximity but randomly distributed, further decreased the success rate of the bears' attempts at predation.

In order to exploit arctic waters successfully throughout the year, ringed seals must be able not only to maintain holes through the ice but to maintain their deep body temperature of approximately 37°C. As with other pinnipeds, core temperature is preserved chiefly by means of the insulating blubber layer and the heterothermism of superficial tissues (Irving and Hart 1957; Fay and Ray 1968; Ray and Smith 1968; Taugbøl 1982). Because subcutaneous fat, not the hair, is the effective insulator in the water, adult seals must circulate significant amounts of blood to the periphery, in order to avoid freezing the skin. Healthy adult ringed seals appear to be thermally neutral in seawater near freezing and, probably, at much lower air temperatures. Taugbøl (1982) gave the lower critical temperature in air as -10°C, but that seems high considering that ringed seals are thermally neutral in water below 0°C. Wind chill temperatures considerably lower than -10°C occur in much of the ringed seals' range during winter. Our data indicate, however, that temperatures inside of subnivean lairs remain above -10°C even when ambient wind chill temperatures are as low as -61°C.

At birth, ringed seals have little or no blubber and rely on a woolly coat, the lanugo, for insulation. The lanugo is an excellent insulator in air but offers almost no protection from cold when wet (Ray and Smith 1968). The blubber layer is deposited during the nursing period and the lanugo is replaced by an adult-like pelage, at about the time of weaning. Before the blubber layer is deposited, ringed seal pups have little tolerance for extreme cold, especially if they are wet. The lower critical air temperature for dry pups in lanugo is close to -25°C (Taugbøl 1982), considerably above common ambient temperatures during the pupping season but much lower than the coldest temperatures we recorded inside of lairs. Taugbøl (1982) has presented evidence that pups in lanugo do escape predators by moving, or being moved, through the water to alternate lairs and that they thereafter can dry and regain thermal neutrality. The relatively great depth of snow drifts in which birth lairs are excavated may serve to provide extra insulation for the thermally vulnerable pups.

The seasonal timing of whelping may be an evolutionary compromise between warmer air temperatures later in the spring and cooler temperatures that favor the integrity of the snow covering lairs earlier in the spring. In late spring, the lairs begin to collapse from excessive warming. Whelping at that time would result in pups being exposed to relatively mild air temperatures but significant wind chills and moisture. The net result probably would be greater heat loss than is experienced by pups born earlier in lairs when outside air temperatures are still quite low.

On several occasions we recorded air temperatures of occupied lairs considerably above freezing. That such high temperatures are common in lairs is evident from our frequent observations of lair interiors showing signs of considerable melting and refreezing of the snow walls and ceiling. Contrary to the observations of Irving (1968), we often have noted signs of melting where seals have lain on the ice. In most lairs, a seal shaped depression was evident on the floor, and in some instances, large icicles hung down from the ceiling above that same depression. Frequently, a thin layer of the ceiling had partially thawed and refrozen as dense ice. That hard layer gives additional strength to the lair (making it harder to penetrate by predators) but, presumably, limits gas exchange with the outside. Lukin and Potelov (1978) suggested that the network of peripheral tunnels excavated by pups might function to increase gas exchange. The large amount of heat given off by seals in lairs indicates that they are perfusing their peripheral tissues with blood, warming the skin to comparatively high temperatures. This supports the idea that such haul-out periods are important for growth and regeneration of peripheral tissues (Fay and Ray 1968). As discussed previously, haul-out inside of lairs probably is important for new hair growth, which can begin even when outside temperatures, as well as water temperatures, would prohibit epidermal regeneration.

Proportion of Seals On the Ice During the Basking Season

Aerial surveys have been used extensively to count ringed seals basking on the ice during the molt in June (Burns and Harbo 1972; Smith 1973a,b; Stirling *et al.* 1977; Smith *et al.* 1978; Burns *et al.* 1981; Finley 1979; Kingsley *et al.* 1985). The greatest numbers of seals generally are visible in the midday period, and surveys usually are flown at that time. Although an unknown proportion of the local population remains unseen and uncounted under the ice, it is thought to be insignificant (McLaren 1966), less than 20% (Fedoseev 1971), less than 30% (Finley 1979), or as high as 50% (Smith 1973a). The counts, however, have been assumed to be reliable as indices of relative abundance when flown in the same midday period, under similar weather conditions.

The proportion of a radio-tagged sample on the ice during an aerial survey would yield an estimate of the proportion of the population that was visible. Such an estimate could be used to correct for the under-ice proportion, hence allowing an estimate of the total population. The variation in proportions of tagged samples on the ice throughout the survey period should be measured to test the assumption that the same relative proportions of local populations are basking in different areas or in the same area in different years. There may well be significant variation in that proportion even under seemingly comparable survey conditions, and estimates of the proportion of seals basking during each survey will be necessary if the area-to-area or year-to-year comparisons are to be reliable.

The timing of the molt, hence of the basking season, undoubtedly varies among individuals, depending on their sex, age, reproductive condition, general health, stability of the ice, and latitude. Harbor seal (*Phoca vitulina*) adults generally molt one month or more after yearlings (Kelly 1981), and a similar lag probably applies to ringed seals. Adult seals also vary as much as one month in the onset of basking, as we observed in both the Beaufort Sea and Kotzebue Sound. Estimates of ringed seal numbers have been made from surveys flown during the empirical peak in haul-out numbers (midday in early to mid-June). Nonetheless, the variance in the proportions of all seals basking may be lowest at a time when some lesser proportion of the population is basking. Estimates of numbers from surveys conducted at those times may be more reliable. The efficacy of aerial surveys as a method of counting basking ringed seals, thus, would be greatly improved by monitoring a sample of radio-tagged seals throughout the entire basking period.

Aircraft support was not available through the basking seasons of 1982, 1983, or 1984. We were able to collect some data on the proportion of seals basking in early June of 1982, but sample sizes were too small in that limited effort to warrant any general conclusions. We examined the effect of the sample size of radio-tagged seals on the variance of a population estimate, based on aerial surveys corrected for the proportion of seals not basking. The variance of that estimate can be approximated using a Taylor series (Mood *et al.* 1974) to combine the variance of observed densities and the binomial variance of the proportion of seals visible. The covariance can be assumed to be zero since the two variance terms are logically independent. In a computer simulation, we found that, for tagged samples of 5 to 10 seals, the combined variance term is smallest when p, the proportion of tagged animals visible, is 0.60 or greater. For $p > 0.60$, the variance is improved little by increasing the number of tagged animals beyond eight. Thus, haul-out data from 8 to 10 radio-tagged seals would be adequate for correcting density estimates from aerial surveys.

Reactions of Ringed Seals to Noise Disturbance

Sound levels of sufficient energy to cause physical harm to seals are extreme (Rausch 1973; Geraci and St. Aubin 1980) and unlikely to result from current methods of petroleum exploration and development. Noise levels of sufficient energy and duration to cause ringed seals to abandon breathing holes and lairs at greater than normal rates can result from seismic profiling with Vibroseis equipment (Burns and Kelly 1982) and probably from other on-ice industrial activities. Assessing the significance of that increased rate of abandonment requires information about the degree of dependency by ringed seals on subnivean structures and the degree of overlap between ringed seal populations and the activities causing abandonment.

Judging from the relative rates of abandonment of seal structures near and at various distances from human activities, we found that ringed seals have highly variable reactions to noise disturbances. Similar variability in response to human disturbances has been reported in harbor seals (Pitcher and Calkins 1979) and walruses (Fay *et al.* 1984). Some ringed seals' structures remained in active use despite close proximity to seismic survey lines, snow machine trails, gravel island construction, and flight paths of helicopters and small planes. Other structures were abandoned quickly when exposed to noises at greater distances. Part of the variation in the response of individuals to noise may have been due to differing levels of ambient background noise. The seals' sensitivity to potentially disturbing sounds may lessen when background noise, such as from wind-driven snow or ice strain, is high. Because individual responses to noise disturbance is so variable, "critical" distances for various activities are difficult to define. Although we found fewer active seal structures within 150 m of seismic lines than beyond that distance, we cannot say how the rate of abandonment changes within that range, which was chosen on the basis of sample size, rather than distance *per se*.

The frequency of occurrence of disturbances may have more influence on abandonment of structures than does the specific source of disturbance. Of the radio-tagged seals within the simulated seismic survey area in 1983, only one seemed to abandon a lair. GI-83 apparently abandoned his lair after human disturbances caused him to flee into the water at least six times, more than any other seal in the study (mean = 2.3). We cannot be certain that the lack of signals from his transmitter after 26 April resulted from him abandoning his lair, but the very high retention rate of transmitters on other seals argues against the possibility of his transmitter having failed or been lost.

The radio-tagged seals spent the majority of time in the water. Little is known about their activities under the ice, although much of it presumably involves feeding and, perhaps, territorial defense. Sound is readily conducted through the sea ice, into the water, and the effects of noise disturbance on seals under the ice remains unknown. The smaller proportion of time that seals spend in subnivean lairs, nonetheless, appears to be essential to the seals' well being, and the dependence on the lairs is especially great for pups. Disturbances that cause them to leave the lair can affect them adversely in several ways. If a pup in lanugo is forced to flee into the water, it may not survive the resultant heat loss. Pups that do survive swimming through the water to an alternate lair will have to expend significant amounts of energy reserves in order to maintain core temperature while drying (Taugbøl 1982). Such pups will be easier prey for polar bears and arctic foxes and will be less able to withstand other stresses. Lair occupation becomes increasingly frequent for older seals throughout the spring months, apparently due to the need to maintain higher epidermal temperatures for new hair growth. Ringed seals are likely to be most negatively affected by noise disturbances when they are most dependent on hauling out, i.e., from late March through June.

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