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Behavioural Adaptations to Arctic Winter: Shelter Seeking by Arctic Hare (*Lepus arcticus*)

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ABSTRACT. Behavioural modifications used by arctic hares, *Lepus arcticus*, to maintain their normal body temperature in late winter, including posture, orientation, the use of natural shelter, and the digging of snow dens, were studied on Ellesmere Island, N.W.T., between 1985 and 1992 and on Bathurst Island, N.W.T., between 1968 and 1992. Hares adopted a near-spherical shape while resting with only the thick pads of the hind feet touching the snow. Hares typically rested together in closely spaced winter groups of up to 28 hares. Huddling did not occur, except in young littermates in summer. Hares in groups did not usually seek shelter, but solitary hares normally groomed, rested, and reingested in the shelter of large rocks. When wind speeds dropped below 10 km·h^{-1}, resting hares shifted from facing away from wind to an orientation towards the sun. As daily mean temperatures increased in April-May, the usual resting posture changed from the tightly curled resting sphere to crouching and sprawling. Hares used natural shelter, especially rocks and snowdrifts, and man-made structures. They also modified snowdrifts by digging snow dens up to 188 cm in length. Thirty-seven dens were seen in 8 of 15 years of observations at Bathurst Island, and seven were seen on Ellesmere Island in 1 of 5 seasons. Snow dens were not used for feeding and their value as safety from predators is likely secondary to their value as shelter.

Key words: arctic hare, shelter seeking, sheltering, winter adaptations, posture

RÉSUMÉ. Cette étude, qui s'est déroulée entre 1985 et 1992 dans l'île d'Ellesmere (T.N.-O.) et entre 1968 et 1992 dans l'île Bathurst (T.N.-O.), porte sur les modifications du comportement qu'affiche le lièvre arctique, *Lepus arcticus*, afin de maintenir sa température corporelle normale à la fin de l'hiver. Ces modifications comprenaient la position et l'orientation du corps, l'utilisation d'un abri naturel et le creusement de gîtes dans la neige. Les lièvres prenaient une position presque sphérique au repos, seuls les épais coussinets de leurs pattes postérieures étant en contact avec la neige. Les lièvres se reposaient généralement en hiver rapprochés les uns des autres, en formant des groupes comptant jusqu'à 28 individus. On n'a pas observé de lièvres serrés les uns contre les autres, sauf durant l'été, parmi les levrauts d'une même portée. Généralement, les lièvres en groupes ne cherchaient pas à s'abriter, mais les lièvres solitaires faisaient habituellement leur toilette, se reposaient et réingéraient à l'abri de grands rochers. Lorsque la vitesse du vent tombait à moins de 10 km·h^{-1}, plutôt que de se détourner du vent, les lièvres au repos s'orientaient vers le soleil. À mesure que la moyenne de la température quotidienne augmentait en avril-mai, les lièvres quittaient leur position de boule serrée pour se tenir sur leur quatre pattes et s'étendre. Les lièvres se servaient d'abris naturels, composés la plupart du temps de rochers et de bancs de neige, ainsi que de structures artificielles. Ils modifiaient aussi des bancs de neige en y creusant des gîtes pouvant atteindre 188 cm de longueur. Durant 8 des 15 années de l'étude à l'île Bathurst, on a recensé 37 gîtes de neige et durant 1 des 5 saisons d'observation à l'île d'Ellesmere, on en a recensé 7. Les lièvres n'utilisaient pas les gîtes de neige pour s'y nourrir et la valeur de ces derniers comme protection contre les prédateurs est certainement secondaire à leur valeur en tant qu'abri.

Mots clés: lièvre arctique, recherche d'un abri, s'abriter, adaptations à l'hiver, position

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INTRODUCTION

Like other northern land mammals with ranges extending to the northernmost points of land in the High Arctic of Greenland and Canada, the arctic hare (*Lepus arcticus* Ross) must cope with the extremes of an arctic winter that might last for nine months. From what is known about other hares and other northern mammals, it can be assumed that during the arctic winter, arctic hares maintain their normal body temperature in the face of mean monthly temperatures of −30°C through a combination of structural modifications, including insulation and piloerection, and behavioural modifications, including posture, orientation, the use of natural shelter, and the modification of the natural environment for shelter.

In winter a thick layer of insulating underfur permits the maintenance of body temperature at the extreme temperatures associated with the high arctic climate. Based on studies of two captive arctic hares from Ellesmere Island, Wang *et al.* (1973) concluded that the effectiveness of the insulation and the reduction of the ratio of volume to surface area allow the arctic hare to maintain a normal body temperature and are sufficient to compensate for a depressed basal metabolic rate. They suggested that a hare could survive for at least 15 days on fat alone at −24°C if fat made up 20% of the body weight.

In terms of behaviour, the arctic hare remains one of the least known of the North American members of the family Leporidae. In recent years, studies in Newfoundland have investigated the dominance relationships in captive arctic hares (Fitzgerald and Keith, 1990) and have shown that arctic hares have no rigid social dominance system (Small *et al.*, 1991). However, the writings of the arctic explorers of the early 19th century (e.g., Sverdrup, 1904; Manniche, 1910) still provide much of the currently available general life history information on this hare in winter.

Recent winter-season observations are limited to general feeding behaviour and the reporting of large winter groups in some parts of their range (Flux and Angermann, 1990; Gray, 1990). Little is known of shelter-seeking behaviour. Scott (1963) defines shelter seeking as "the tendency (of animals) to seek out optimum environmental conditions and to avoid dangerous and injurious ones." The term shelter seeking as defined by Scott is broad enough that I have also used the more specific term sheltering, meaning to take shelter, the active seeking of a place of protection in or under a component of the outside environment that is either already

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there or that the animal itself creates. Sverdrup (1904) and Freuchen (1935) noted that hares sheltered behind rocks and oriented towards the sun in spring. Bonnyman (1975) described briefly some of the basic postures used by arctic hares during spring and summer on Ellesmere Island but her terminology is not clear. Parker (1977) studied the feeding ecology and reproductive state of arctic hares on Axel Heiberg Island in late winter, documenting feeding habits and noting the use of forms for sheltering in summer. Both Inuit hunters (Gunn *et al.*, 1988) and early explorers (Osborn, 1856; Sverdrup, 1904) have noted that arctic hares in certain coastal areas moved out onto the sea ice to shelter behind grounded sea ice or ice blocks formed at tide lines or pressure ridges. Manniche (1910) and Manning (1976) considered the possibility that sheltering behind rocks could serve as protection from aerial predators, especially the snowy owl, *Nyctea scandiaca*. The use of snow dens by arctic hares in Greenland and the Canadian High Arctic is mentioned in some of the earliest explorers' accounts of these areas (Great Britain, 1852; Osborn, 1856; Feilden, 1877; and Greely, 1886).

In Scotland, mountain hares (*Lepus timidus*) shelter from the wind and modify the snow surface in winter by digging snow scrapes for resting sites (Thirgood and Hewson, 1987) and also keep ground burrows open by digging through the snow (Flux, 1970). Mountain hares are also known to make short tunnels in snow for protection from adverse weather or aerial predators (Flux and Angermann, 1990). Pulliainen (1982), working in Finland, concluded that temperatures as low as −30°C were of minimal importance to the mountain hare in habitat selection.

This paper describes the shelter-seeking behaviour of arctic hares during the late winter breeding season (mid-April through mid-May) in the Canadian High Arctic. This study is part of a larger project to provide basic information on life history and behaviour, especially courtship behaviour (Gray and Hamilton, 1982; Gray, 1989) and reproduction (Aniskowicz *et al.*, 1990) in the northern part of the arctic hare's range.

STUDY AREAS

The primary study area was the central part of Sverdrup Pass (79°08′N, 79°45′W), an 80 km pass crossing Ellesmere Island, Northwest Territories (N.W.T.) (Fig. 1a). This area was chosen because the hare population, though relatively small, was thought to be relatively consistent and restricted geographically. The study area is approximately 600 m above sea level and bounded on the north and south by mountains and icecaps rising to over 1500 m above sea level. Within the 7 km stretch of the pass that forms the study area, sandy or gravel flats in mid-valley with scattered clumps of arctic willow are interspersed with better vegetated meadows and sparsely vegetated slopes leading up to scree slopes. At the terminus of a large valley glacier are fields of boulders and mounds of glacial till. Extensive areas of moraine with boulders ranging up to 4 m in height occur throughout the pass.

The late winter climate in Sverdrup Pass is characterized by a gradual increase in average daily temperature from −30°C in early April to −20°C in early May. Winter is defined as the period when the mean air temperature remains below 0°C (Maxwell, 1981). Average monthly wind speeds in late winter ranged from 11 to 20 km·h^{-1}. Periods of calm occurred only infrequently with a major shift in wind direction. The maximum recorded wind speed in April was 63 km·h^{-1}. Snowstorms and blizzards occurred in both April and May. In the boulder areas snowdrifts were several metres deep, but in the centre of the pass and on the scree below the talus slopes on the north side the wind kept large areas virtually snow free. By mid-May average daily temperatures rose to −12°C. At Sverdrup Pass 24 h daylight occurred from mid-April to late August.

The Bathurst Island study area is 140 km^2 of high arctic tundra surrounding the Canadian Museum of Nature's High Arctic Research Station at Polar Bear Pass (75°43′N, 98°25′W). Polar Bear Pass has a small and scattered hare population but includes sites where hare snow dens are seen regularly. The research station overlooks the mid-point of the pass, a wide, flat valley extending east-west across Bathurst Island for 40 km, with many small streams, ponds, and shallow lakes (Fig. 1b). Hills to the north and south of the valley reach a maximum elevation of 240 m within 8 km of the station. Extensive wet sedge meadows in the floor of the pass are gradually replaced by polar desert on these hills (see Gray, 1987, for a more detailed description of the study area). Few large boulders are present but there are localized outcrops of ancient coral reefs standing up to 10 m high.

In mid-winter (December-March) the average monthly temperature was from −30°C to −40°C. Mean monthly wind speeds in the winter of 1970-71 varied from 13 km·h^{-1} in April to 26 km·h^{-1} in January. The mean monthly wind speed for May over five years was 19 km·h^{-1}. The period with the sun below the horizon lasts from the first week in November to early February. The period of 24 hours of daylight begins during the last week of April and ends in mid-August. Late winter weather (April-May) is characterized by moderate winds, frequent periods of ice fog, moderate snow cover, and mean temperatures below −10°C. The five-year mean monthly temperature for April is −22°C and for May −13°C. May also features increased cloudiness, with some snowfall and steadily increasing temperatures.

METHODS

Observations on shelter-seeking behaviour were made during a study of courtship behaviour of arctic hares in late winter (April-May) in five years between 1986 and 1992 at Sverdrup Pass and in mid-May at Polar Bear Pass in 1988 and 1992 (Fig. 2). Observations in late summer (August) or early winter (September-October) were also made at Sverdrup Pass in 1985, 1986, 1987, and 1990. At Polar Bear Pass incidental observations of hare behaviour were made throughout the winter of 1970-71 and in late winter in seven years between 1968 and 1979 during studies of the social behaviour of muskoxen (*Ovibos moschatus*) (Gray, 1987). Observations were also made during short periods in five other years between 1968 and 1979 and between 1986 and 1992. Other limited incidental observations were made during muskox studies at Sverdrup Pass in 1981 and at Mokka Fiord on Axel Heiberg Island in late winter 1975.

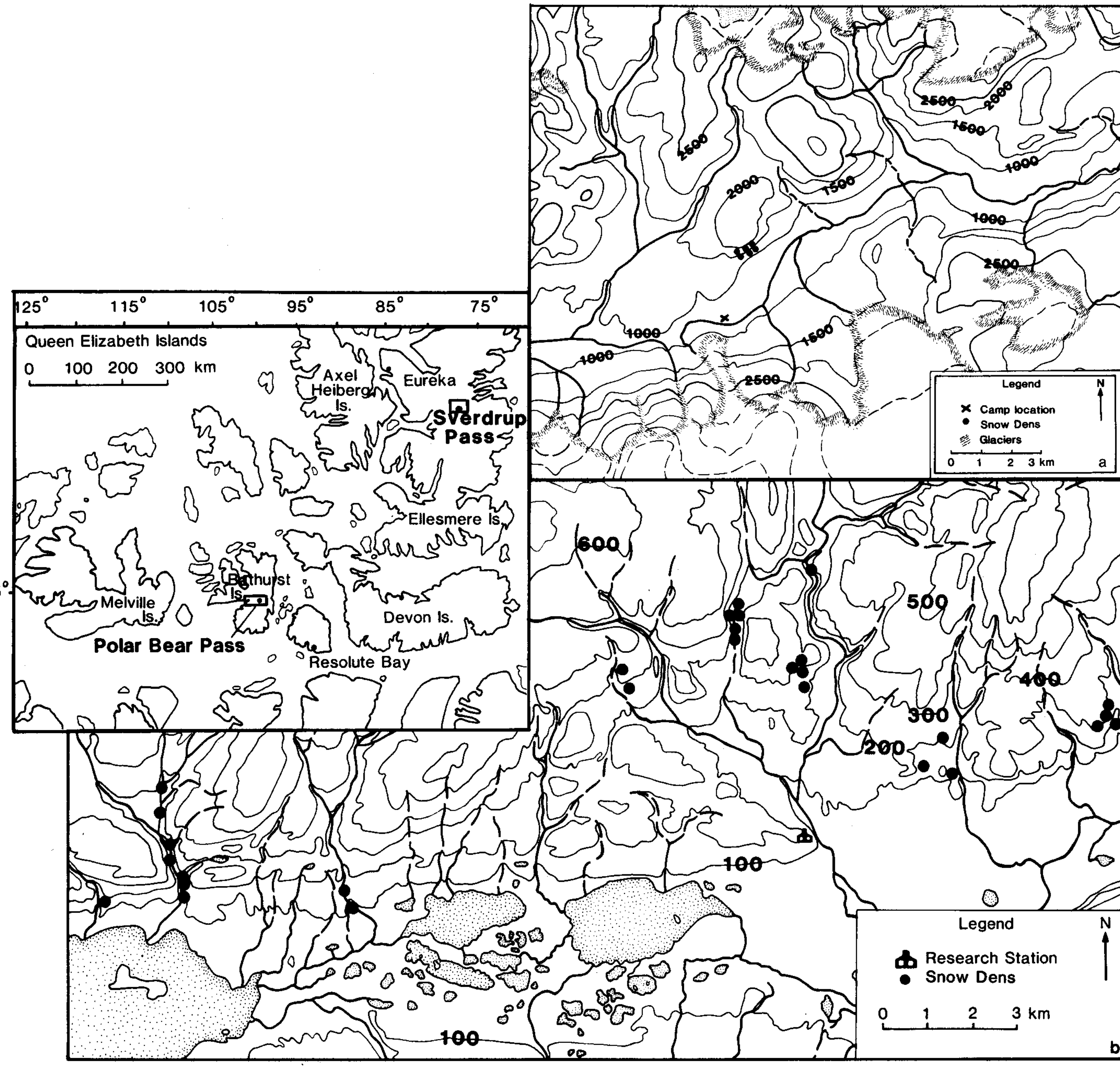

FIG. 1. Maps of the two study areas, Sverdrup Pass (a) and Polar Bear Pass (b), and their location in the Queen Elizabeth Islands of Canada's High Arctic. Locations of snow dens are indicated by solid circles.

Arctic hares were located by searching the study areas from standard points of high elevation near the camp or by walking surveys through areas not visible from the camp. In times of low numbers, hares were located by tracking in fresh snow. Visual counts of hares were made at least twice daily, and numbers of hares in the study area were estimated by making visual counts throughout the study area within as short a time as possible. The presence of tagged hares helped ensure accurate estimates.

Arctic hares were live-trapped with #208 Tomahawk double-door wiremesh live-traps, using both single- and double-opening systems and dried apples as the primary bait. Hares were weighed, measured, colour-marked with picric acid, and tagged with small Allflex coloured and numbered ear tags. Twenty-four hares were ear tagged: 16 adults and 4 young at Sverdrup Pass between April 1985 and September 1986, plus 2 adults in each of 1988 and 1990; and 4 at Polar Bear Pass, 2 adults in April 1971 and 1 adult and 1 young hare in September 1990.

Young hares could be distinguished from adults visually by pelage colour and by relative size at least until October. Sex of trapped hares was determined visually and confirmed by observation of behaviour patterns. Adult males were particularly easy to identify due to the extensive visibility of the penis in late April and early May during the spring breeding season (Gray and Hamilton, 1982).

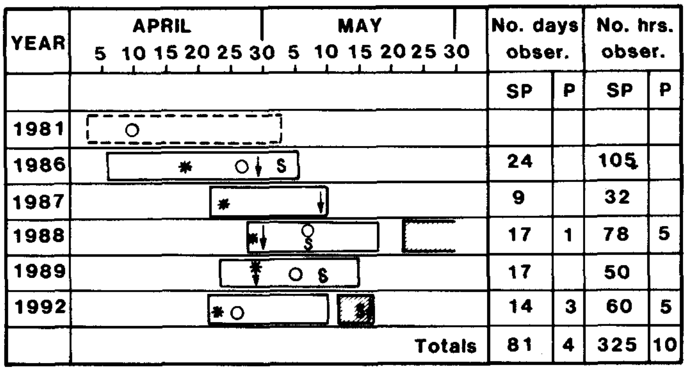

FIG. 2. Late winter observation schedule, numbers of days and hours of behavioural observations, and first occurrence recorded of certain postures and events at Sverdrup Pass and Polar Bear Pass. Open circles indicate first appearance of crouch postures while resting, "s" indicates first sprawl posture, asterisk (*) indicates first evidence of shedding, and vertical arrow indicates first temperature above −10°C.

Over 320 h of behavioural observations were recorded in April and May at Sverdrup Pass between 1985 and 1992 (Fig. 2). Although some observations were made at all times throughout the 24 h day, we attempted to record observations during periods of hare activity in the early to mid-morning and in mid-afternoon. Although weather conditions and the difficulty of locating hares prevented observations on some days, we were able to observe hares for a daily average of 3.9 h. Groups of hares were also monitored during resting periods to allow us to continue with observations of the same individuals when activity resumed. Behavioural observations were made using focal animal sampling for ear-tagged animals and all-occurrences sampling for selected behaviour patterns. Specific behaviour patterns recorded of relevance to sheltering were resting and feeding postures, digging in snow, movements to shelter, sheltering, plus timing of changes in behaviour and activity. Hare behaviour was documented with 35 mm cameras, super 8 and 16 mm movie cameras, and a video 8 camera-recorder.

Snow scrapes and snow dens were located through regular (but not systematic) survey trips throughout the study areas on foot, skis, and snowmobiles. At Polar Bear Pass, areas used by hares and known to have had dens in previous years were checked during snowmobile surveys each year. In a few instances, dens were located initially by the presence of hare faecal pellets on the snow at the den entrance. Snow scrapes and most dens were measured and photographed, and twelve of the longest dens were cut open with a saw at the end of the study period in order to measure the internal structure. Den use was determined by removing tufts of newly shed wool from den entrances and by checking for tracks in fresh snow.

Standard Aviation Weather Reports measuring cloud, visibility, wind, temperature, and precipitation were made twice daily at both study areas. Wind speeds were measured at dens and other potential shelter sites and in open feeding areas, using a Lambrecht 1438 hand-held anemometer. The wind velocity was measured at 1.5 m above the ground or snow surface (in order to compare with the standard Aviation Weather data), at 1 m above the ground or snow, and at 18 cm above the ground (the height of the instrument and the approximate height of a resting hare). Wind velocity inside dens was measured by placing the anemometer into a hole in the den floor and taking a reading from outside.

Statistics

Statistical tests are based on Sokal and Rohlf (1969). All tests are two-tailed. Values given in the paper are means ± SD. The statistical analyses of wind speeds near boulders and snow dens were performed using the General Linear Models procedure on the SAS statistical package (SAS Institute, 1986).

RESULTS

General Observations Relating to Sheltering

The highest daily count of arctic hares in the Sverdrup Pass study area in late winter ranged from 56 in April 1986 to a low of 2 in April-May 1987. In late winter hares were seen in groups of up to 28 individuals (Fig. 3a), in pairs, or alone. A group is defined as 2 or more hares separated by less than 5 m and resting or feeding at the same time. Hares in large winter groups fed within a few metres of each other and maintained individual distances of about 1 m by agonistic behaviour, chasing and striking with forelegs. When resting, hares stayed 1-2 m apart and resting hares moved (Fig. 3b) and struck out with their forepaws if a passing hare came within about 1 m. Single hares or small groups of 3-6 individuals were seen each year in Polar Bear Pass. In May 1992, 12 hares (in three groups) were seen, the highest daily count recorded. The maximum group size seen in late winter was 10. Most late-winter groups contained males and females.

The activities of arctic hares in groups were synchronized — they fed and rested at about the same time. A simple activity pattern for two tagged hares living in various groups at Sverdrup Pass in April and May shows an active period in early to mid-morning and again in the early to mid-afternoon (Fig. 4). Hares rested for about 4 h from late morning to early afternoon. A shorter rest period occurred around 18:00.

The first signs of a winter moult were seen at Sverdrup Pass in mid- to late April, when daily mean temperatures were still about −25°C. The earliest noticeable shedding of loose wool ranged from 18 April 1986 to 29 April 1989 (Fig. 2).

Shelter-Seeking Behaviour

Orientation: When feeding in low or calm winds, even at temperatures of −30°C or lower, hares moved with no obvious orientation to the wind or other natural features, such as terrain or sunlight. With increasing winds, orientation became more obvious. While feeding in moderate to strong winds (25-45 km·h^{-1}), hares faced downwind. When changing location, they turned and faced into the wind and moved upwind.

While resting in winter, arctic hares in the open almost always sat with their backs to the direction of the wind. When sheltering behind snow or rocks, hares positioned themselves

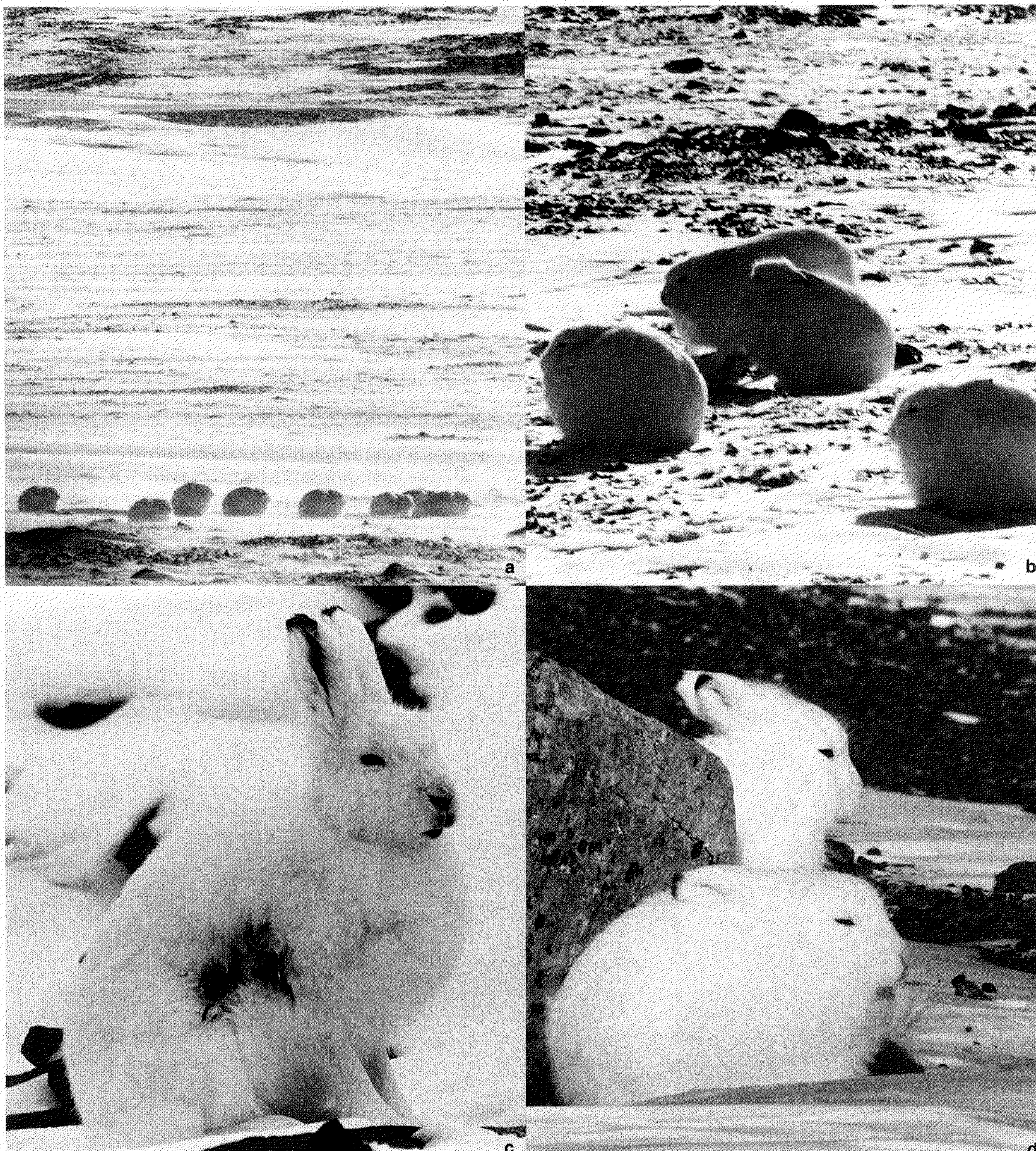

FIG. 3. Arctic hare postures and behaviour patterns: a) part of a late winter group at rest showing spacing between resting individuals; b) agonistic reaction by resting hare when another moved too close; c) sitting alert posture showing shedding on hare's side; d) hares sheltering with their backs to a rock.

in the lee of the rock with their backs to the rock and thus also to the wind direction (Fig. 3c).

In late April and May, when the wind speed approached 0 $km \cdot h^{-1}$ for up to an hour as the wind shifted from east to west, resting hares shifted from facing away from the wind to facing towards the sun. As wind speed increased again, hares reoriented with their backs to the wind.

Posture and Positioning: While feeding, an arctic hare's weight rested mainly on the hind feet, as the hares dug at the snow with the forefeet in a drumming motion, breaking

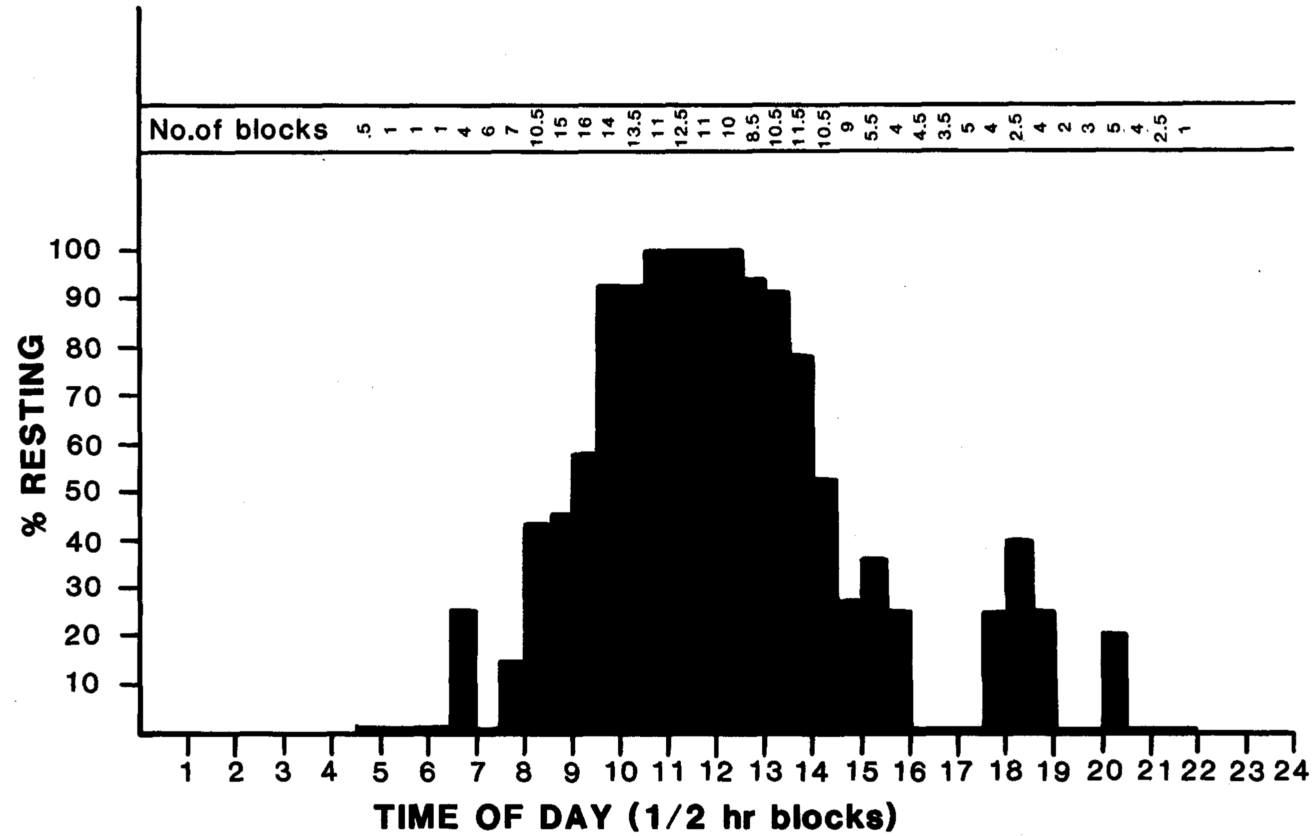

FIG. 4. Simplified arctic hare activity cycle at Sverdrup Pass showing percentage of time spent resting in each .5 h period of the 24 h day. Graph is based on 117.25 h of observation on activity of two tagged adult males living in groups in 1986 and 1989. At top of graph is the number of .5 blocks of observation made in each time period. All behaviours are grouped under resting (including grooming) or active (feeding, moving, courtship, etc.).

it away from the food plants underneath. During feeding, hares normally kept their ears lifted up from the shoulders or in an upright position. During winter storms, when the wind speed reached approximately 25 $km \cdot h^{-1}$, hares held their ears tightly against the neck and back, giving the appearance of being earless (Fig. 5a). Even in such strong winds, the ears were raised at frequent intervals, though they were held tightly together with no space between them. In blowing or drifting snow, i.e., wind speeds at more than 25 $km \cdot h^{-1}$, each time a hare turned upwind to change feeding location, it first lifted up the fore part of the body, with the forepaws dangling, and shook briefly before moving (Fig. 5b).

Grooming, the active care of the coat by licking and scratching with the paws, was seen at the end of each feeding period before the hares began resting and also at the end of each rest period. For example, in six complete resting periods recorded for an adult male hare in April, a bout of grooming occurred at the beginning of all six, at the end of four, and during two resting periods. Grooming usually took place in the same location as resting. When hares moved to shelter after feeding, grooming followed after the move. Grooming after resting also took place at the shelter site.

In winter, after a feeding period and usually following a short bout of grooming, arctic hares assumed a typical posture before resting. Hares sat up on their hind legs, folded their forepaws and tucked them into their chest fur with a quick paddling or rolling motion, at the same time as they lowered themselves down onto their hind feet. They flattened their tails down, lowered their ears down into the fur on their backs, and settled into a nearly spherical shape. I have termed this posture the "resting sphere" (Fig. 3a,b), as it has not previously been clearly described. During winds accompanied by drifting or blowing snow, hares lifted themselves up about 5 cm higher off their hind feet when settling into the resting sphere posture. In the resting sphere position only the thick pads of the hind feet touched the ground and the hare's body was centred over the hind feet. The eyes were often closed to mere slits.

The resting sphere position was broken regularly, even in extreme cold and strong winds, by reingestion behaviour or coprophagy (Flux, 1970). At intervals of about 15 minutes, arctic hares sat up with head lifted before bending the head down to ingest the soft faecal pellets directly from the anus, thus exposing the forelimbs, belly, and ears for about 15 seconds (Fig. 5c).

With the exception of brief grooming bouts, reingestion, and occasional moves, hares spent the entire resting period in early April in the resting sphere posture, a minimum of 4 or 5 h a day (Fig. 4). As daily mean temperatures increased in April-May, resting posture became more variable, changing from the tightly curled resting sphere (Fig. 6a), to the sitting crouch in which the forepaws are placed on the ground under the body with the tips of the paws showing (Fig. 6b). In the lying crouch the body is lowered further, with the forelegs extended (Fig. 6c). Eventually a sprawling

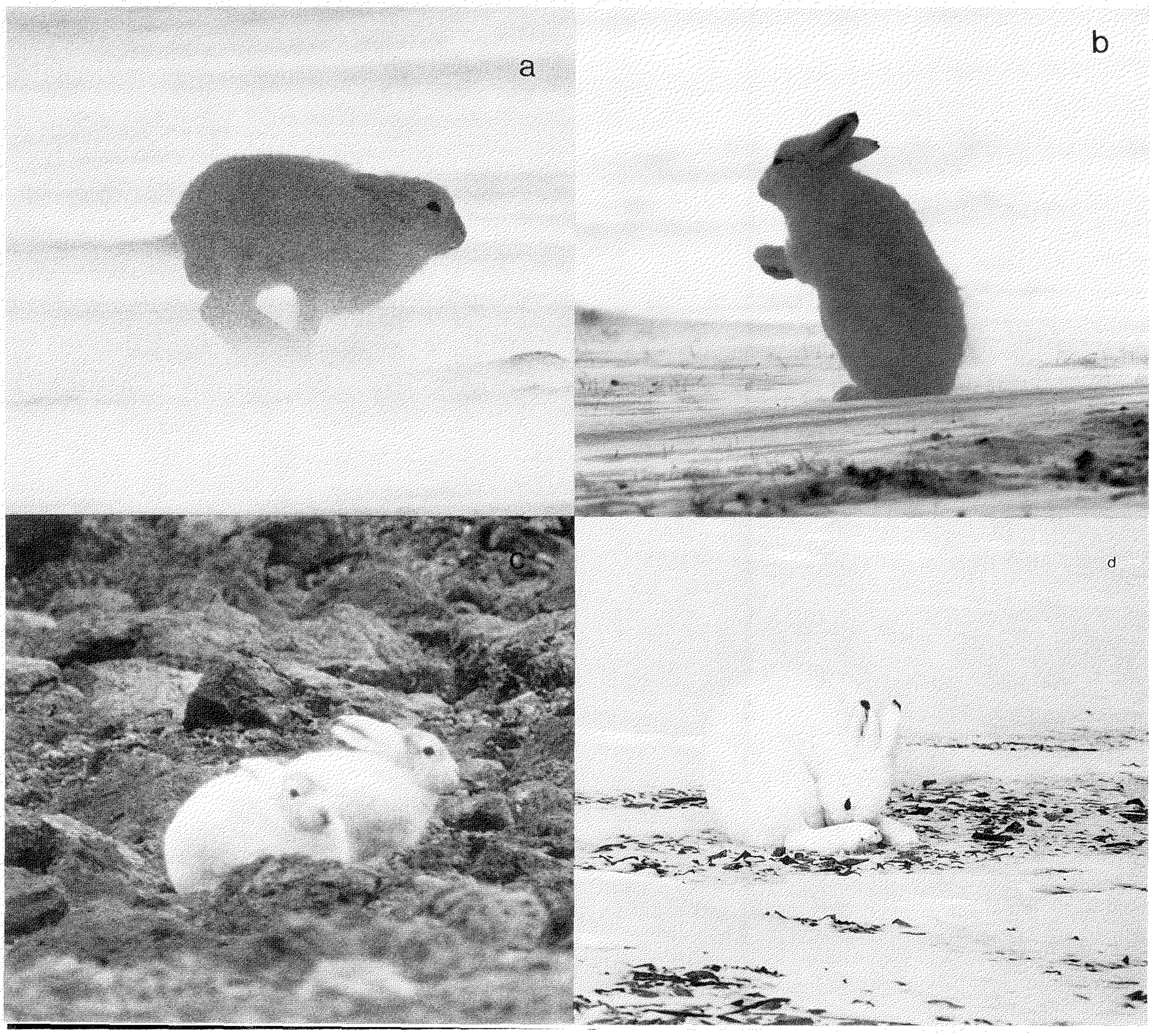

FIG. 5. Arctic hare postures and behaviour patterns: a) hare moving between feeding sites during wind storm, with ears held tightly to back and neck; b) hare shaking snow from fur before moving and resuming feeding; c) two young hares huddling at nursing site in mid-August just prior to weaning; d) hare reingesting faeces during resting.

position occurred with all four legs extended out and the side or belly touching the ground (Fig. 6d). The first observed occurrence of non-spherical crouching postures while resting were between 10 April and 7 May at temperatures of -12 to -25°C (Fig. 2). First observations of the "sprawl" posture occurred in early May (3-9 May) at temperatures of -10 to -15°C. In 1992 the temperatures in May were about 10°C below the previous years' average and the sprawl was not seen in Sverdrup Pass up to 9 May, the end of the observation period, and was first seen at Polar Bear Pass on 15 May (-13 to -16°C). In early winter, the resting sphere posture was first seen as early as 5 September in 1986 (at -10°C).

Huddling: Although hares typically rested together in closely spaced groups, huddling together with actual body contact did not occur with adults at any season. Only in the case of young littermates in summer was huddling observed (Aniskowicz *et al.*, 1990). At Sverdrup Pass in 1986, on each of the five days before weaning on 22 August, hares 2 months of age and at least ¾ adult size huddled together for 22-43 minutes ($\overline{x} = 30.50 \pm 9.52$ min) while awaiting the mother (Fig. 5d). Although up to five weaned young were seen resting and feeding together in late August and early September in four years, no huddling during resting was observed.

Use of Natural Shelter: When resting at ground level with no shelter from rocks or snowdrifts, hares received some protection from the wind, just by being close to the ground. In a frequently used meadow area near a field of glacier-deposited boulders at Sverdrup Pass, the wind speed during

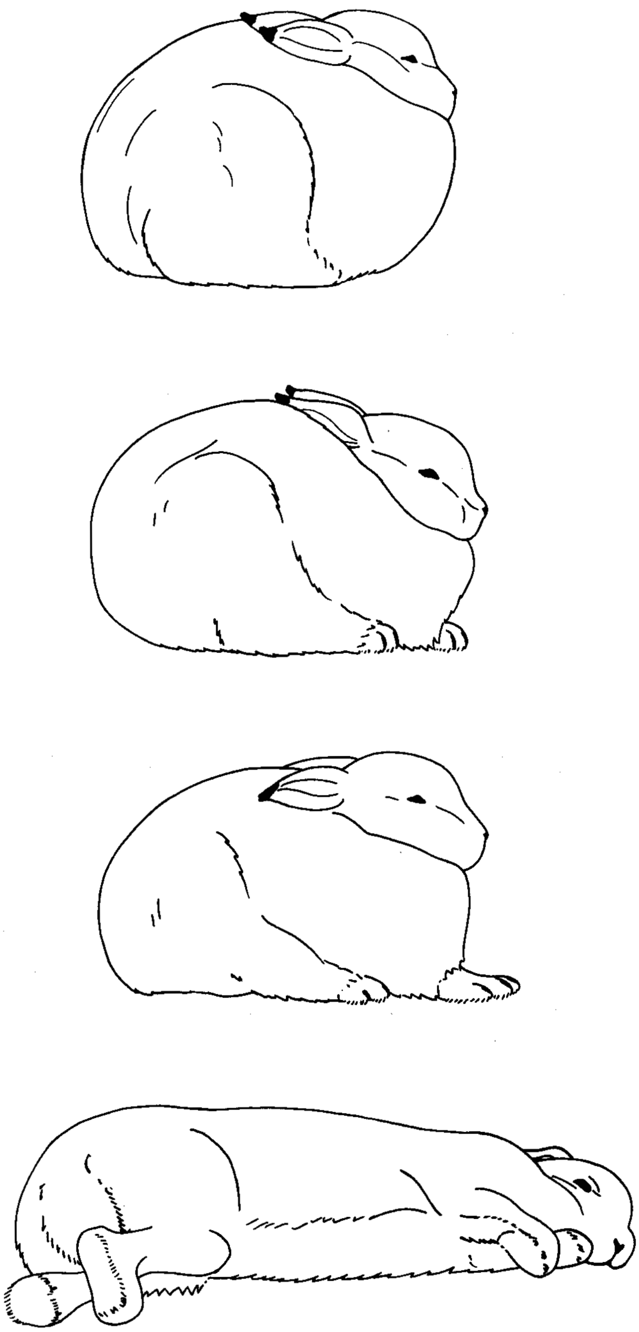

FIG. 6. Late winter resting postures of arctic hare: top to bottom: resting sphere, sitting crouch, lying crouch, sprawl.

a mid-April winter storm was measured at 20 sites, 10 m apart, across the meadow. There was a significant drop in the average wind speed from 35.32 ± 3.83 km·h^{-1} at 1.5 m, to 30.68 ± 5.88 km·h^{-1} at 1 m (t-test, p = .005), and also from 30.68 ± 5.88 km·h^{-1} at 1 m to 19.00 ± 4.33 km·h^{-1} at 0.18 m above the snow surface (t-test, p = .000001) (Fig. 7).

In winter, single hares usually sought shelter from the wind during the long rest periods. Hares rested in the lee of large and small rocks, even rocks smaller than the hare itself (Fig. 7b). In near-blizzard conditions with an average wind speed of 35.32 ± 3.83 km·h^{-1} at 1.5 m, the wind speed at ground level in the lee of rocks less than 35 cm high was not significantly different from the speed at the same height in the open meadow (t-test, p = .112). The shape of the rock in relation to the wind direction influenced the wind speed in the lee.

At Sverdrup Pass, hares sheltered in the lee of large boulders (at least 2 m high) in an extensive moraine area. They typically rested on the top of snowdrifts about 1 m from the rock, as indicated by both direct observations of hares and the location of accumulations of pellets. Wind velocities measured at three heights around five such boulders during a moderate wind storm decreased significantly on the lee side of the boulder ($F_{3,56}$ = 24.25, p = .0001), with the lowest wind speeds being at the surface of the drifts 1 m from the rocks, rather than at the foot of the boulder in the wind hollow (Fig. 7). Wind speeds were significantly lower at all three levels on the lee side ($F_{2,56}$ = 46.84, p = .0001).

Hares also sheltered behind wind-sculptured snowdrifts (sastrugi), in the wind channels around the base of large rocks, and in naturally formed cavities in snowdrifts or cornices on banks or cliffs. Hares did not use open wind-blown tunnels under the boulders.

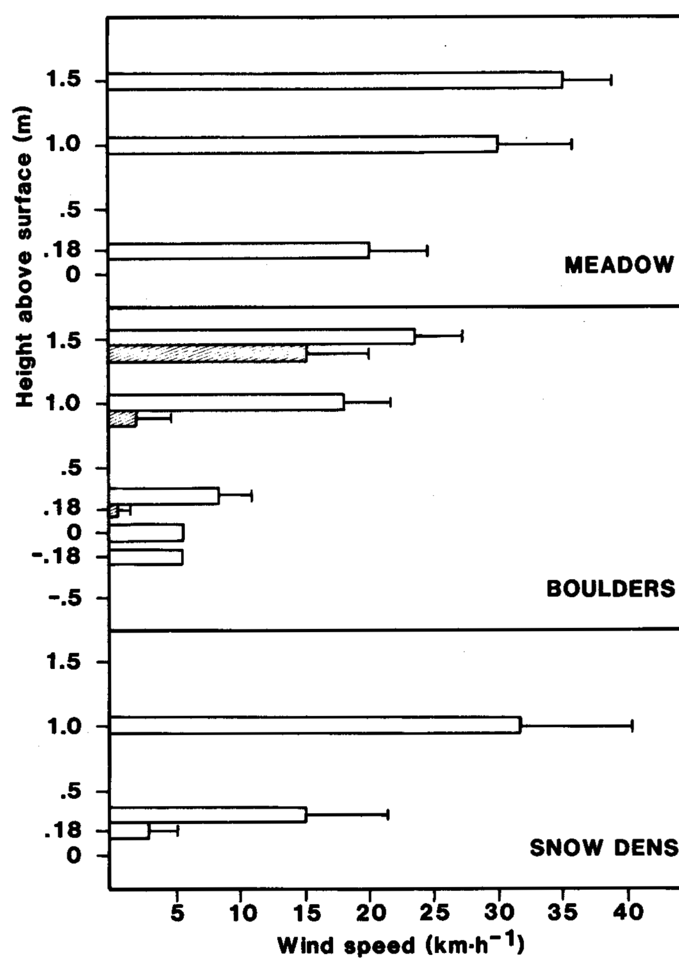

FIG. 7. Wind velocities (mean ± SD) in three habitats in Sverdrup Pass, measured at three standard heights, late April 1992: a) in feeding meadow; b) at boulders used for sheltering (hatched bars represent lee measurements, all of which are significantly different from open bars), and c) at four snow dens on the lee side of large boulders (three measurements at .18 cm are outside den, at entrance, and inside den).

Individual hares sometimes moved up to 100 m to shelter at specific rocks or boulders at the end of feeding periods. Certain sites were used repeatedly by the same hare as well as by different hares at other times. At Polar Bear Pass hares sheltered under the same snow cornice in at least three different years when a natural opening extended for 150 cm along the drift.

In large groups of up to 28 hares feeding in extensive meadows or on exposed slopes, few individuals moved to seek the shelter of nearby boulders. All hares usually rested within the group. When individual hares did move away from a feeding group to groom and rest in the lee of a boulder, they usually returned to the group within 20 minutes and stayed with them for the remainder of the resting period. If a group of hares was feeding near a single boulder, as many as 8 hares from the same group sheltered around the boulder even though only 1 or 2 would have received the maximum shelter available.

A tagged male hare, 1 of only 2 hares seen in the Sverdrup Pass study area in 1987, was observed at the end of 16 active feeding periods over a period of 13 days from 23 April to 4 May. He moved to the shelter of a rock or boulder to begin grooming or resting 13 times (81%), remaining in the exposed feeding area only 3 times (19%). A different tagged adult male, observed in groups of 2-28 hares on 25 days between 9 April and 4 May 1986, moved to a rock to shelter only 5 times (20%) and stayed with the other hares to groom and rest in the feeding area 20 times (80%) (Fig. 8).

In summer, hares also rested beside rocks, under overhanging rocks, in horizontal crevices and in cavities under boulders. As in winter, individuals returned to the same rock to rest many times over the observation period. That certain of these boulders have been used by hares over many years

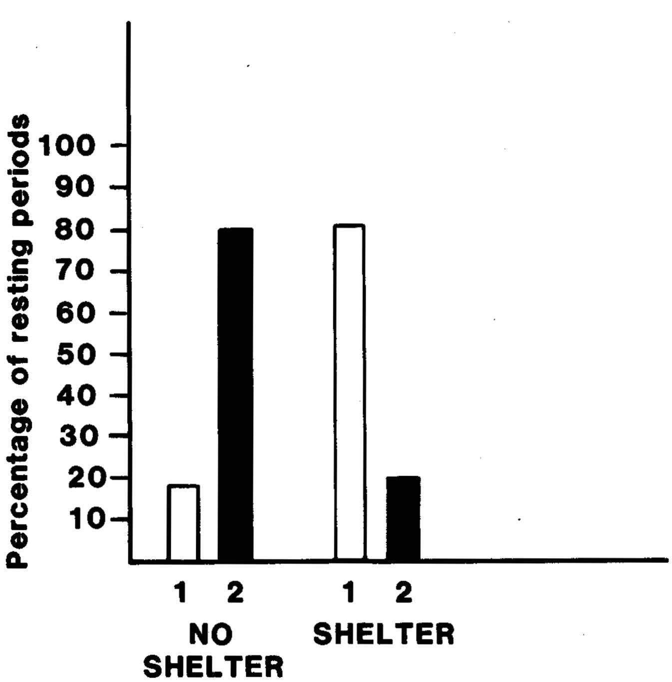

FIG. 8. Percentage of late winter resting periods in which two male arctic hares sought shelter before resting after feeding activity. Male no. 1, open bars (1987), and male no. 2, solid bars (1986).

was shown by accumulations of hundreds of faecal pellets. Arctic hares dropped the hard round pellets regularly at short intervals during active feeding, but not during resting. However, as a hare got up from a resting position or as it stretched before moving away, one or two pellets were usually dropped, leading to an accumulation at resting or sheltering sites.

Hares also sheltered behind man-made structures such as fuel drums, food caches, and huts and under structures such as the research station building at Polar Bear Pass.

Habitat Manipulation: Ground Scrapes — In summer in both study areas, hares occasionally dug shallow hare-sized depressions in the soil. Although these summer scrapes or forms (Flux, 1970) likely provided shelter from wind, hares at Polar Bear Pass were also found on two separate occasions in July using deep scrapes during warm weather (+4-10 °C) where the overall effect on the hare would have been cooling. There was no indication that summer scrapes were used as shelter in early winter before or during the development of the snow cover.

One instance of a hare digging a burrow in the ground was observed at Sverdrup Pass in August 1986. A hare had enlarged an opening under a large rock (144 cm × 80 cm × 72 cm high), forming a chamber 72 cm deep, 56 cm wide, and 24 cm high inside. This "den" was not used in late summer or late winter in any other year.

Snow Scrapes — In winter, arctic hares rested on snow rather than on bare ground. After grooming, hares frequently dug briefly at the snow, then turned, shuffled back and forth, and stamped their hind feet, before settling into the resting sphere or crouch posture. These movements resulted in a shallow (less than 1 cm) depression in the snow. At Sverdrup Pass, hares also modified the wind hollows between large rocks and the snowdrifts around them by digging out small flat areas or enlarging wind-sculpted hollows on the drifts, creating a shallow depression.

Other, more extensive modifications of the snow surface by hares were called snow scrapes, following the terminology of Flux (1970, 1981) and Thirgood and Hewson (1987). For the purposes of this paper, a snow scrape is defined as a small hare-sized cavity with two sides, a level floor, and an overhanging roof of less than 30 cm, made by hares digging into a snowdrift (Fig. 9b). Seventeen snow scrapes were found, 3 at Sverdrup Pass and 14 at Polar Bear Pass. The length of the overhang of scrapes at Polar Bear Pass ($\overline{x}$ = 14.40 ± 6.13 cm, N = 10) was less than half their mean length ($\overline{x}$ = 38.16 ± 15.68 cm, N = 12). The mean height and width of the scrapes were 27.73 ± 8.34 cm (N = 11) and 18.30 ± 3.33 cm (N = 10). Five of the 14 ended at a rock face. Three scrapes that did not appear to have been used were dug into drifts against a riverbank where the hare had stopped digging before it reached the bank.

At Sverdrup Pass all three scrapes were dug only part way into drifts in the lee of boulders and only one had been used for sheltering based on the presence of tracks, pellets, and fur.

Snow Dens — Larger structures dug more than 30 cm into snowdrifts and consisting of an entrance and tunnel or chamber were termed snow dens. Snow dens were large enough to contain a hare in the resting sphere or crouch

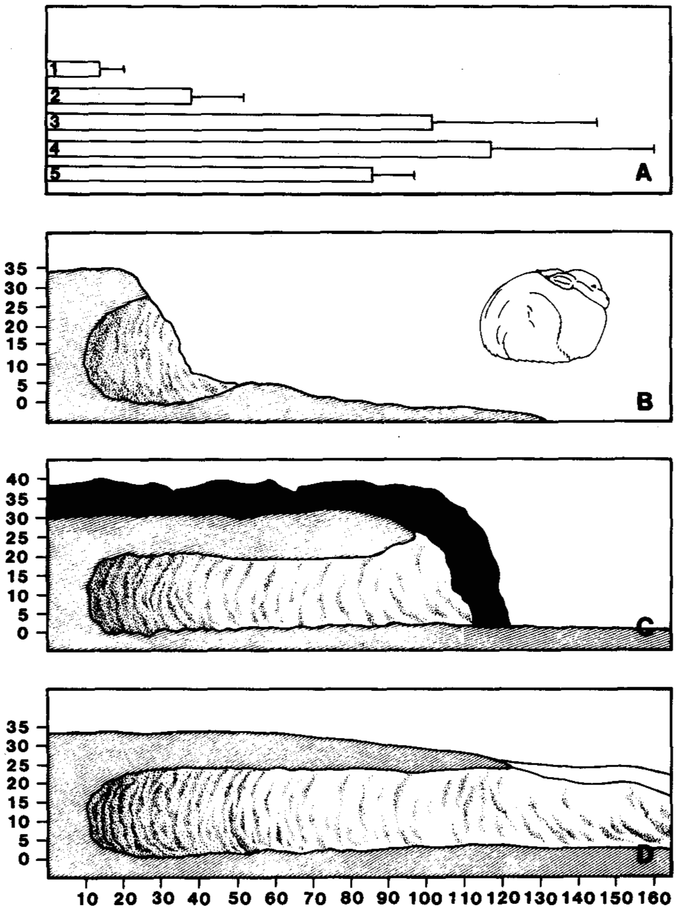

FIG. 9. Dimensions and shapes of snow scrapes and snow dens (in cm): a) mean length (±SD) of scrapes and dens at both study areas: 1 = scrape overhang, 2 = scrape length, 3 = snow dens near rock or hummock (Polar Bear Pass), 4 = snow dens in extensive snowdrift (Polar Bear Pass), and 5 = snow dens at Sverdrup Pass; 3, 4, and 5 are not significantly different; b) cross-section of average scrape with size of resting hare to scale; c) mean size of snow dens in drift behind rocks at Sverdrup Pass; d) mean dimensions of snow dens at Polar Bear Pass.

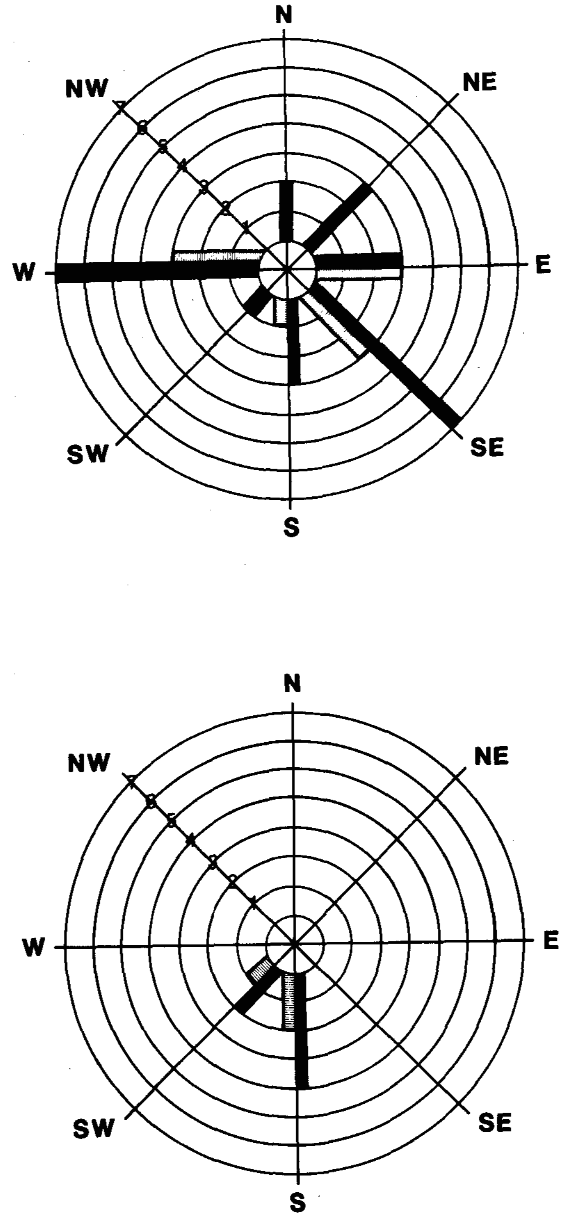

FIG. 10. Orientation of 13 snow scrape entrances (cross-hatched) and 32 snow den entrances (solid). Above, at Polar Bear Pass; below, at Sverdrup Pass. (Orientation recorded as one of 8 compass points only, due to irregularity of entrances.)

posture with a roof of snow extending completely over the hare.

Six snow dens were seen in Sverdrup Pass in April 1992, all within a 1 km² area, where up to five hares were observed. Five of the six dens were excavated in snowdrifts formed on the southeast side of large (2 × 3 m) boulders. This area has little snow cover, much ground is exposed throughout the winter, and there were no other major snowdrifts in that area. The rock wall was partially exposed in the entrance and tunnel in all six dens and den length was restricted by the size of the drift. Den length ranged from 76 cm to 102 cm ($\overline{x}$ = 86.60 ± 11.62 cm) (Fig. 10). Each of the six dens terminated in a slightly expanded chamber. The den openings all faced south or southwest.

At Polar Bear Pass, 37 snow dens were found in April or May in 8 years out of 15. Snow dens were all found in areas where hares were normally seen in small numbers in both late winter and summer (Fig. 1). The number of dens found each year varied from 1 in 1987 and 1989 to 16 in 1992. Five of the 1992 dens were in small drifts between hummocks in one valley and 7 were along the base of one narrow ravine. One den and several scrapes in the latter area were at the base of 25 m rock cliffs. The dens at Polar Bear Pass were dug into extensive snowdrifts (28) or into smaller drifts against a rock or hummock face (9). Four of these dens had slightly expanded chambers at the end of the tunnel. In 2 cases there was a 20 cm increase in width and up to 5 cm in ceiling height and 1 den had two terminal chambers branching from the entrance tunnel. The orientation and size of these dens was not restricted by the snowdrift or the presence of rock or ground. The mean length of 16 dens dug into extensive drifts, either in wind-sculptured sastrugi or relatively flat snow, was 102.60 ± 44.41 cm (range 50-188) (Fig. 9a).

For 9 snow dens (all found in 1992) dug into drifts in the lee of rocks, at the base of cliffs, or against a hummock, it appeared that the direction, slope, and height of the den were at least partially determined by the rock or ground formation. Most dens curved to one side, following the exposed surface. Only 3 dens had an enlarged terminal chamber 20-40 cm wide. The mean length of 9 such dens ($\overline{x}$ = 117.30 ± 46.37 cm) was not significantly different from that of the previous type, nor were they significantly different in length from the dens at Sverdrup Pass (Fig. 9a).

Den entrance orientation was variable (Fig. 10). In extensive drifts formed on the south-facing slopes of low hills, the den entrance usually faced south, southeast, or east. Dens in smaller drifts beside rocks faced north, west, and southwest to southeast. Five of the 1992 dens in the ravine were on the east side and thus the entrances faced west. The mean entrance height and width of 16 dens was 25.38 ± 6.63 cm and 19.47 ± 2.80 cm.

No snow scrapes or dens were observed at Mokka Fiord in late winter 1975 in the area in which a herd of about 250 hares spent at least part of the winter (Parker, 1977). The herd was seen in late March moving away from an area with hundreds of feeding craters, tracks, pellets, and urine spots, but with no obvious signs of sheltering.

Although arctic hares usually fed in shallow snow, they did occasionally dig into deeper drifts, forming craters up to 30 cm long and 20 cm deep. When digging for food in deep or drifted snow, hares used their forepaws to scrape and loosen the snow using rapid, alternating pawing movements similar to when feeding in shallow snow. They then scooped the snow out between the hind feet, shifting sideways with a slight hopping motion as the snow was pushed out. One individual took 4 minutes to dig a crater almost deep enough to conceal a hare (34 cm × 20 cm × 17 cm deep). The vertical claw marks on the walls inside snow scrapes and dens are the same as those seen on the walls of deep feeding craters (Fig. 11a,b). In most cases snow dens were dug into uniform, relatively hard wind-packed drifts. Excavated snow was piled in front of the entrance. Most snow piles were marked with tracks, droppings, or urine of arctic fox (*Alopex lagopus*) and one with wolf (*Canis lupus*) and short-tailed weasel (*Mustela erminea*) sign.

Although hares dug some den tunnels almost at ground level, all dens had a floor of snow. The floor of the tunnels was usually close to ground level and hares seem to have dug into the area of crystalline snow (known as depth hoar) just above ground level. The roof of all dens in both study areas varied in thickness, with a maximum of 10-36 cm (Fig. 9).

There was no indication of hares having dug dens to reach vegetation under the snow, nor was there any evidence of hares having fed inside. In one den at Polar Bear Pass the side of a well-vegetated hummock was exposed, but there were no signs of feeding.

Few faecal pellets were seen in snow dens. Only 6 of 19 dens checked had from one to five pellets inside ($\overline{x}$ = 2.83 ± 1.72). All dens had more pellets outside near the entrance than inside the den. Three dens at Polar Bear Pass where six hares were present each had over 20 pellets on the snow surface near the entrance and one had over 100 (Fig. 11c,d). Fourteen dens had well-used runways from 20 to 150 cm long ($\overline{x}$ = 65.82 ± 38.05) leading to the den entrance.

Wind velocities measured inside four dens on the lee side of large boulders in Sverdrup Pass were 0 km·h^{-1} during winds of 37 km·h^{-1}, with gusts up to 65 km·h^{-1} at 1.5 m above the den (Fig. 8c).

Timing of Construction and Use of Snow Dens: During the winter of 1970-71 at Polar Bear Pass, signs of hare feeding activity were seen from January to April and two hares were seen in a known late winter feeding area in February and March. However no dens were found until early May. In all other years observers were not in the study area until April or May, at which time dens were already present, so the time of earliest use of dens is unknown.

At Sverdrup Pass a den that was trampled by muskoxen and partially drifted in with snow some time before it was found on 23 April was redug and extended between 29 April and 1 May. Another 100 cm den, filled in with drifted snow during a storm on 5 May, was dug out again to a depth of 50 cm by 7 May. Two days after I opened this den on 7 May, a hare had redug at the entrance forming a new 20 cm chamber. Two other dens had at least been visited, if not used for shelter, between 29 April and 3 May. Hares were not seen entering or leaving dens at Sverdrup Pass, although the dens were not observed continuously throughout a 24 h period.

At Polar Bear Pass continuous observations of hares in the vicinity of dens were limited to 10 h, all between 0900 and 1700. Hares were observed at the entrance to dens on ten occasions from 23 April to as late as 5 June (Fig. 11c). On 16 May 1992, two hares from a group of five were seen briefly entering one of five dens in the area. One hare of the group chased another from the entrance, then entered the den itself twice for only 4 and 8 seconds. The first hare returned later to the same den and also entered twice, again for only 4 and 6 seconds. Hares were never flushed from inside dens. Dens at Polar Bear Pass that were blown full of snow between 12 and 15 May 1971 were not reexcavated before the melt.

One hare sitting at a den entrance remained there even as two observers approached to within 10 m. When the hare finally moved, it did not enter the den but ran off. Observers watched a snowy owl stoop at a group of arctic hares at both study areas, and both times the hares ran, even though once they were near several dens.

DISCUSSION

Although the arctic hare is well adapted structurally to the extremes of the long arctic winter, it is apparent that some behavioural modifications, from posture and orientation to the use of natural shelter and snow dens, are necessary in order to maintain the normal body temperature while at rest.

Hares conserve heat in winter by adopting a sphere-shaped posture while resting. Wang *et al.* (1973) noted the importance of the near-spherical shape of resting hares in decreasing heat loss, though at an ambient temperature of 15°C their captive hares probably would have rested in the sitting crouch rather than the resting sphere. Flux (1970) described a resting posture in the mountain hare in the Scottish winter, similar to the resting sphere, in which the forepaws

FIG. 11. Arctic hare snow scrape and snow dens: a) snow scrape and debris pile in lee of rock, Sverdrup Pass; b) hare at entrance to den in extensive drift at Polar Bear Pass; c) two adjacent dens at base of ravine at Polar Bear Pass; d) two hares near entrance to dens shown in b); note faecal pellets on snow.

are folded against the chest. Bonnyman (1975) referred to the "sitting crouched" posture as the characteristic posture of arctic hares in cold, rainy, or windy weather but did not mention the resting sphere posture. At the time she was observing hares (late May to August) the resting sphere posture would likely have been replaced by the sitting crouch.

The orientation of hares to wind direction plus the frequent shifting of position while resting in blowing snow conditions and the regular shaking movements while feeding in drifting or blowing snow probably ensure that the insulative qualities of the fur are not affected by the build-up of snow.

Although Banfield (1974) suggested that arctic hares sometimes huddle together for shelter in their winter snow forms, there was no evidence of huddling by hares in winter during this study. The huddling together seen in young hares in summer (Aniskowicz *et al.*, 1990) is restricted to the period before weaning. Similar huddling in young brown hares (*Lepus europaeus*) is thought to decrease the chances of predation and reduce the effect of extreme temperature changes (Schneider, 1979). Although young arctic hares, like adults, did rest together in closely spaced groups, even littermates did not huddle once they had joined mixed age and sex groups after weaning. This difference in behaviour, depending on location and social circumstance, suggests that huddling by young approaching the time of weaning was more a social response than a response to environmental conditions.

Grooming, important in the maintenance of the insulative quality of the coat year-round, is of increased importance in late winter because of the moult beginning when temperatures may still be as low as −25°C. Although Banfield (1974) states that the annual moult for arctic hares starts in June and occurs later on Ellesmere Island, the present observations and those of Manniche (1910), who noted hares moulting in April, clearly indicate an earlier moult.

Arctic hares are more exposed to the wind while reingesting and grooming, and during the late winter moult skin is exposed as they twist and stretch while grooming. Seeking shelter before grooming lessens the effects of such direct exposure and the general decrease in insulation caused by shedding.

Hares in groups do not usually move from the group to shelter at the end of the feeding period. Those that do move return to rest within the group, suggesting that social contact and interaction during the breeding season may be of greater importance than the benefits of shelter seeking.

The use of snow dens seems to be restricted to Greenland and the Canadian High Arctic. However, the lack of information on snow dens may partly be a reflection of the general lack of knowledge of the behaviour of many arctic animals in winter (Gray, 1990). In those areas where snow dens have been reported, they are not common. Most historical records are of a single observation, although Greely (1886:365) "saw several burrows in the snow, which had been temporarily occupied by hares." Manniche (1910:29) noted that although hares "will sometimes dig long channels for shelter" into winter snowdrifts, he usually found them sitting on snow by a rock, even in the severest winter cold. After travelling from Greenland through Canada's eastern and central Arctic, Freuchen (1935:74) noted that the arctic hare "very rarely burrows down into the snow for cover." At Mould Bay on Prince Patrick Island, MacDonald (1954:219) noted that hares "often excavate dens in the large, hard-packed snowdrifts." The four or five snow dens MacDonald observed were close together, in extensive flat drifts, and less than 1 m in length (S. MacDonald, pers. comm. 1992). In Jameson Land, northeast Greenland, snow dens are uncommon (H. Thing, pers. comm. 1992). During extensive travels with Inuit hunters on southern Ellesmere Island, B. Jesudason (pers. comm. 1992) saw only one snow den. Tom Smith (pers. comm. 1992) observed snow dens on western Victoria Island.

It is unlikely that arctic hare snow dens were missed in this study, as most are impressive structures and relatively easy to spot. One of Penny's exploring parties (Great Britain, 1852) found a hare at the entrance to a den 8 ft (240 cm) in length on Cornwallis Island in mid-May 1851. Feilden's (1877) observation from Grinnell Land, northwest Greenland, describes a hare starting from a 4 ft (120 cm) snow den in mid-February 1876 at a temperature of −49 °C. The den was discoloured from the hare's passage, with a quantity of hair on the sides and much sign of feeding around the den.

Although the absence of pellets inside dens indicates that hares only used dens for short periods at a time, probably while resting, the numbers of pellets and abundance of tracks outside some dens indicated considerable long-term use.

Although Osborn (1856) suggested that hares dig tunnels in snow to seek food, this study shows that feeding was not a factor in den construction. Even in the few cases where vegetation was exposed within a tunnel, there was no evidence of feeding.

The presence of snow dens in any area may be related to the amount of naturally occurring shelter. The relative number of snow dens seen at Polar Bear Pass compared to Sverdrup Pass is perhaps due to the comparative lack of rocks and boulders there suitable for sheltering. The type and number of dens are also very likely influenced by the amount, type, and timing of major winter storms.

It is unlikely that arctic hares use snow dens in escaping from mammalian predators, as wolves could easily dig hares out of a den and are probably attracted to dens by the obvious entrance. However a hare was seen to take refuge in a den after being shot (T. Smith, pers. comm. 1992). Dens would protect hares from aerial predators such as gyrfalcons (*Falco rusticolus*) and snowy owls, although our limited observations of interactions with avian predators indicate that hares run to rough or rocky terrain even when snow dens are nearby. The benefit of concealment in using a den may be negated by the inability of a hare to monitor the presence and activity of the predator once inside the den.

That hares were still using dens and keeping them open in late April and early May at both Sverdrup Pass and Polar Bear Pass is at first surprising in view of the steadily improving weather conditions. However, the fact that hares are undergoing a moult at this time suggests that there may be a need for extra shelter.

Thomas (1987) suggested that arctic hares, like other Leporidae and grouse species, have little metabolic resistance to winter fasting and must feed regularly to maintain the energy balance. Hares acquire small energy reserves, feed regularly for short periods, and emphasize energy conservation rather than energy acquisition. The most important method of energy conservation appears to be the resting sphere posture, as this is used in all late winter weather conditions and not always in conjunction with shelter. The use of snow scrapes and snow dens, even for relatively short periods of time, is an additional efficient, but not essential, method of conserving energy. The use of snow burrows by various grouse species has been shown to result in large savings in energy (Thomas, 1987). Within a 150 cm long, snow-covered snow den with walls and floor of snow and no wind even during storms, arctic hares would obviously lose less heat to the atmosphere than if they remained out in the open. The energy requirements for the digging of the dens in mid-winter are probably minimal and are compensated for if the dens are used until winter's end.

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