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Timing and Re-interpretation of Ringed Seal Surveys

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Abstract

We used VHF radio telemetry to estimate the proportion of ringed seals (*Phoca hispida*) visible resting on the ice surface during the spring months in 1999, 2000, 2001, 2002, and 2003. Changes in the number of seals counted during ground-based, visual surveys of seals resting on the ice corresponded to changes in the number of radio-tagged seals basking. Tagged seals spent 16% ($SD = 10\%$) of their time out of the water while using subnivean lairs and 55% ($SD = 22\%$) of their time out of water after emerging from those lairs. Emergence from the lairs was related to structural failure of the snow pack, and passive microwave emissions—indicative of liquid moisture in the snow—predicted lair abandonment ($r^2 = 0.982$, $p = 0.001$). Active microwave (Ku-band) backscatter also detected snow melt but responded to an anomalous rain event.

Inter-annual and spatial comparisons of seal densities based on aerial surveys have not adequately accounted for the proportion of seals concealed within subnivean lairs. Previous models of the factors influencing the density of seals detected in aerial surveys have been based on densities observed during surveys conducted under limited ranges of conditions. We used the probability of radio tagged seals being visible as our response variable to determine which environmental factors were most important in explaining the availability of seals to be counted. The most important variables were time of day, date, wind speed, air temperature, and days from snow melt as determined by passive microwave emissions. Modeling of the probability that seals were visible during past aerial surveys indicated that the fraction of seals visible varied from less than 0.40 to more than 0.75 between survey years. Future surveys should be conducted after seals have emerged from their lairs and should employ telemetry to determine the probability that seals are visible.

Radio-tagged ringed seals remained close to their capture and release sites in April, May, and early June. The mean home range size (based on breathing holes and lairs visited by tagged seals) during the breeding season was 1.73 km² ($SD = 4.19$), and 94% of the home ranges were less than 3 km². Inter-annual fidelity to breeding sites was observed in 3 adult ringed seals (2 males and 1 female) and suggests fitness costs to displacement of seals and an unexpected level of population structuring.

Introduction

Accurate estimates of the number of ringed seals (*Phoca hispida*), believed to be the most numerous pinniped in the northern hemisphere, remain elusive (Scheffer 1958; Smith 1987, Kelly 1988, Reeves 1998) due to inadequate knowledge of the species' population structure, ecology, and behavior. Distributed throughout the seasonally ice covered seas (and some lakes) of the northern hemisphere, ringed seals are thought to comprise six subspecies (Scheffer 1958, Reeves 1998), but population structure is largely unknown.

Local densities and, by extrapolation, population size of ringed seals have been estimated based on aerial surveys (e.g., Chapman et al. 1977, Stirling et al. 1977, Harwood and Stirling 1992, Frost et al. 2002, 2004; Garner et al. 1999; Moulton et al. 2002) typically without reference to population structure. Seasonal peaks in the number of seals out of the water (hauled out) vary by demographic class, and the timing of those peaks may vary from year to year depending on food availability as well as temporal and environmental variables (Green et al. 1995, Daniel et al. 1999, Jemison and Kelly 2001). Nonetheless, spatial and temporal comparisons often have been made under the implicit assumption that the proportion of animals visible is constant from survey to survey (Caughley 1977, Drummer 1999). In surveys of harbor seal (*Phoca vitulina richardsi*) populations, that assumption has been tested using radio telemetry (Withrow and Loughlin 1995, 1996, Huber et al. 2001). Frost et al. (1999b) used another approach in which they ignored the unseen fraction of a population and analyzed trends by adjusting counts of harbor seals to standardized conditions based on environmental and temporal covariates. That approach assumes that a similar (unknown) proportion of the population is visible when survey data collected under those conditions are compared. The approach also depends on selecting covariates that can predict the peak number of animals and on surveys that adequately represent all demographic classes and span a broad range of conditions relative to the covariates (Ver Hoef and Frost 2003). Simpkins et al. (2003) suggested that, when harbor seal surveys are corrected for covariates, they account for 81–86% of the local population.

Analyses of ringed seal surveys generally have been less intensive and have not taken into account seasonal changes in the visibility of ringed seals resting on the ice. When out of the water during the winter months, ringed seals are concealed from view within subnivean lairs excavated above breathing holes in the sea ice (Chapskii 1940, McLaren 1958, Smith and Stirling 1975). In late spring, the seals begin to emerge from

those lairs, and some are visible resting on top of the ice. Others, however, remain hidden from view either under the ice or on top of the ice but still concealed under the snow (Kelly 2005). Surveys of ringed seals typically have been conducted in late May and early June when the seals begin their annual molt. Regeneration of the epidermis requires that they elevate skin temperatures (Feltz and Fay 1966, King 1983), which they do by lying in the sun—hereafter referred to as “basking”. The greatest numbers of seals are visible on the ice “just before the ice break-up in most mid arctic localities” (Smith 1973a). Burns and Harbo (1972), however, pointed out that “extensive water on top of the fast ice, from melt and overflow of rivers” reduced the number of seals visible, and Frost et al. (1999a) observed that “it is difficult to predict when breakup will begin and how long the survey window might be in a particular year.” Nor has the onset of the survey window been explicitly defined. Rather, most surveys of ringed seals depend on the assumption that all seals have abandoned their lairs and, hence, are available to be counted when out of the water.

The Alaska Department of Fish and Game and LGL Ltd. surveyed ringed seals in the Beaufort Sea off of Alaska and corrected their counts for environmental influences using multivariate models (Moulton et al. 2002; Frost et al. 2004). In both of those studies, the response variable was the number of seals visible on the ice during aerial surveys. Thus, their models could not include information about seals hidden under snow cover, and their analyses of covariates were limited to conditions suitable for flying in light aircraft. Thus, their models were constructed without benefit of contrasting conditions of daylight, fog, and high winds.

Comparisons of local densities of seals visible on the ice have been used to assess the effects of human activities on ringed seals (Frost and Lowry 1988, Kelly et al. 1988, Richardson and Williams 2000; Moulton et al. 2005). Those human activities most often occur in winter or early spring (when snow and ice conditions are suitable to occupying the ice), while the seal surveys are conducted in late spring when seals are basking. An implicit assumption is that local seal distributions and densities are static in the interim. Some ringed seals, however, appear to move away from their winter range when they emerge from their lairs to bask. At least four of thirteen seals tracked telemetrically near Prudhoe Bay in the 1980s “hailed out at new sites . . . several kilometers” from those occupied prior to the beginning of snow melt (Kelly and Quakenbush 1990). Two of ten seals tracked in the Canadian arctic basked at sites several kilometers from lairs they occupied earlier in

the spring (Kelly 2005). During intensive aerial surveys conducted near Prudhoe Bay over eight days in 1999, the density of seals visible near shore decreased while the density offshore increased (Moulton et al. 2000). The authors interpreted those changes in densities as a large-scale movement of seals, but no such shift was evident in similar surveys conducted in 2000 or 2001 (M. Williams, pers. comm.). We do not know what determines whether ringed seals bask at the same breathing holes they used during their months under the ice and snow.

Ringed seals can be counted during visual surveys only if (1) they are on top of the ice, (2) they are not concealed in subnivean lairs, and (3) sightability is not impaired by fog, blowing snow, or a complex visual field such as a mosaic of snow cover and melt ponds. Ringed seals tend to bask on the ice whenever the weather is warm and calm. Those conditions occur only rarely in fall and winter months, and basking seals are rare in those seasons. Warm, calm conditions occur increasingly frequently in the spring months, and seals begin to abandon their lairs in favor of resting on top of the snow and ice.

We explored environmental factors that might predict when lairs are abandoned and then analyzed the covariates influencing the probability of seals being on top of the ice for the period after lair abandonment but before the development of extensive melt ponds on the ice surface.

We used VHF-radio telemetry to determine where and when ringed seals were visible on top of the snow and ice near Prudhoe Bay, Alaska in April, May, and early June of 1999–2003. Seal behavior was monitored 24 hours per day in all weather conditions. At the same time, we monitored weather and snow conditions on the ice adjacent to the seals to determine the relationships between environmental variables and the availability of seals for counting. Our response variable was the probability of tagged seals being visible on the ice, and we modeled the influence of covariates, including days before snow melt (hence the seals’ emergence from subnivean lairs), on that proportion.

Our objectives were to:

1. Determine the relationship between environmental variables (including snow conditions) and the number of seals visible during spring surveys.
 - Hypothesis: The transition from resting in lairs to resting in the open will be complete when the

snow becomes saturated with melt water.

- Hypothesis: The degree of saturation will better predict the abandonment of lairs than will calendar dates.
 - Hypothesis: The timing of saturation and of lair abandonment will vary regionally.
 - Hypothesis: Variation in the proportion of seals visible on the ice surface will decrease after seals cease to rest in lairs.
2. Determine the best methods for monitoring snow conditions and determining optimal survey times.
 - Hypothesis: Ku-band backscatter data can indicate optimal survey times by consistently identifying the point at which snow on the sea ice becomes saturated with melt water.
 - Hypothesis: Optimal survey times can be determined using on-shore coastal snow data as a proxy for snow conditions on the sea ice.
 3. Re-analyze previous ringed seal surveys from the Beaufort Sea of Alaska.
 - Hypothesis: The proportion of seals visible during past surveys can be estimated based on historical, coastal snow data used as a proxy for snow conditions on the sea ice.
 - Hypothesis: Relationships between seal densities and offshore development activities will be better represented when survey data are corrected for estimates of the proportion of seals observed.

Methods

Study area

We collected field data in the near shore Alaskan Beaufort Sea (70°29'23"N 148°41'52"W) between Prudhoe Bay, Reindeer Island, and Northstar Island (Figure 1) in April, May, and June 1999 through 2003. The area is shallow (water depths mostly less than 9 m, maximally 15 m), and usually covered by shorefast ice from October to July (Wise and Searby 1977). Snow falls mainly during September and October when open water in the Beaufort Sea provides moisture (Dingman et al. 1980, Walker et al. 1980) and is redistributed by winds throughout the winter (Benson et al. 1975). The snow cover is shallow over flat ice and drifts on the windward and leeward sides of pressure ridges and other deformities in the ice surface. Subnivean lairs are excavated by ringed seals in wind-packed snow greater than 20 cm deep (Smith and Stirling 1975).

Locating seal holes

Specially trained Labrador retriever dogs indicated the location of subnivean breathing holes by digging in the snow where they detected the odor of ringed seals (Kelly and Quakenbush 1987). We used avalanche probes to penetrate the snow and precisely locate the breathing hole in the underlying ice. We also used the probes and visual observations to determine whether a subnivean lair was excavated above the breathing hole. Each hole was marked with a numbered wooden stake and its location (± 10 m) was determined using a Global Positioning System (GPS).

Capturing, tagging, and tracking seals

We captured seals in nets that pursed below them when they entered breathing holes (Kelly 1996). We transported the seals to our ice camp where we recorded weights, estimates of age, and axillary girths. Annuli on the claws of the front limbs provided estimates of minimal age, since the earliest annuli are worn away from the distal end of the claws. We also photographed the unique pelage patterns of each seal and assigned identification codes. We compared the pelage patterns of each seal captured to those previously photographed in this and an earlier study (Kelly and Quakenbush 1990) to determine whether the seal had been previously captured.

We glued a 26 g VHF radio transmitter (Advanced Telemetry Systems, model MM170) with a unique frequency to the hair on each seal's back. To extend our observations of seal haulout bouts and movements beyond the annual molt, we attached a second 23 g VHF radio transmitter (Advanced Telemetry Systems, model MM420) to one hind flipper of each seal by way of a cattle ear tag (Temple Tag, Inc., model 73200) in 2002 and 2003.

We monitored radio signals hourly from stations equipped with 8-element Yagi antennas on 11 m high masts and within 5 km of the seal capture sites. We rotated the antenna through 360° while monitoring and recorded the direction from which each signal was received. Each time a seal came out of the water, as indicated by the presence of its radio signal, we determined its location using a mobile receiver and hand-held directional antenna array. The directional antenna array consisted of two H-antennas communicating with the acoustic receiver by way of a null combiner. Thus, the bearing from the array to a transmitter was indicated by a null surrounded by high amplitude signals. Typically, five or more bearings

(with an accuracy of approximately $\pm 3^\circ$) from points surrounding a tagged seal were obtained, and the seal's position was read as the intersection of those bearings. Once the seal's position was determined, we recorded whether each seal was concealed within a lair or visible on the snow surface.

Spatial and temporal patterns of lair use

The locations of breathing lairs and basking sites used by the tagged seals were plotted using MapSource (Garmin Corporation), transferred to an ArcView shape file, and the home ranges were delineated as minimum convex polygons (Worton 1987). The areas of those polygons were calculated to estimate home range sizes. The estimates did not account for water depth which did not exceed 9 m in any the areas used by seals in this study.

Diel patterns of haulout bouts were examined over periods ranging from 22 to 52 days for each tagged seal. The frequency distributions of haulout bouts at each hour of the day were plotted and the circular mean and standard deviations were calculated (Batschelet 1981). The frequency and duration of haulout bouts were examined separately for haulout bouts in lairs and haulout bouts at basking sites. The probability that the timing of haulout was the same when seals were in lairs and when they were basking was tested using Watson's U^2 statistic (Batschelet 1981). Rao's Spacing Statistic (U) was used to evaluate deviations from uniformity in the times at which seals were out of the water (Batschelet 1981).

To verify that the behavior of tagged seals was representative of the behavior of the overall population, we counted all seals visible on the ice daily (approximately 16:00 Alaska Daylight Time) in May each year. We used binoculars (Leica 10 \times 42) to make the counts from the roof of a building about 62 m above the ice at the southern edge of the study area.

Recording snow and weather conditions

Environmental variables that might influence when seals were visible on the ice were measured in the study area. Additional data were obtained from the airport in Deadhorse (70°11'41.9"N 148°27'54.6"W), the West Dock of Prudhoe Bay (70°24'47.5"N 148°31'57.3"W), the man-made Northstar Island (70°29'23.4"N 148°41'51.9"W), as well as from satellites collecting active and passive microwave data.

In the study area, we recorded air temperature, snow temperature (from ice surface to snow surface at 5 cm intervals), wind speed, and wind direction every

30 minutes. The data were stored on a CR10 data logger and SM192 storage module (Campbell Scientific). We examined changes in the distribution of liquid water in the snow pack, snow depth, the size and morphology of snow grains, and the overall snow landscape to monitor the transformation of the snow pack during snowmelt (Liston and Sturm 2002). We compared the snow temperature record for our study area with snow temperatures collected by V. E. Romanovsky on the tundra near the West Dock in Prudhoe Bay (70° 22.47'N 148° 33.13'W) in 1999, 2000, and 2001.

Records obtained from the airport in Deadhorse included air temperature, wind speed, and wind direction. Wind speed and direction and air temperature data also were obtained from a seawater treatment plant (STP) operated by BP Alaska at the West Dock of Prudhoe Bay. Solar radiation data and additional temperature records were obtained from the Northstar Island.

Snow melt in the study area is hastened by flooding of the Sagavanirtoq and Kuparuk rivers on to the sea ice. Breakup dates of the Kuparuk River were obtained from the U. S. Geological Survey and were defined by a rapid increase in flow rates.

We also used satellite-borne Ku-band backscatter data to monitor changes in the liquid content of the snow pack in our study area in 2000, 2001, 2002, and 2003. The Jet Propulsion Laboratory in California provided active microwave data (14 GHz backscatter) reported from the satellite, QuikSCAT. Backscatter data were collected at 0600 and 1800 hrs daily for our study area. The microwave backscatter is highly sensitive to the amount of liquid moisture in snow, and the difference in backscatter amplitude between the morning and evening passes of the satellite indicated the degree of diurnal freezing and thawing in the snow cover (Tjuatja et al. 1992; Nghiem et al. 1995).

We also monitored snow melt using passive microwave data collected from the NOAA/NASA Pathfinder AVHRR Land Program satellite. The date of snow melt on the sea ice in our study area was estimated using two variants of the Advanced Horizontal Range Algorithm (Drobot and Anderson 2001); the Passive Microwave Surface Temperature Algorithm (PMSTA) and the Mean Differences and Standard Deviation Analysis (MDSDA) algorithm (Belchansky et al. 2004).

Re-interpreting past surveys

We used generalized additive models (binomial family, logit link, and spline smooth) to explore the relationship between the probability of a seal basking

and environmental variables (Hastie and Tibshirani 1990).

Each of the 2,163 hourly observations on 61 tagged seals were treated as a binomial response (the seal was basking and visible to an aerial observer or the seal was hidden from view, in a lair or under water). We minimized variance by confining the model to periods when aerial surveys in the Alaskan Beaufort Sea were conducted (26 May to 12 June) and to the shore fast ice area near Prudhoe Bay (sector B3) included both in Frost et al.'s (2002) surveys and our telemetry study. Frost et al. (2002) collected wind speed measurements from airport weather stations and from survey aircraft and reported them as meta data to the National Oceanographic Data Center. We developed a linear regression equation that corrected those measurements to wind speeds measured on the sea ice.

We reanalyzed the Alaska Department of Fish and Game surveys (Frost et al. 1999, 2002) estimating the proportion of seals visible during each of their surveys based on our telemetric observations and environmental covariates we measured in the field. We used the GAM function in Splus to build models and test the significance of covariates. We used univariate models and our best multivariate model to predict the probability of seals basking during each observation based on covariates from Alaska Department of Fish and Game surveys. The probabilities were averaged for each year and compared to the densities reported by Frost et al. (2002). Raw data were not available for surveys conducted by LGL Limited (Moulton et al. 2002). We compared the probability that tagged seals were visible with corrected density estimates obtained in LGL Limited's aerial surveys.

Results

Locating seal holes

In each year of the study, we located over 100 seal breathing holes, nearly half of which had subnivean lairs above them (Table 1). The percentage of all lairs that showed signs of a pup were low overall and varied from 4% in 2000 and 2001 to 9% in 2002, but the differences were not significant ($\chi^2 = 1.95$, $df = 4$, $p > 0.50$).

Breathing holes and lairs often were distributed in linear arrays reflecting the distribution of refrozen cracks and pressure ridges in the study area (Figures 2–6).

Capturing, tagging, and tracking seals

We set nets one or more times in 124 seal holes for a total of 180 sets (Table 2). Including recaptures, we caught seals in 60% of those holes or 41% of the nets set. Time to capture ranged from 15 minutes to 5 days with 56% of captures occurring within 48 hours of the time a net was set (Figure 7). Capture rates were higher in May (49% of 80 nets set) than in April (37% of 100 nets set) reflecting less frequent freezing of the nets and more frequent visits by seals. Seals entered 50% of the nets set in April and 66% of the nets set in May.

We captured 62 individual ringed seals, and we tagged and tracked 31 females and 29 males (Table 3). The number of annuli visible on the pectoral claws of captured seals ranged from 4 to 9 with a median of 7 for both male and female seals.

Spatial and temporal patterns of lair use

The location of each tagged seal was determined 1 to 32 ($\bar{X} = 12.8$, $SD = 7.02$) times when they rested on the ice. The number of resting sites identified for each seal ranged from 1 to 8 ($\bar{X} = 3.4$, $SD = 1.53$) and likely underestimates the actual number of holes used, as the seals' locations were not determined for every resting bout. The number of holes used increased with the number of times sites were identified and reached an asymptote at 4.5 holes per seal (Figure 8).

Home ranges were determined for 58 of the seals tracked in 1999–2003 (Figures 2–6) and ranged from 0.03 to 28 km² ($\bar{X} = 1.73$, $SD = 4.19$). Most (94%) of the home ranges were less than 3 km² (Figure 9). Two of the larger home ranges included lairs ≥ 7 km apart between which seals moved repeatedly. In 2000, the home range of an adult female seal (OC00) included two lairs 8.6 km apart, and in 2001, an adult male (MK01) used two lairs separated by 7 km. The home ranges of two seals tracked in 2002 exceeded 3 km² only in early June when they began basking 20 km (RO02) and 40 km (RN02) from the sites they used in May.

Nine seals were recaptured within the same breeding season, 1 to 20 days after their initial capture. Each was captured within 1300 m of their initial capture site. Three seals were recaptured in the subsequent breeding season, 371–377 days after their initial capture. Their recapture sites were 746, 1400, and 2000 m from the sites at which they were captured in the previous year. The home ranges of those three seals were similar in size, configuration, and number of lairs occupied in successive breeding seasons (Figure 10).

Seals spent more time out of the water once they began emerging outside of lairs. Tagged seals spent

16% (SD = 10%) of their time out of the water before abandoning lairs and 55% (SD = 22%) of their time out of the water after first emerging on the ice outside of a lair. Twenty-six of 43 seals monitored before and after their first emergence from lairs occupied lairs one or more times after emergence. They spent an average of 3% (95% CL: 1–4%) of their time in lairs and an average of 37% (95% CL: 32–41%) of their time basking after the first emergence. Resting bouts on the ice (Figure 11) were of longer duration (Median = 9 hrs) when the seals were basking than when they occupied lairs (Median = 6 hrs). Intervals between on-ice resting bouts (Figure 12) tended to be shorter (Median = 14 hrs) when seals were basking than when using lairs (Median = 27 hrs).

Most tagged seals exhibited a significant diel pattern in the proportion of time spent on the ice (Figure 13). Individuals varied in their preferred on-ice times, but most shifted from resting on the ice primarily between 1800 hrs and 0600 hrs (overall \bar{X} = 0110 hrs, SD = 6.10 hrs) when using lairs to resting on the ice primarily at mid day when basking (overall \bar{X} = 1646 hrs, SD = 1.46 hrs). The shift to coming out of the water in late afternoon was highly significant ($U^2 = 1.591$, $p < 0.001$). The variance in when seals were out of the water was greater during lair occupation (Rao's $U = 149.63$, $0.10 > p > 0.05$, $n = 41$) than when seals were basking (Rao's $U = 286.78$, $p < 0.01$, $n = 59$). The probability of a seal being out of the water during any hour rarely exceeded 0.50 when occupying lairs, but when the seals were basking, the probabilities often exceeded 0.50, especially in the afternoon hours.

Relationship between snow conditions and number of seals visible

No seals were visible resting on snow surface prior to 28 April in any of the five years of observation. Tagged and untagged seals began appearing on the surface on 21 May 1999, 8 May 2000, 4 May 2001, 5 May 2002, and 28 April 2003, and the number of seals visible generally increased thereafter until late May or June. The number of tagged seals visible in the study area generally increased with the total number of seals visible, although counts of tagged seals were less variable, because those seals were detected and located even when visibility was poor (Figure 14). The proportion of tagged seals visible explained more than 60% of the variance in the total number of seals visible every year except 2002 (Table 4). In that year, an early snow melt forced all seals out of their lairs by 18 May.

The first seals were recorded resting on the ice

outside of lairs earlier each year from 1999 through 2003, and the transition (time when the first to last tagged seal began basking) varied from 14 days in 2002 (5 May–18 May) to 36 days in 2000 (8 May–12 June) and 2003 (28 April–2 June) (Figure 15).

Snow temperature at the ice surface warmed throughout April and May and reached 0°C in late May or early June (Figure 16). The rise from about -2°C to 0°C was abrupt in contrast to the gradual rate of increase prior to that point and corresponded with the entire snow pack becoming isothermal (Figure 17). The abrupt shift likely reflected liquid water running freely through the snow pack. While the date on which the last tagged seal abandoned lair occupation varied widely between years (ranging from 18 May in 2002 to 12 June in 2000), each year it was within 4–6 days of the day on which the snow became isothermal (Table 5). The abrupt increase in snow temperature to 0°C preceded the date of final lair use in 1999, 2000, and 2003 and occurred after lair abandonment in 2001 and 2002. Thus, snow temperature was a poor predictor of lair abandonment ($y = 1.1016x - 14.92$, $r^2 = 0.663$, $p = 0.093$).

The variance in the proportion of seals visible decreased after the transition from lair use to basking was complete. During the transition period, the mean proportion of tagged seals basking was 0.19 and the coefficient of variation (CV) was 117.92. After lair abandonment was complete, the mean proportion of tagged seals basking was 0.75 and the CV was 27.93.

Methods for determining snow conditions and survey times

While the abrupt increase in snow temperature at the ice surface occurred within one week of the final date of lair abandonment each year, monitoring snow temperatures is impractical as a means of determining suitable survey times. Therefore, we explored more practical, remote methods of determining when failure of the snow cover was imminent and lair abandonment was complete. We regressed the date of final lair abandonment against the date the first seal was observed out of a lair, the break up date for the Kuparuk River, the date of substantial snow melt indicated by passive microwave backscatterometry, and the date of substantial snow melt indicated by active microwave imagery.

The date of first lair abandonment was a poor predictor of the final date of lair abandonment ($y = 0.4281x + 98.781$, $r^2 = 0.136$, $p = 0.542$) reflecting substantial inter-annual variability in the duration of

snow melt.

In 2000, 2001, and 2003, the diurnal difference in the amplitude of backscatter first exceeded 2 dB 7–8 days prior to the date on which the snow became isothermal. In 2002, however, an early rain event in late April caused the diurnal difference in the amplitude of backscatter to exceed 2 dB 17 days prior to the snow becoming isothermal. The date on which the diurnal difference in backscatter first exceeded 2 dB preceded the date of final lair abandonment by 3–13 days in 2000, 2001, 2002, and 2003 ($y = 0.8447x + 31.874$, $r^2 = 0.847$, $p = 0.080$).

We also examined snow temperature data from an on-shore monitoring site at West Dock in Prudhoe Bay as a potential proxy for snow conditions on the sea ice. Snow temperature on the tundra was consistently colder than the snow over the ice and it reached 0°C later in the season each year (Figure 18). Overall, snow temperature on the tundra was a good predictor of snow temperature on the sea ice ($y = 1.0289x + 6.1609$, $r^2 = 0.883$, $p = 0$).

Abrupt flow rates on the Kuparuk River are another indication of breakup, and we regressed dates of lair abandonment against melt dates indicated by river discharge. The discharge did not predict lair abandonment well ($y = 0.7043x + 47.506$, $r^2 = 0.3436$, $p = 0.4138$).

We regressed date of final lair abandonment against date of snow melt estimated by passive microwave data using two different algorithms. The PMSTA algorithm estimated date of snowmelt as 21–35 days after the date of final lair abandonment ($y = 0.8841x - 5.3768$, $r^2 = 0.697$, $p = 0.078$). The MDSDA algorithm estimated snow melt dates within 3 days of the date of final lair abandonment ($y = 0.9308x + 11.221$, $r^2 = 0.982$, $p = 0.001$) for each year of the study.

Re-analysis of ringed seal surveys in the Beaufort Sea

We modeled the proportion of seals visible as a function of the environmental variables that significantly influenced the haulout behavior of the tagged seals. We examined, date, time of day, air temperature, wind speed, wind direction, barometric pressure, solar radiation, and days from snow melt based on the active microwave radar and the MDSDA algorithm (Figure 19).

The probability of seals basking increased as solar radiation increased. Because radiation was highly correlated with time of day, however, we dropped radiation from the model. The prevailing east winds provided little contrast for analysis, and wind direction

was not a significant covariate in the final model. We observed no correlation between barometric pressure and the basking behavior of seals.

Time of day, day of year, days from snow melt, air temperature, and wind speed all had significant effects on the probability of seals basking (Figure 19). We found a strong diel effect during the aerial survey period with a peak probability of seals basking at 1500 h Alaska daylight time. The probability of seals basking continued to increase with date through mid June when our observations ceased. The probability also increased during the 20 days preceding snow melt as estimated from the MDSDA data. There was little change in the probability of basking for the next 10 days and then an increasing probability for at least the next 20 days. We observed a rapid increase in the probability of basking as air temperature rose from -5°C to 0°C and a slower increasing probability with further warming. The probability of basking changed little with wind speeds under 3.5 m/s but declined at higher wind speeds.

Our best model included time of day, date, days before snow melt, air temperature, and wind speed (Table 6). Applied to the Alaska Department of Fish and Game surveys in the Prudhoe Bay region (Frost et al. 1999, 2002), the model (Figure 20) indicated that the mean probability that seals were visible during the surveys ranged from 0.39 (SD = 0.16) in 1999 to 0.76 (SD = 0.07) in 1985.

For most years, the error associated with the estimated probability that seals were visible during the Alaska Department of Fish and Game surveys was large, reflecting the diversity of covariates that influence seal behavior. The probability of seals being visible was more strongly influenced by some covariates than by others (Figure 21). The surveys mostly were restricted to the hours between 1100 and 1700 h AST, and time of day appeared to have had little influence on probability of seals being visible. Survey dates were more variable from year to year, and our model indicated that twice as many seals were available to be counted on the days surveyed in the 1980s than in the 1990s. Late snowmelts reduced the probability of seals basking during the surveys in 1986 ($\bar{X} = 0.24$, SD = 0.03) and in 1999 ($\bar{X} = 0.27$, SD = 0.05).

Wind speed had minimal effect on the probability of seals basking during the surveys (Figure 21), most likely because surveys were not conducted at higher wind speeds (Frost et al. 1999, 2002). Air temperature, however, did not influence when surveys were conducted, and variability in air temperature increased variability in the proportion of seals visible.

Aerial surveys conducted by LGL Limited in 1999–2002 encompassed our study area (Moulton et al. 2005). The densities they reported in each of those years were positively correlated ($r^2 = 0.7546$, $p = 0.13$) with the proportion of our tagged seals that were basking (Table 7). The overall densities reported by LGL Limited, however, were substantially lower than those reported for the same area by the Alaska Department of Fish and Game (Table 8).

Discussion

Snow cover is important to ringed seals, especially the young, as it insulates them from cold (Smith and Stirling 1975; Kelly and Quakenbush 1990) and helps protect them from predators (Lydersen and Smith 1989; Smith and Lydersen 1991). In winter and early spring, ringed seals rest when out of the water in subnivean lairs. In late spring, they begin to bask on top of the ice after the lairs collapse or after excavating their way out of the lairs. Thus, snow conditions influence when ringed seals are available to be counted in visual surveys. Our hypothesis that the transition from resting in lairs to resting in the open would be completed when the snow became saturated with melt water was supported by the observation that the seals abandoned the last lairs within 4–6 days of the snow becoming isothermal. The liquid moisture content of the snow as measured by microwave emissions was even more strongly correlated with lair abandonment.

We attempted to test the hypothesis that the timing of saturation and of lair abandonment varies regionally by enlisting students and other observers to monitor emergence from lairs near Kaktovik and Barrow. We were unsuccessful, however, in recruiting help for the Barrow effort, and the Kaktovik site recommended by local hunters had insufficient numbers of seals for quantifying emergence. Other investigators, however, have reported regional variation in snow melt dates with the melt dates being consistently earlier near Kaktovik than near Barrow (Stone et al. 2002). Given the close relationship between snow melt dates and lair abandonment, the regional variation in snow melts likely translates into regional variation in when seals are available to be counted. Furthermore, along the northern coast of Alaska, snow melt dates have advanced over the past three decades (Stone et al. 2002), with the earlier melts corresponding to an increased variability of May air temperatures since 1990 (Arctic Climate Impact Assessment 2004). The combination of regional and temporal variation in snow melts indicates that the timing of ringed seal surveys should take snow

conditions into account.

The timing of aerial surveys, however, typically has been based on calendar date and general assessments of weather conditions. Surveys in the Alaskan Beaufort Sea have been conducted after the onset of lair abandonment but not necessarily before abandonment was completed. Between the onset and completion of lair abandonment, less than 20% of the tagged seals were basking and available to be counted. Once abandonment was complete, an average of 75% of the tagged seals were visible basking. As hypothesized, the variance in the proportion of seals visible was substantially less after abandonment. The low numbers and high variance in the proportion visible before all seals have emerged from their lairs argues for commencing surveys only after emergence is completed. Comparisons of densities estimated from previous surveys that took place during the transition period when variances would have been high may be misleading. For example, Frost et al. (1997) reported that in 1985–1987, ringed seal densities in the industrial zone around Prudhoe Bay were similar to densities in surrounding areas, while in 1996, the density in the industrial zone was half that of the surrounding areas. With the addition of three more years of surveys (1997–1999), they reported observing 31% fewer ringed seals on the shore fast ice of the Alaskan Beaufort Sea in the 1990s than in the 1980s (Frost et al. 2002) with especially pronounced decreases in the Prudhoe Bay area (Frost et al. 1999b). They noted, however, that the reduction in numbers of seals observed might be a function of a shift to earlier survey periods in the 1990s rather than of a population decline. Indeed, our modeling results suggested that the change in timing of the surveys could account for a 50% reduction in the number of seals available to be counted. Survey timing relative to snow melt was an especially strong influence and negatively biased density estimates in 1986 and 1999.

Determining the effect of snow melt on the probability of seals basking requires proxy data from which past snow melts can be reliably inferred. Our preliminary results in 2000 (Kelly et al. 2000) encouraged us to hypothesize that active microwave (Ku-band) backscatter data would indicate optimal survey times by consistently identifying the point at which snow on the sea ice becomes saturated with melt water. An abrupt increase in the diurnal difference in backscatter amplitude did correspond to wet snow associated with snow melt and lair abandonment in 2000, 2001, and 2003. The backscatter signal also indicated wet snow associated with a rain event 17 days prior to snow melt and lair abandonment in 2002. We

conclude that backscatter is a useful indicator of snow conditions in seal habitat, but only when interpreted with appropriate meteorological information.

We do not have a historical record of backscatter data, and we examined proxy data that might allow us to infer snow conditions on the ice during previous ringed seal surveys. We hypothesized that the completion of lair abandonment and, hence, optimal survey times could be determined using on-shore snow temperatures as a proxy for snow melt on the sea ice. Snow temperature on the tundra at West Dock was a good predictor of snow temperature on the sea ice in our study area, but the tundra record was limited to the years 1999–2001. Changes in discharge rates for the Kuparuk River did not correlate well with lair abandonment in our study area. The river discharge likely responds more to the conditions inland than to near shore conditions.

Snow melt determined from passive microwave emissions proved to be a good indicator of lair abandonment, especially when analyzed with the MDSA algorithm (Belchansky et al. 2004). The relationship between snow melt and lair abandonment likely reflects the importance of snow integrity to maintaining subnivean lairs, which conceal ringed seals. Other studies have ignored snow melt, implicitly assuming that the effect can be accounted for by date. We observed substantial interannual variation in the dates of snow melt, however, and a general trend toward later snow melts consistent with the climate record for the arctic coast of Alaska (Stone et al. 2002). Passive microwave data are especially attractive as proxy data as they are available from 1979 forward and for the entire Arctic Ocean. Future visual surveys of ringed seals should be conducted only after substantial snow melt as indicated by passive microwave data.

After the snow melt, the probability of ringed seals being visible was most strongly influenced by time of day, wind speed, and air temperature. The time of day effect was more pronounced in the analysis of our telemetric studies than in analyses based on counts collected in aerial surveys. Burns and Harbo (1972) conducted surveys in Alaska between 1000 and 1600 hours (presumably Alaska Daylight Time) “based on previous general observations” of when the most seals were expected to be visible. Smith (1973a,b) made repeated counts throughout the day to determine when the most seals were visible resting on the ice. He concluded that, for a site in the eastern Beaufort Sea, the optimal survey times were between 0900 and 1500 hours (again, presumably local time). The Alaska Department of Fish and Game adopted a protocol that

called for conducting ringed seal aerial surveys between 1000 and 1600 hours local time (Burns and Kelly 1982, Frost et al. 1988, 1998). An analysis of the effects of covariates on ringed seal density in the Beaufort Sea during surveys in 1996–1998 suggested a nearly three-fold linear decrease in densities between 1000 and 1800 hours local time (Frost et al. 1999a). Moulton et al. (2002) reported highly significant declines in the densities of seals observed between 0900 h and 1700 h (apparently local time) in 1997 and 1998 but a highly significant midday peak in densities in 1999. When considered in a multivariate model, however, they found no significant effect of time of day on seal densities. Frost et al. (2004), on the other hand, reported that in 1996, 1997, and 1998, densities increased significantly between 1000 h and 1200 or 1300 h (Alaska daylight time). In 1999, however, they observed a significant increase in densities throughout the survey hours with the highest numbers after 1700 h. As with Moulton et al.’s (2002) model, Frost et al. (2004) found that time of day did not remain significant in their multivariate model. Their samples provided little contrast in times of day, however, since “most surveys occurred between 1100 and 1700 h.”

In contrast, our monitoring of tagged seals showed a strong relationship between time of day and the probability that tagged seals were visible. Less than 10% of tagged seals typically were visible at 0400 h and 70% were visible on average at 1600 h. The inconsistent time-of-day effects reported by Moulton et al. (2002) and Frost et al. (2004) may reflect the lack of contrast in the timing of their surveys. Our samples included all hours of day and night which better anchored the model. The analysis of time-of-day effects based on aerial surveys may also be confounded by visibility effects associated with changing sun angles.

The probability of tagged ringed seals being visible decreased with increasing wind speed. Both Moulton et al. (2002) and Frost et al. (2004) reported inconsistent results in their analyses of the effects of wind speed on ringed seal densities. Their surveys necessarily were conducted in a narrow range of wind speeds, however, and the lack of contrast may have masked real effects. They attempted to minimize the influence of wind speed by limiting surveys to wind speeds of 10 m/sec or less. Our modeling of ringed seal behavior indicated, however, that at wind speeds of 10 cm/sec the probability of seals being visible was less than half the probability under calm conditions.

For air temperatures between -10 and 8°C, the probability of tagged ringed seals being visible increased

with temperature. Air temperatures vary irregularly during aerial survey periods, and the overall effect is to increase variance in survey counts.

Frost et al. (2002), Moulton et al. (2002), and others modeled the influence of covariates on the number of seals observed in aerial surveys. We modeled the influence of covariates directly on the probability of tagged seals being visible and applied the model to each of the surveys conducted by Frost et al. (2002) in the Beaufort Sea in the 1980s and 1990s. The re-analysis indicated that the portion of seals that were visible during those surveys varied from less than 0.40 to more than 0.75. We had hoped that our re-analysis would permit us to correct the density estimates taking into account the probabilities of seals being visible, but such corrections seemed imprudent given the large variances around the estimated probabilities.

Moulton et al. (2002) corrected their counts of seals in our study area using a Poisson regression model that included date, ice deformation, cloud cover, distance from the ice edge, water depth, percentage of ice covered by melt water, and air temperature. The proportion of tagged seals visible varied from 0.08 to 1.00 during the period in which those surveys were conducted (Table 6), and the resulting density estimates were positively correlated ($r^2 = 0.75$) with our estimates of the proportion of seals visible. Their results likely would be strengthened by incorporating date of snow melt and correcting for seals concealed in subnivean lairs. It is not clear why their density estimates were consistently lower than the Alaska Department of Fish and Game estimates (Frost et al. 2004). The differences may reflect differences in covariate models and/or in observer abilities.

Density estimates based on counts of molting seals are strongly influenced by the timing of the molt, which may vary among demographic classes of seals. The probability of ringed seals basking increased with date through our latest observations in mid June (Figure 19). Thus, our study (and the Alaska Department of Fish and Game and LGL Limited aerial surveys) were conducted prior to the peak molting period. It may also be that the number of ringed seals available to be counted varies seasonally among age classes as is the case in harbor seals (Daniel et al. 1999, Jemison and Kelly 2001). Our sample, however, did not include juvenile ringed seals. If, as is the case for harbor seals (Kelly 1981), juvenile ringed seals molt prior to the adults, the “peak” counts in ringed seal surveys may be indicative only of the adult segment of the population.

The optimal survey window for ringed seals is the

period after lair abandonment is complete but before formation of melt ponds interferes with sightability. Both the onset and duration of snow melt vary widely from year-to-year (Kelly 2005), however, as do other factors, such as ice deformation, that influence sightability. While melt ponds and ice deformation appear to substantially decrease sightability, their influence has yet to be adequately quantified. The high variability in the onset and duration of the optimal survey window—coupled with the array of variables influencing the probability of seals being visible—suggests that inter annual comparisons of observed ringed seal densities need to be corrected using simultaneous telemetrically derived estimates of the proportion of seals visible similar to the corrections made by Withrow and Loughlin (1995, 1996) for harbor seals surveys.

The small home ranges maintained by ringed seals in winter and early spring have implications for the potential impact of human on-ice activities and for the utility of aerial surveys for counting seals. The three seals that we recaptured in successive breeding seasons all came back to small home ranges within 2 km of the sites used the previous year. Furthermore, in each case the breeding home ranges used in subsequent years were similar in size, number of lairs, and the spatial arrangement of those lairs. If that site fidelity is typical of ringed seals, it suggests that there may be fitness costs associated with displacement of ringed seals by the activities of humans or predators. Fidelity to breeding sites by adult seals also would beg the question of philopatry. If ringed seals, in fact, are returning to their own natal sites to breed, then there likely is substantial structuring of their populations and local impacts would be of greater consequence than if genes are exchanged over broad areas. We have begun investigating stock structure with movement data and analysis of micro satellite DNA and mtDNA extracted from skin samples of breeding seals.

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Reports and publications resulting from this project:

- Kelly, B. P., L. T. Quakenbush, and B. D. Taras. 1999. Correction factor for ringed seal surveys in Northern Alaska. Annual Report for 1999 to Coastal Marine Institute, University of Alaska Fairbanks. Pp. 51-64.
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- Harding, O. R., B. P. Kelly, L. T. Quakenbush, and B. D. Taras. 2001. Importance of snow for ringed seal pups. In Abstract Book. Aquatic Sciences Meeting. American Society of Limnology and Oceanography. February 12-16, 2001. p. 64.
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- Kelly, B. P. 2005. Correction factor for ringed seal surveys in northern Alaska. Final Report, OCS Study MMS 2005-006. Coastal Marine Institute, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks. Fairbanks, Alaska.

Study Products

Presentations on this project have been delivered in several venues.

VENUE	DATE	PRESENTER
Univ. Alaska Southeast, Juneau	Feb. 1999	O. Harding
Coastal Marine Institute, Fairbanks	Feb. 1999	B. Kelly
Coastal Marine Institute, Fairbanks	Mar. 2000	B. Kelly
Research Experiences for Undergrad's, Univ. Alaska Southeast, Juneau	Jul. 2000	O. Harding
Am. Soc. Limnology & Oceanography, Albuquerque, N.M.	Feb. 2001	O. Harding
Coastal Marine Institute, Fairbanks	Feb. 2001	L. Quakenbush
Biomonitoring/Global Change, Ascona, Switzerland	Feb. 2001	B. Kelly
MMS Information Transfer, Anchorage	Apr. 2001	B. Kelly
U.S.-Russia Marine Mammal Project, Santa Cruz, CA	Apr. 2001	B. Kelly
Mt. Film Festival, Telluride, CO	May 2001	B. Kelly
Biennial Conf. Biol. Marine Mammals, Vancouver, B.C.	Dec. 2001	B. Kelly
Coastal Marine Institute, Fairbanks	Feb. 2003	B. Kelly
MMS Information Transfer, Anchorage	Apr. 2003	O. Harding
Natl. Academy of Science, Anchorage	Mar. 2003	B. Kelly
MMS Scientific Committee, Anchorage	Apr. 2003	B. Kelly
Research Experiences for Undergrads, Univ. Alaska Southeast, Juneau	Aug. 2003	J. Conway
Research Experiences for Undergrads, Univ. Alaska Southeast, Juneau	Aug. 2003	K. Hildebrandt
54 th Arctic Science Conference, Fairbanks, AK	Sept. 2003	O. Harding
SEARCH Open Science Meeting, Seattle, WA	Oct. 2003	B. Kelly
34th International Arctic Workshop, Boulder, CO	Mar. 2004	J. Conway
IEEE Internatl. Geosci. & Remote Sensing Symposium, Anchorage, AK	Sept. 2004	S. Nghiem

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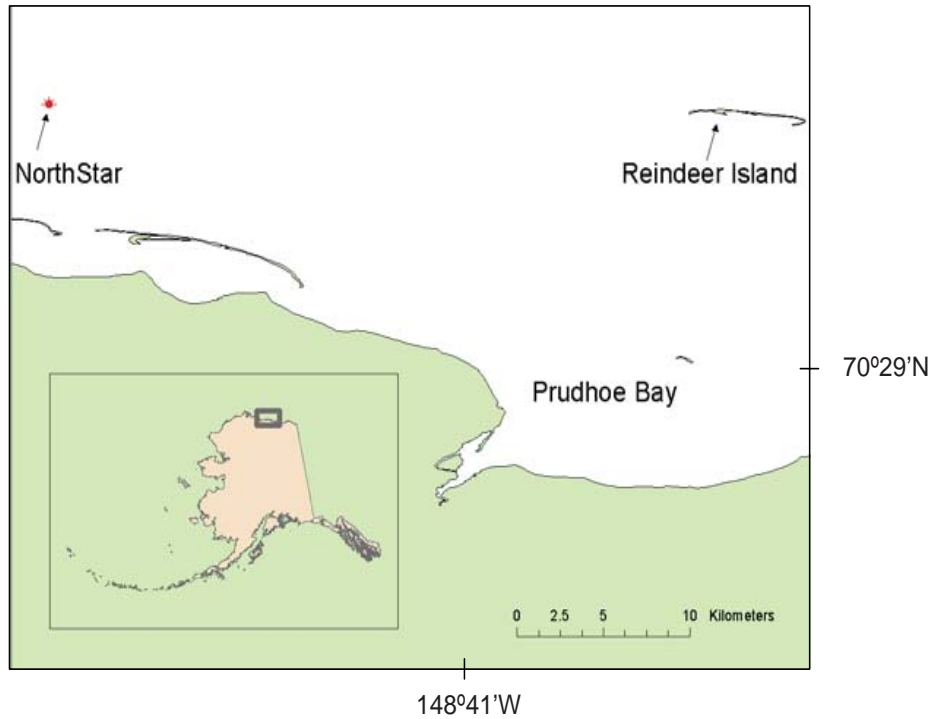


Figure 1. The study site on the shorefast sea ice of the Beaufort Sea between Prudhoe Bay, Reindeer Island, and the man-made Northstar Island.

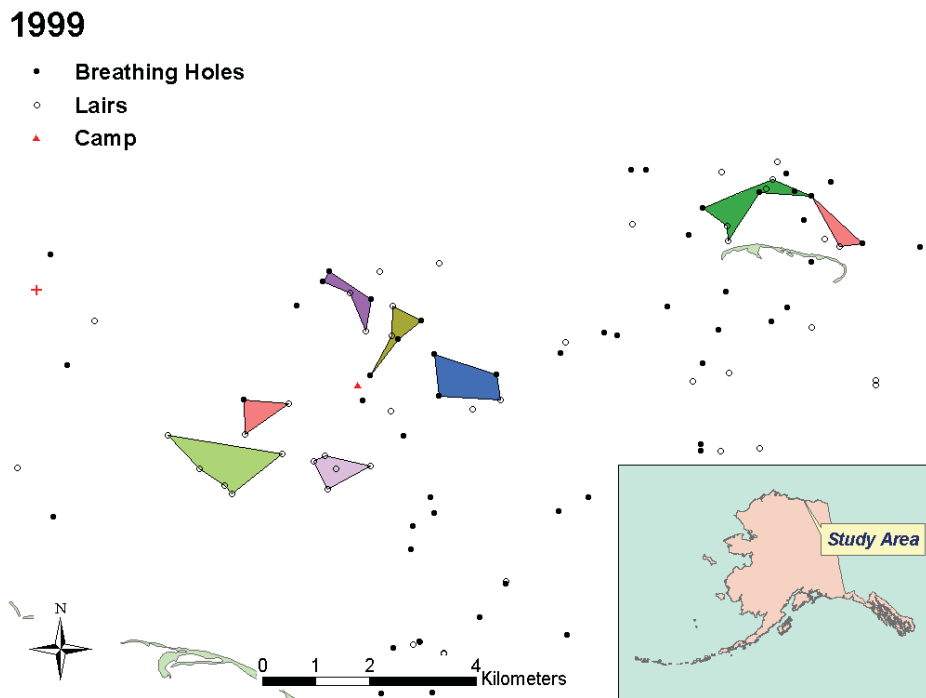


Figure 2. Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 1999. Also shown are the minimum convex polygons delineating the home ranges of 8 ringed seals based on on-ice resting sites.

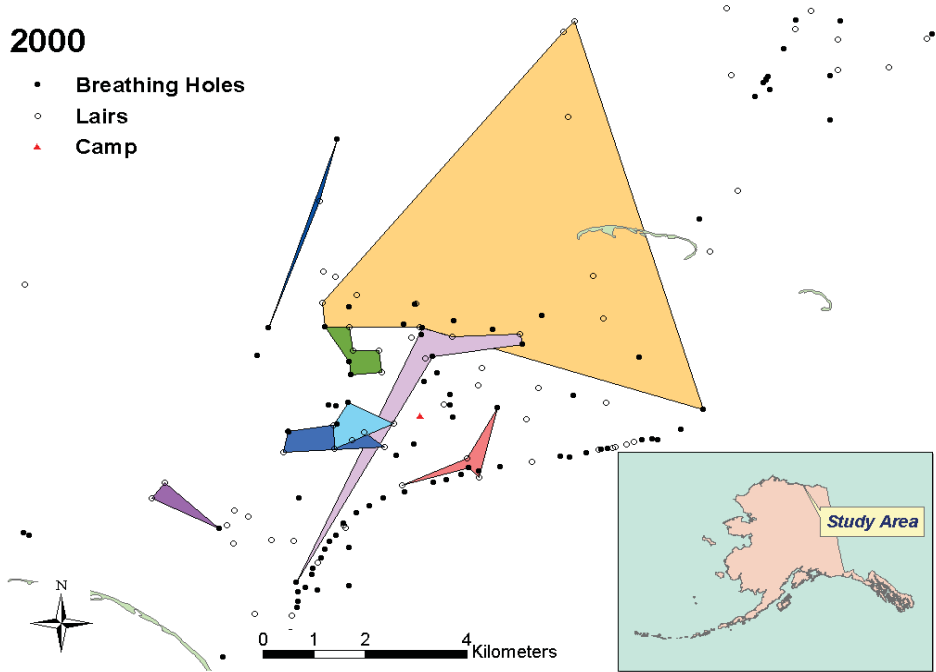


Figure 3. Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 2000. Also shown are the minimum convex polygons delineating the home ranges of 8 ringed seals based on on-ice resting sites. The home ranges of 2 radio-tagged seals were not determined.

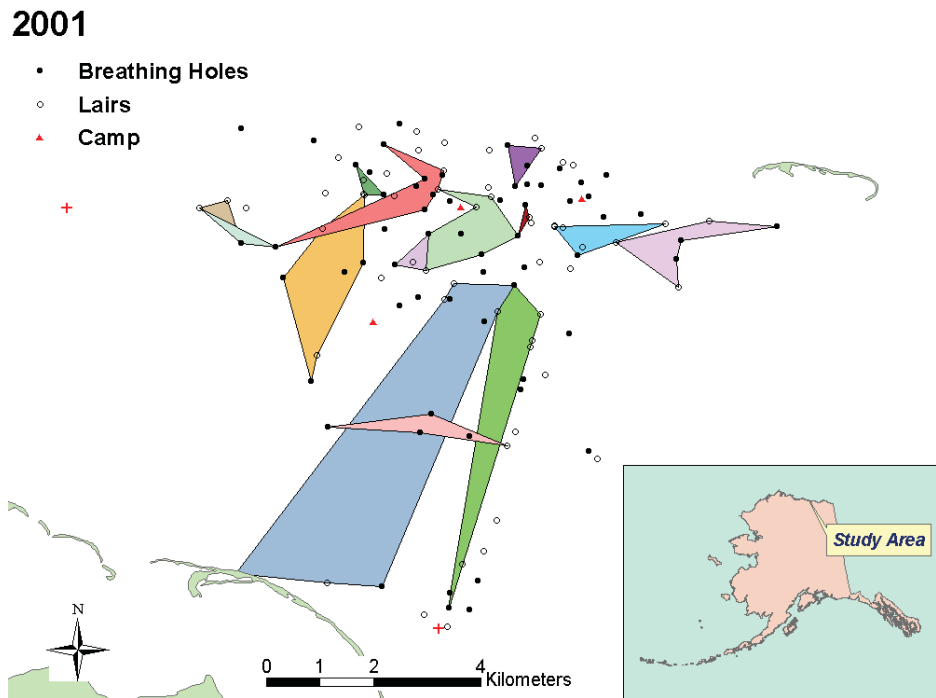


Figure 4. Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 2001. Also shown are the minimum convex polygons delineating the home ranges of 14 ringed seals based on on-ice resting sites.

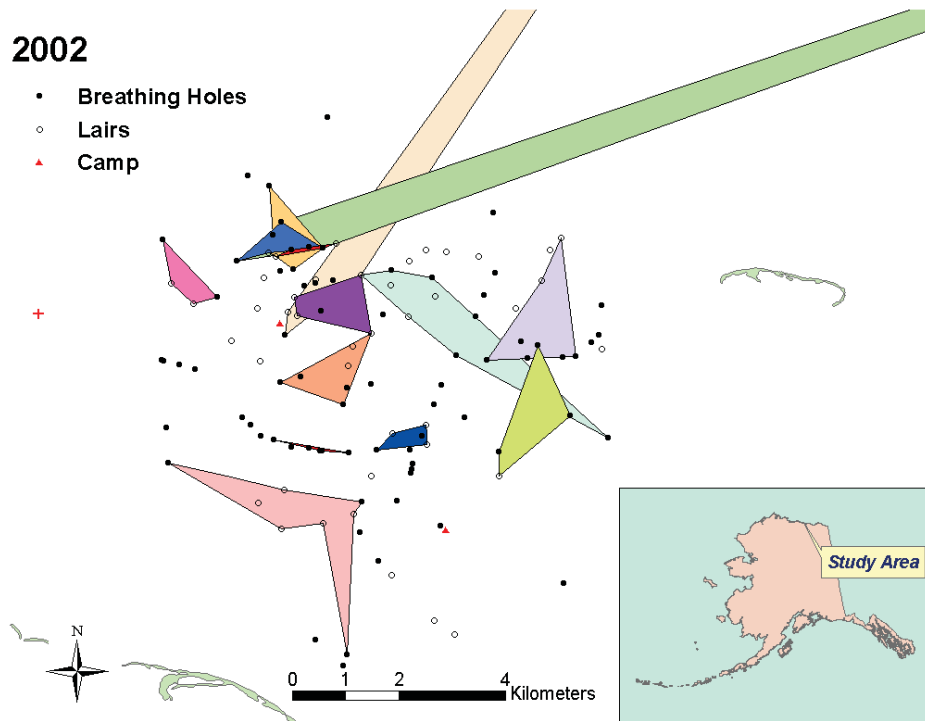


Figure 5. Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 2002. Also shown are the minimum convex polygons delineating the home ranges of 14 ringed seals based on on-ice resting sites. The home ranges of 2 radio-tagged seals were not determined.

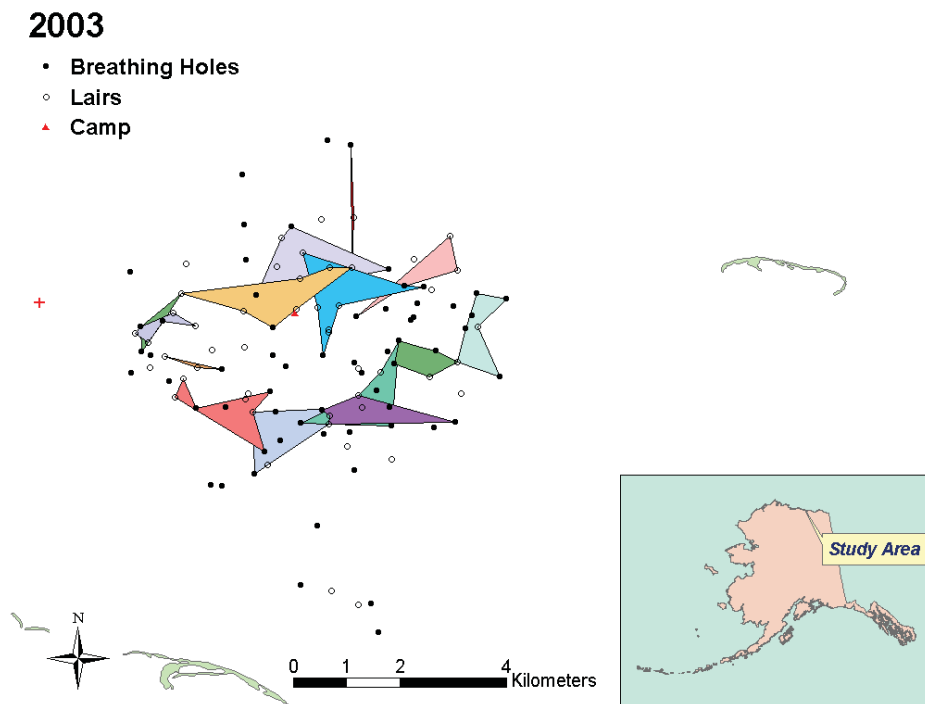


Figure 6. Locations of the monitoring camp and the subnivean breathing holes and lairs located by the trained dogs in 2003. Also shown are the minimum convex polygons delineating the home ranges of 14 ringed seals based on on-ice resting sites. The home range of 1 radio-tagged seal was not determined.

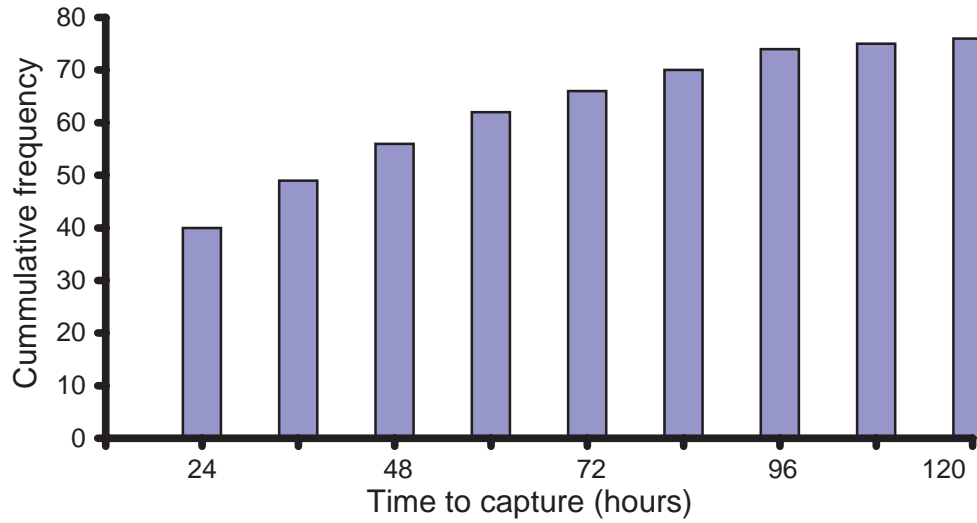


Figure 7. Duration of net sets for 75 captures of ringed seals in the Beaufort Sea in 1999, 2000, 2001, 2002, and 2003.

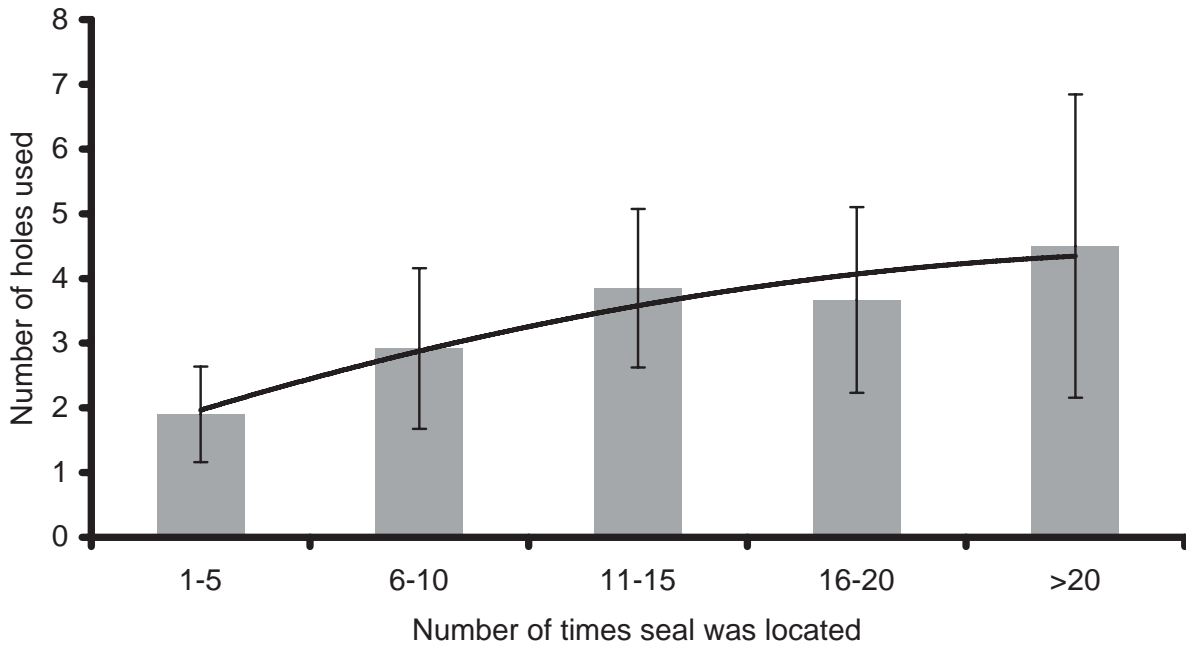


Figure 8. Mean (and SE) of the number of holes used by radio tagged ringed seals as a function of the number of times haulout locations were determined. The asymptote is 4.5 holes per seal.

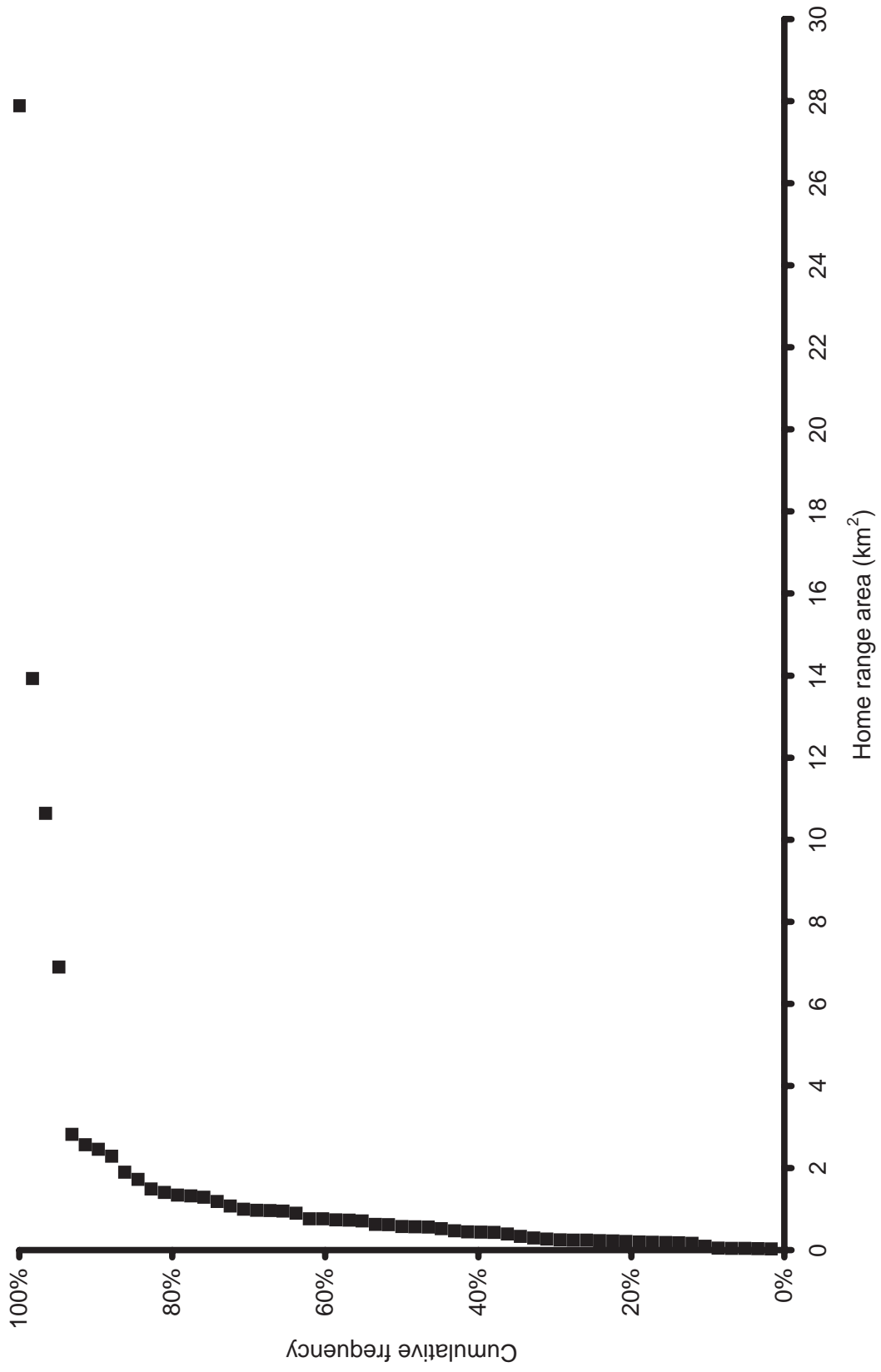


Figure 9. Cumulative percent frequency of home range size (minimum convex polygon) for 58 ringed seals radio tracked between 1999 and 2003.

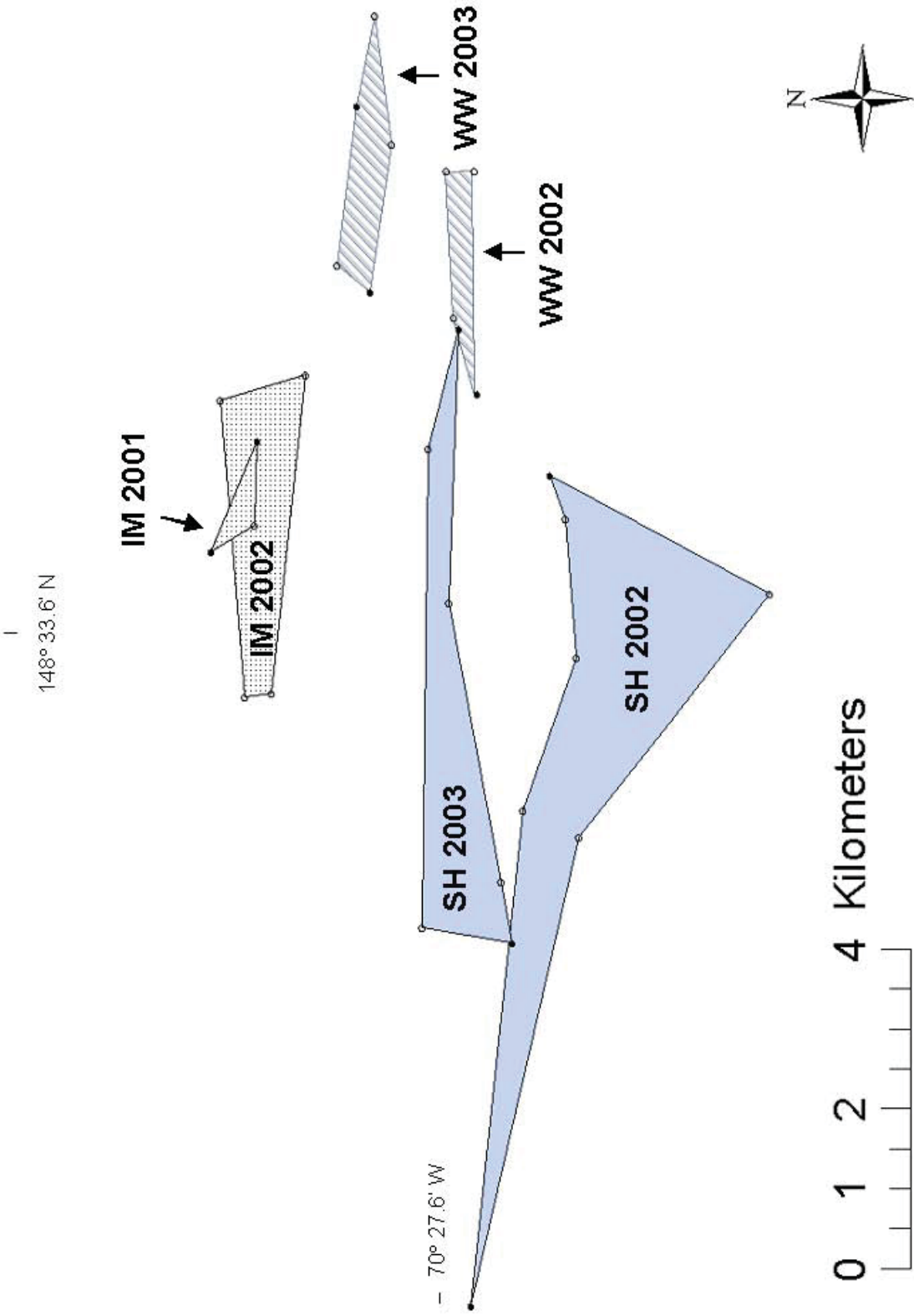


Figure 10. Minimum convex polygons delineating the home ranges of 3 ringed seals each tracked during two successive breeding seasons. IM was an adult male tracked in 2001 and 2002. SH was an adult female tracked in 2002 and 2003. WW was an adult male tracked in 2002 and 2003.

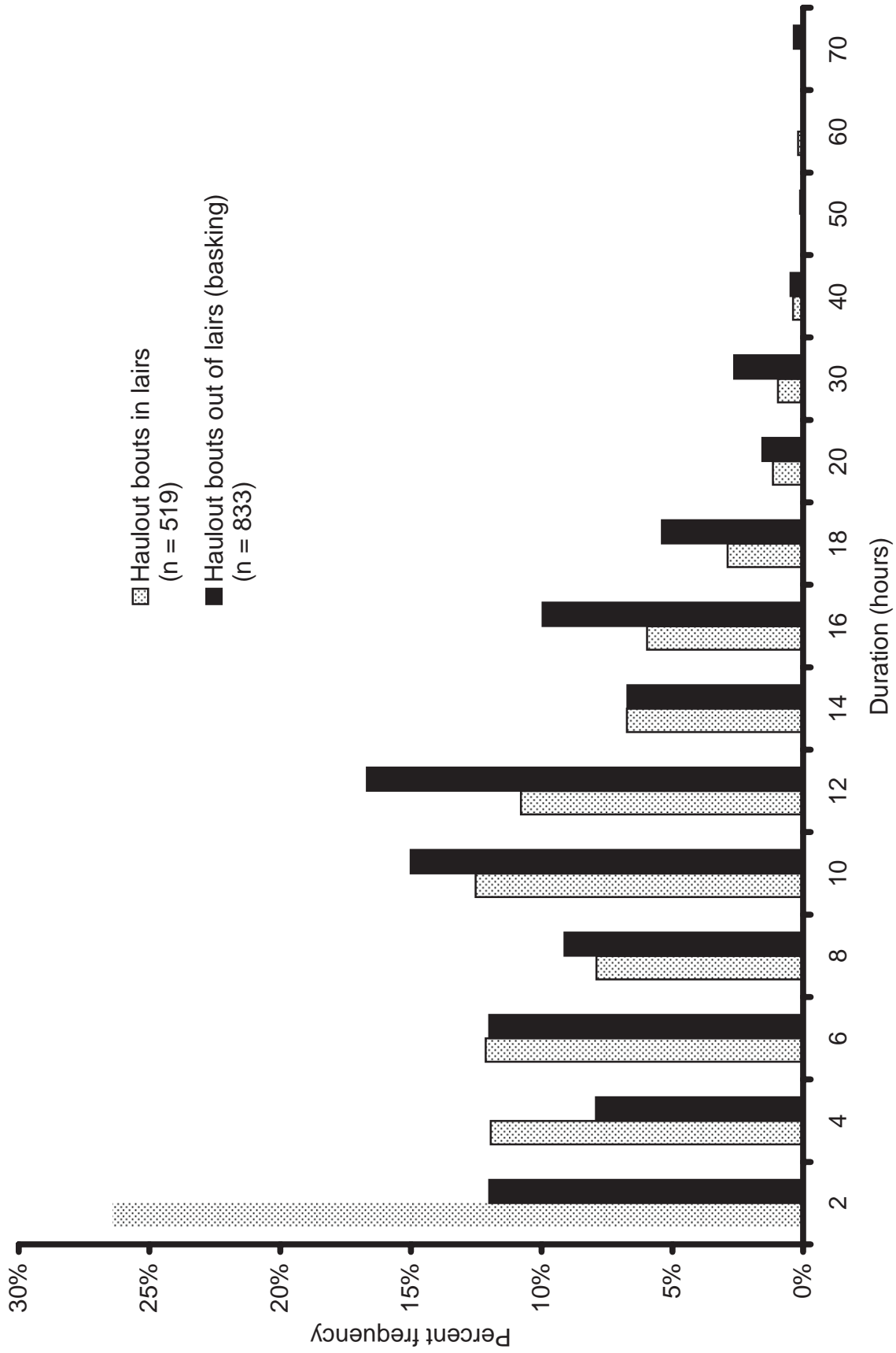


Figure 11. Duration (hrs) of haulout bouts in subnivean lairs and out of lairs (basking).

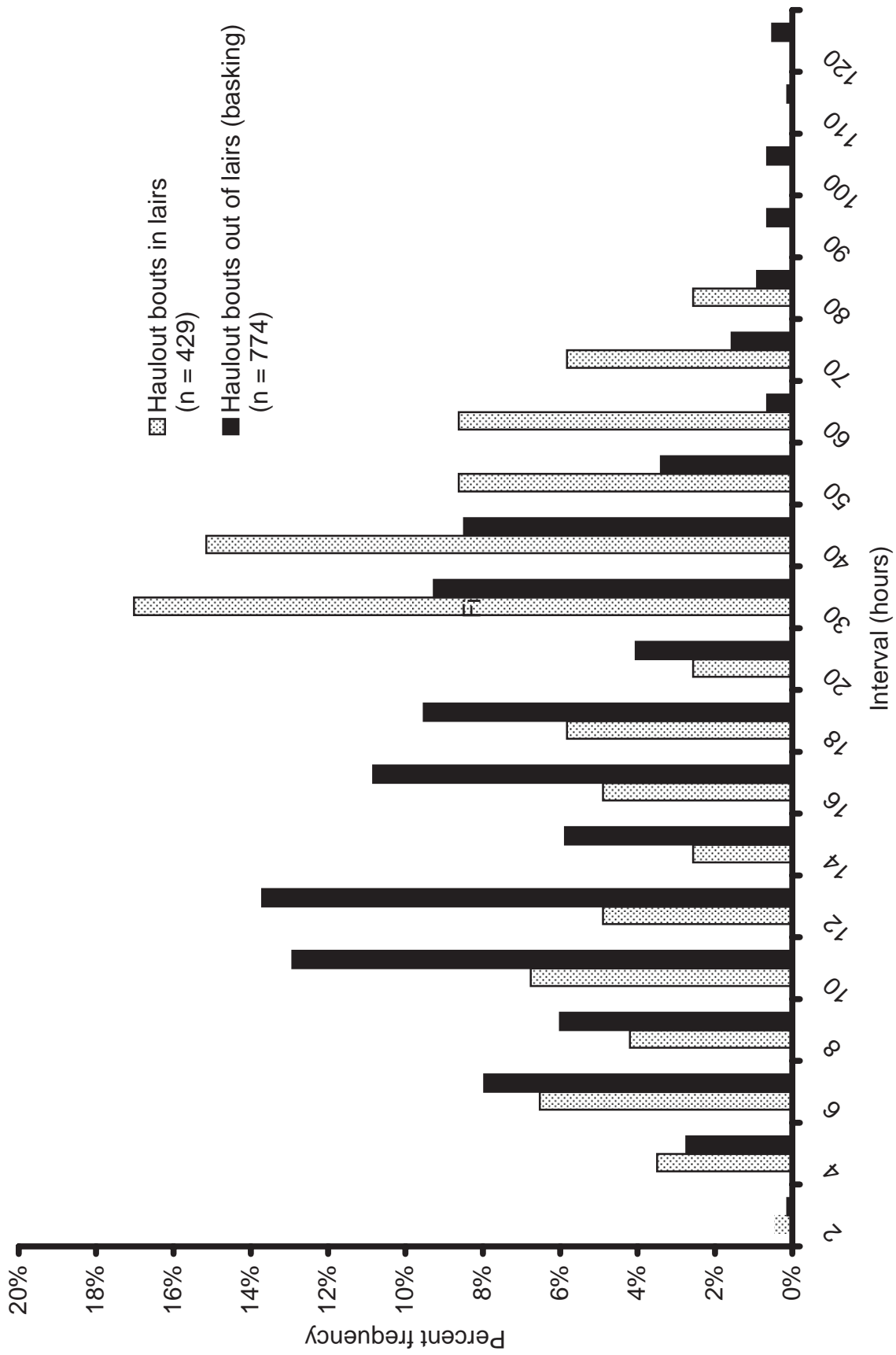


Figure 12. Interval (hrs) between haulout bouts in and out of subnivean lairs.

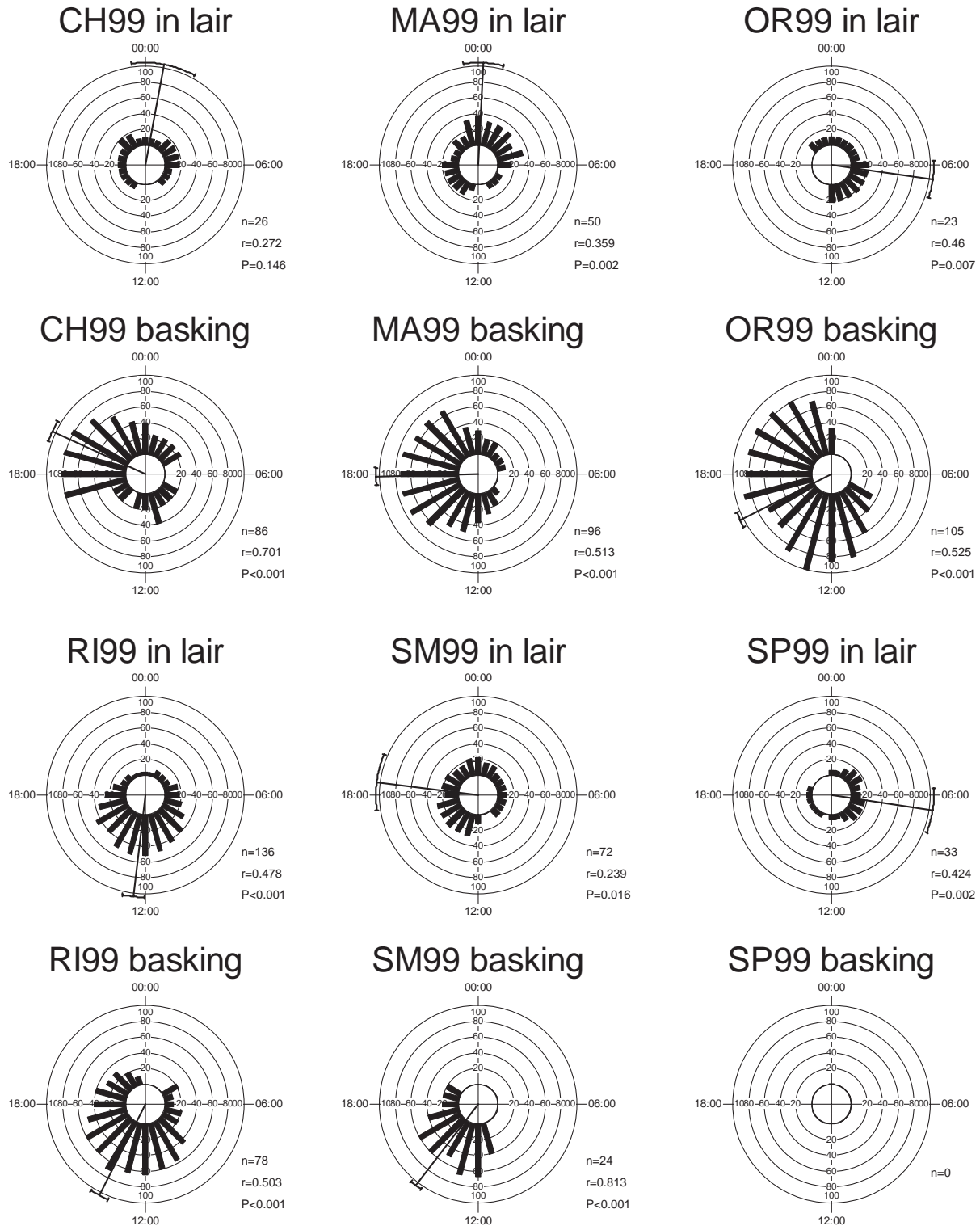
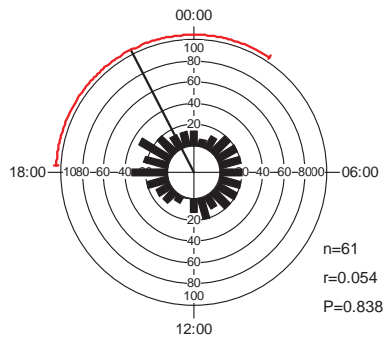
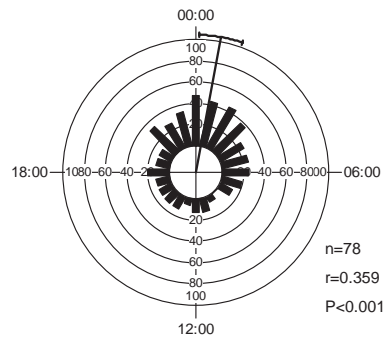


Figure 13. Diel haulout patterns of radio tagged ringed seals while using subnivean lairs and while basking. Each graph shows the percentage of monitoring periods when the seal was out of the water for each hour of the day. Thin radial lines indicate the mean hour of haulout, and the perpendicular bar shows the 95% confidence limits around the mean. The mean vector length (r) is shown along with the probability that the distribution of hourly haulout times is different from a random distribution.

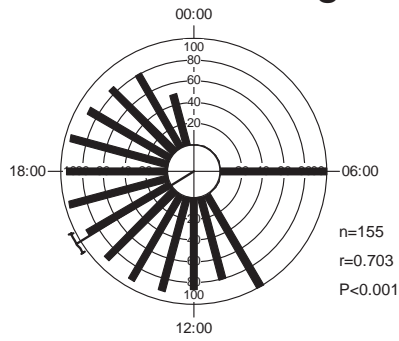
SW99 in lair



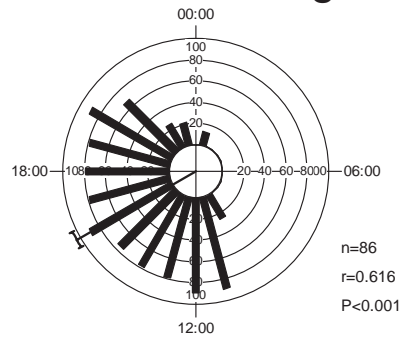
VR99 in lair



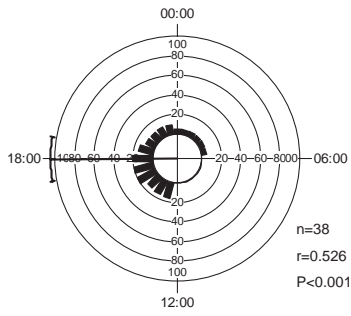
SW99 basking



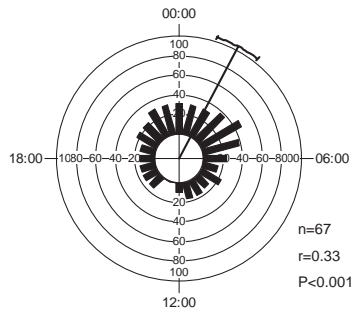
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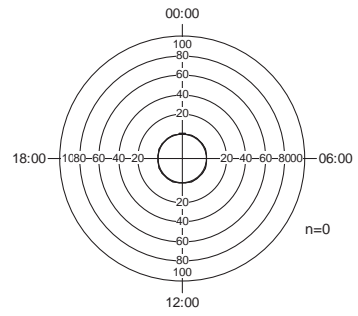
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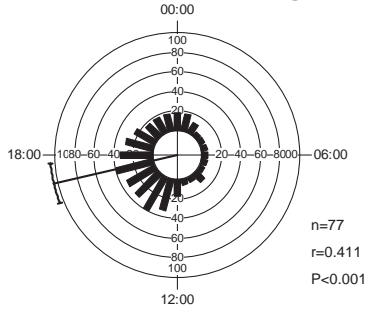
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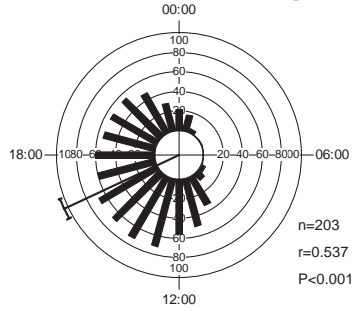
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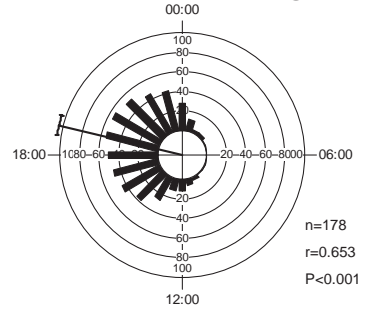
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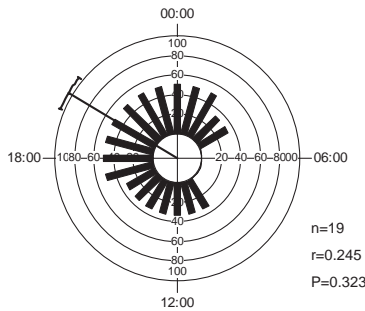
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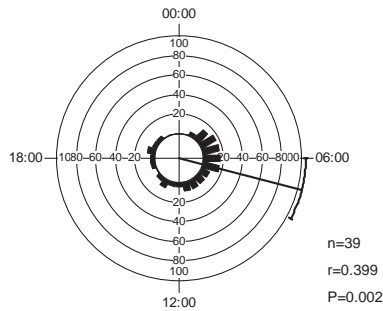
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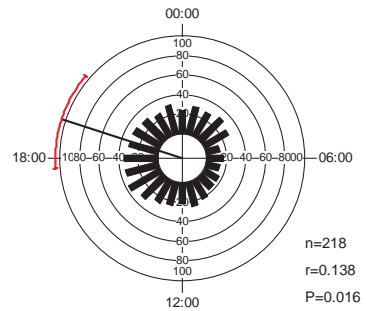
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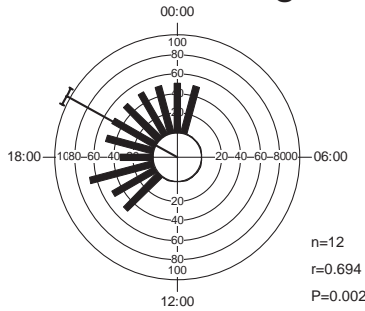
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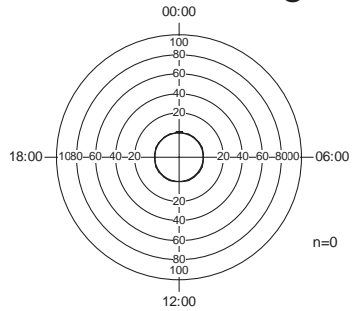
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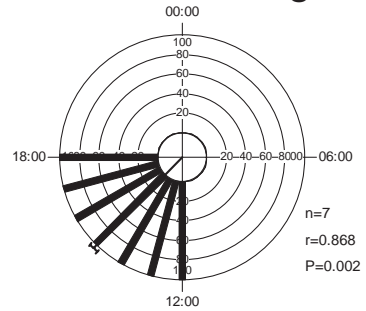
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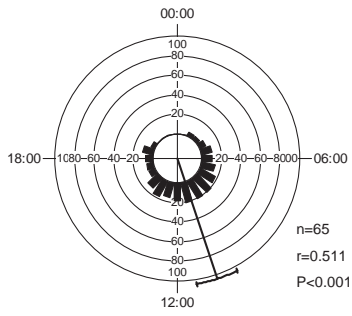
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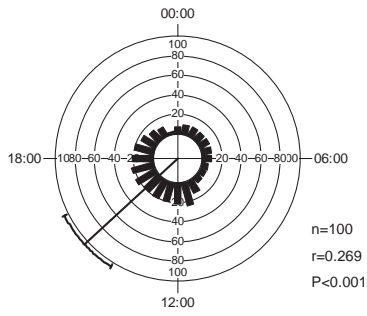
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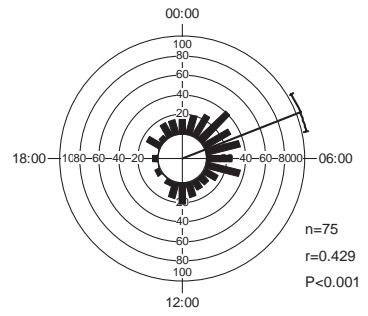
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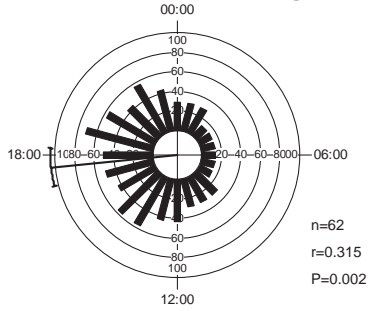
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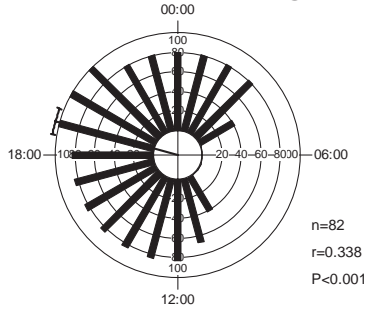
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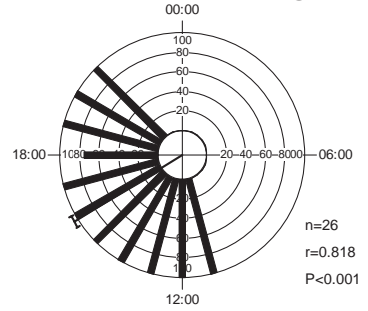
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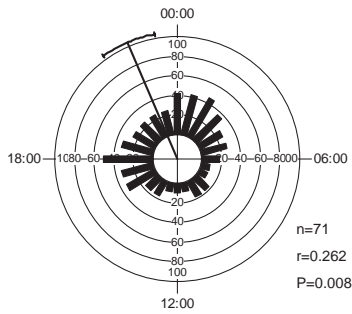
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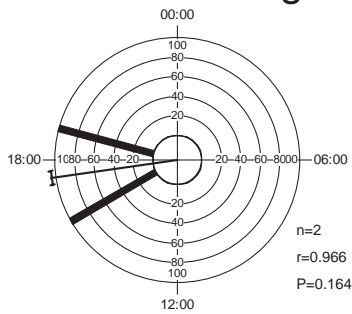
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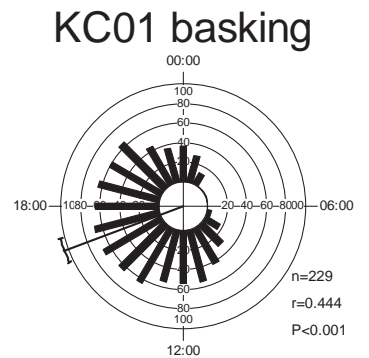
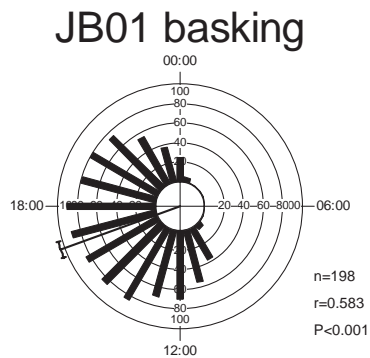
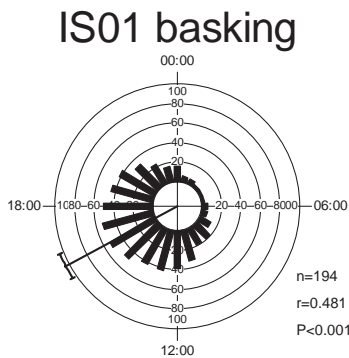
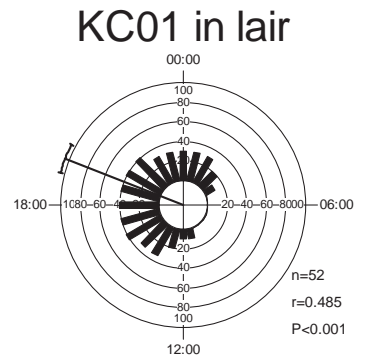
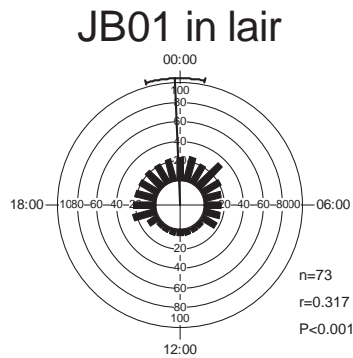
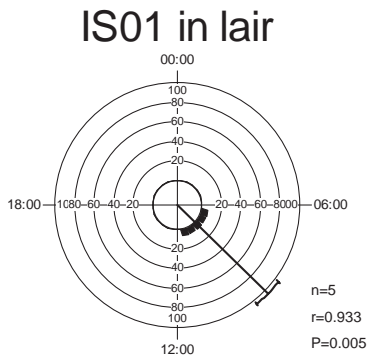
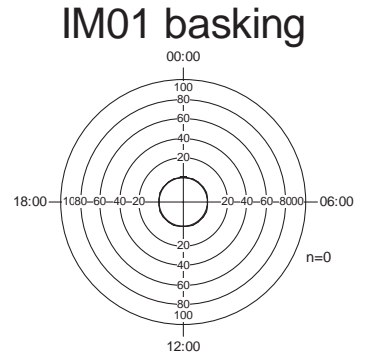
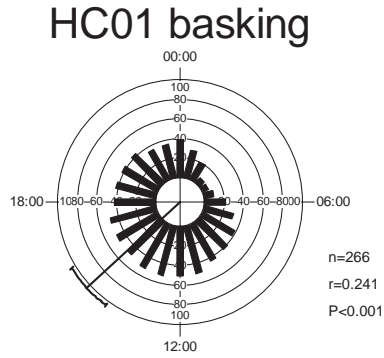
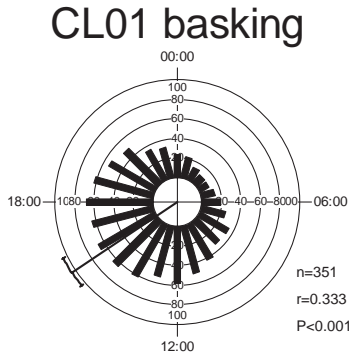
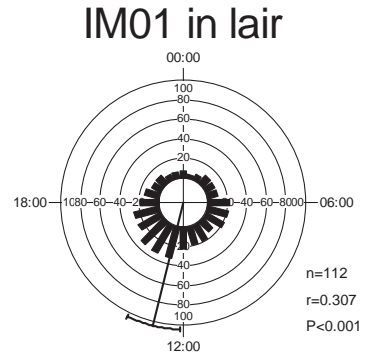
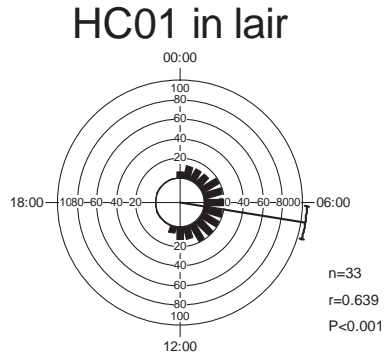
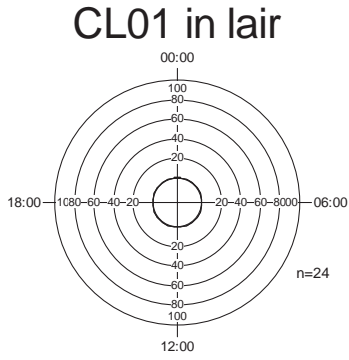


SL00 in lair

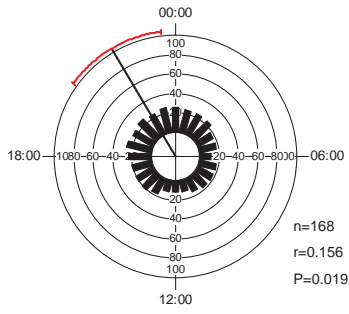


SL00 basking

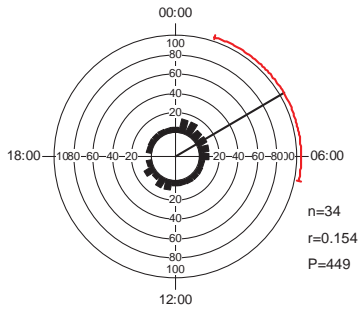




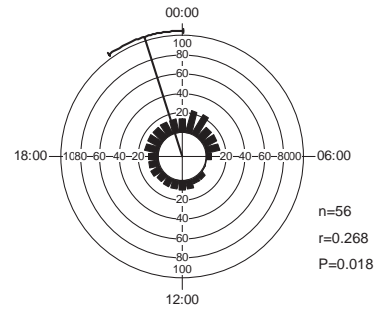
KK01 in lair



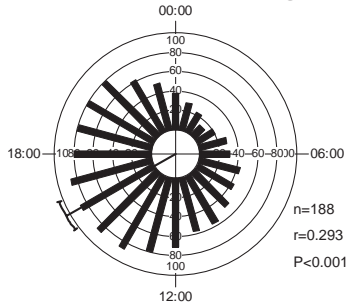
LH01 in lair



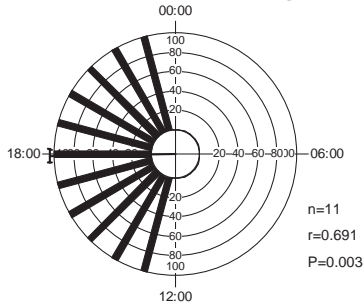
MH01 in lair



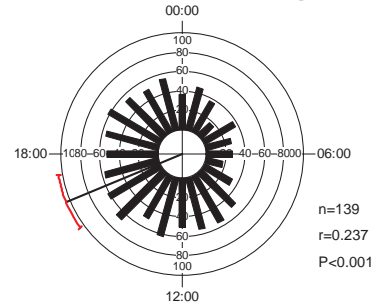
KK01 basking



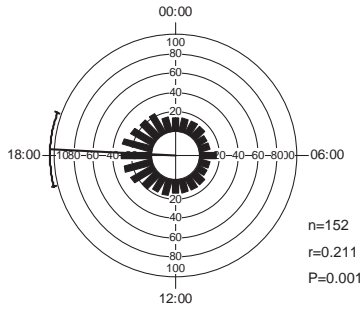
LH01 basking



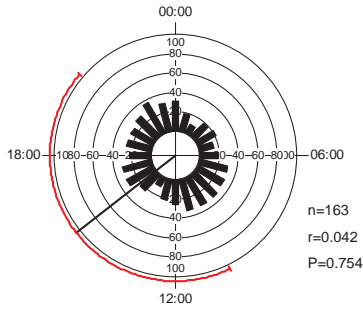
MH01 basking



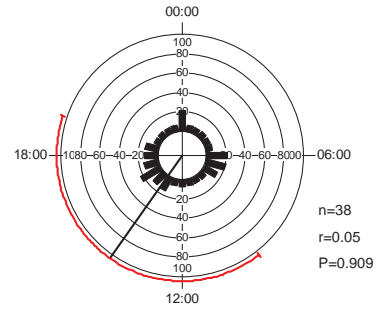
MK01 in lair



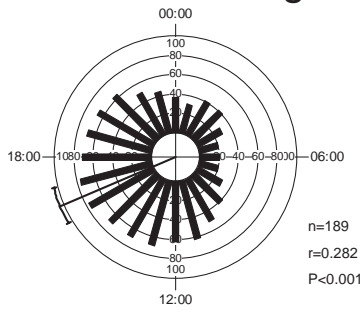
PO01 in lair



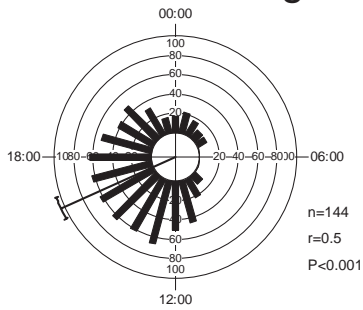
SI01 in lair



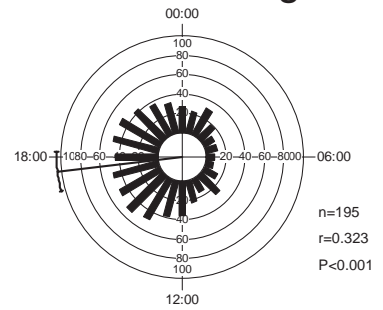
MK01 basking



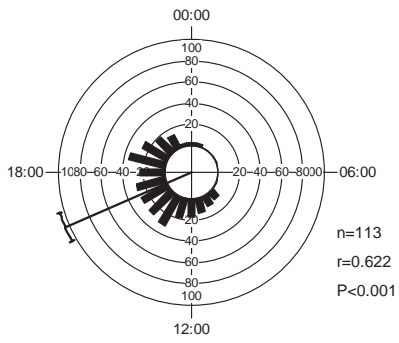
PO01 basking



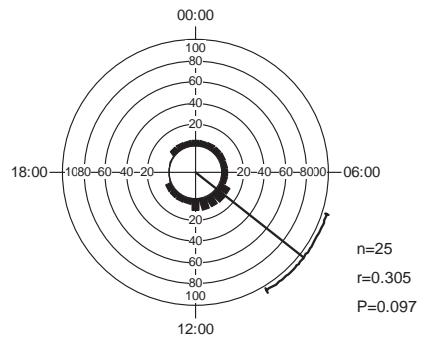
SI01 basking



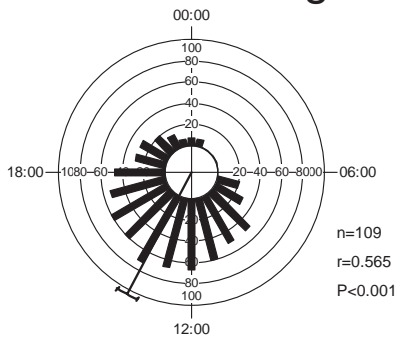
TS01 in lair



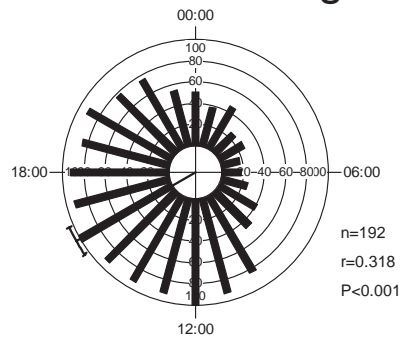
WC01 in lair



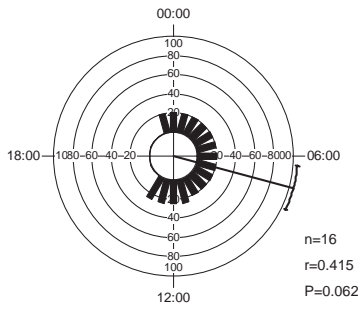
TS01 basking



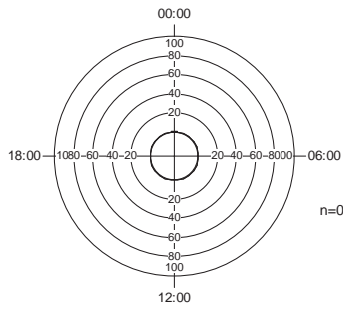
WC01 basking



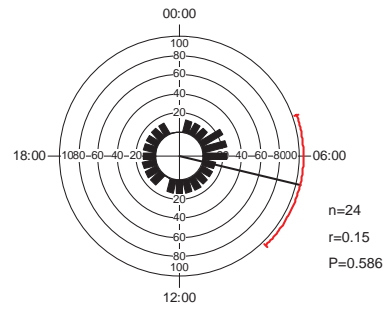
BC02 in lair



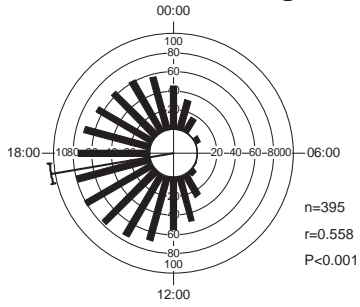
EF02 in lair



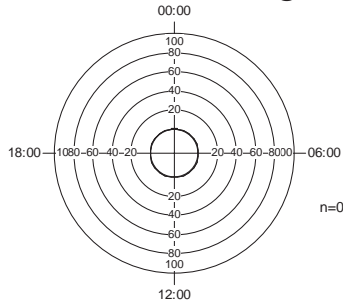
EV02 in lair



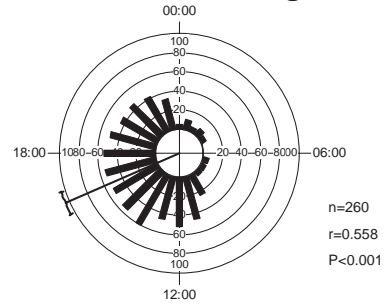
BC02 basking



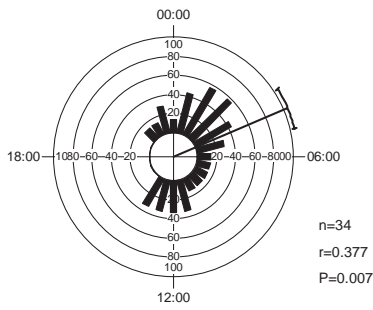
EF02 basking



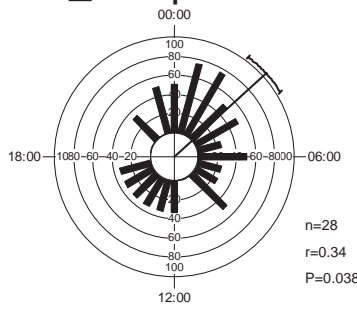
EV02 basking



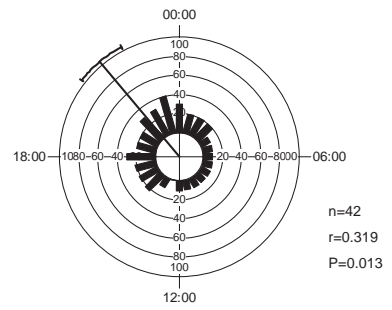
HM02 in lair



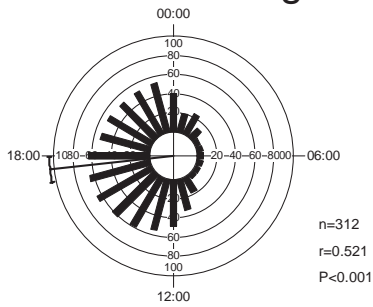
IM01_recapture in lair



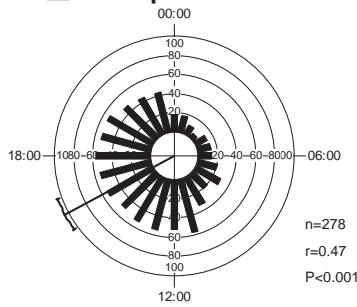
JN02 in lair



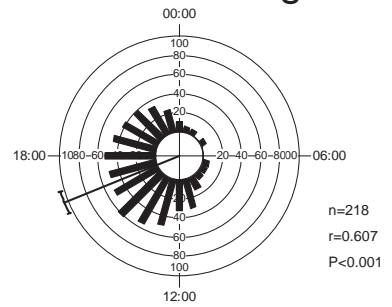
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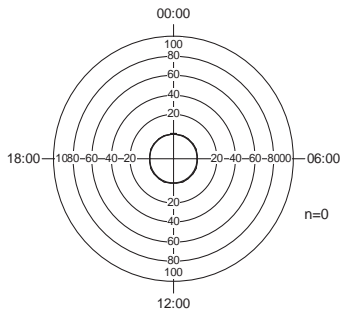
IM01_recapture basking



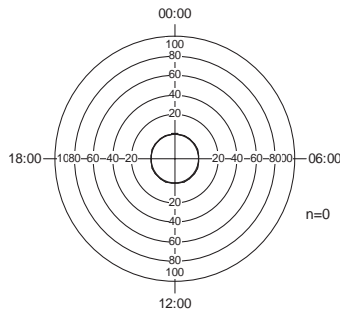
JN02 basking



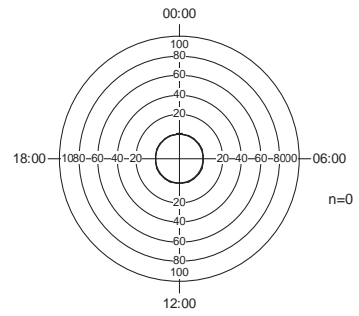
JU02 in lair



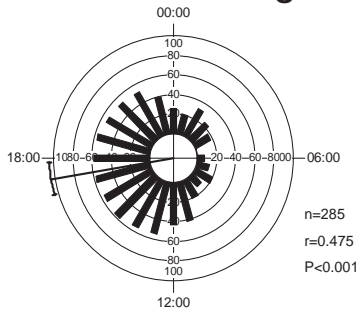
KK02 in lair



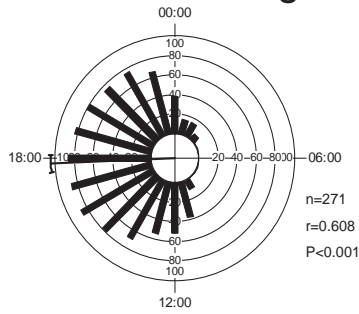
MW02 in lair



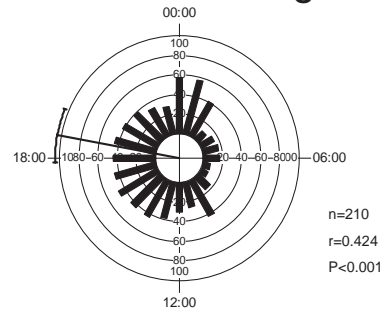
JU02 basking



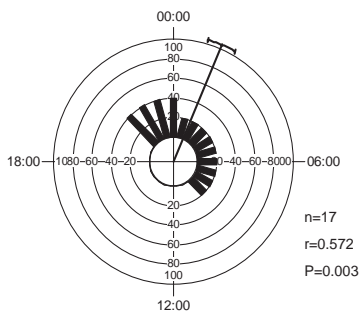
KK02 basking



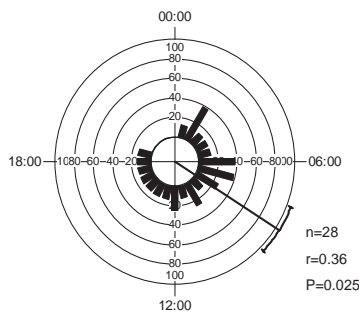
MW02 basking



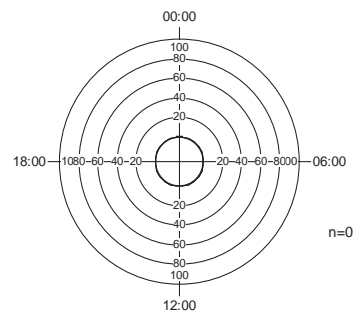
NA02 in lair



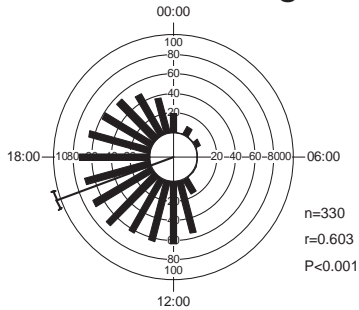
ND02 in lair



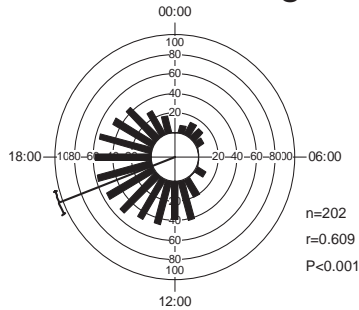
RN02 in lair



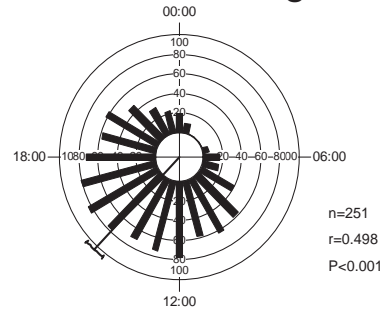
NA02 basking



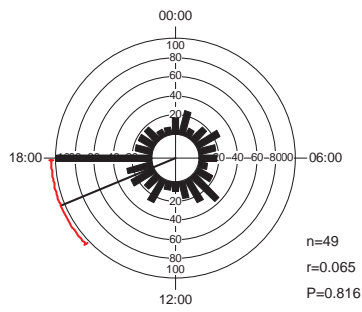
ND02 basking



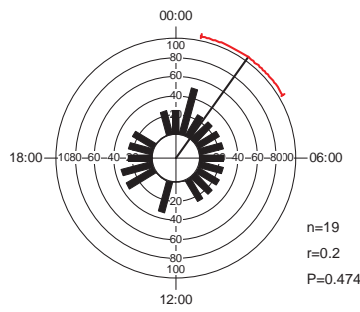
RN02 basking



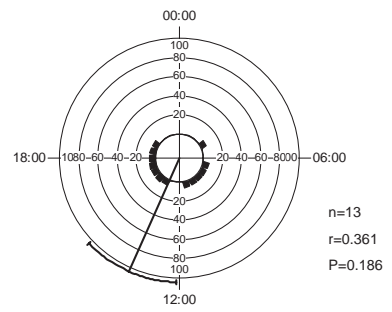
RO02 in lair



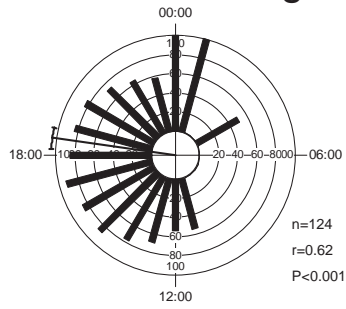
SH02 in lair



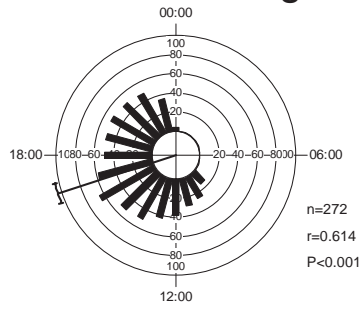
TR02 in lair



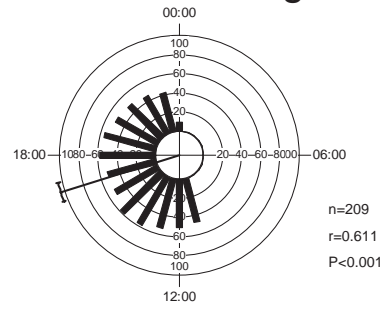
RO02 basking



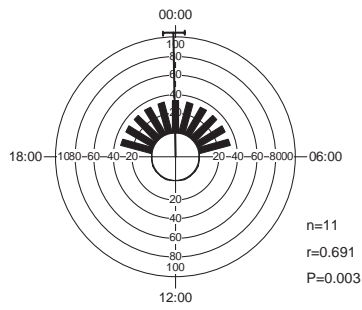
SH02 basking



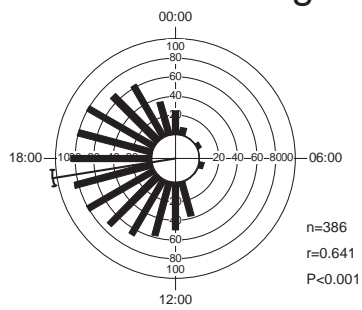
TR02 basking



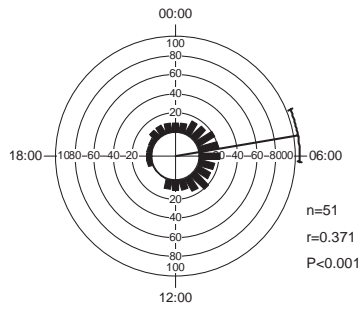
WW02 in lair



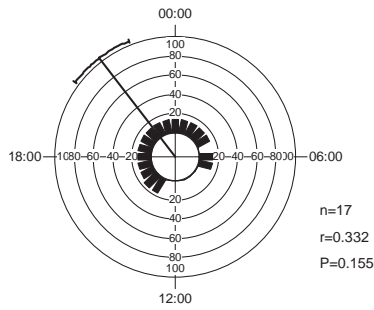
WW02 basking



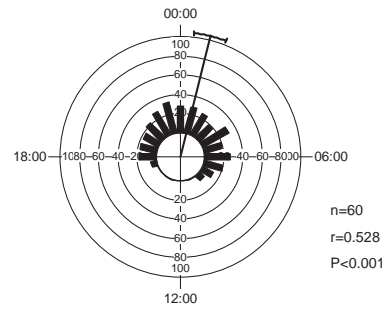
FI03 in lair



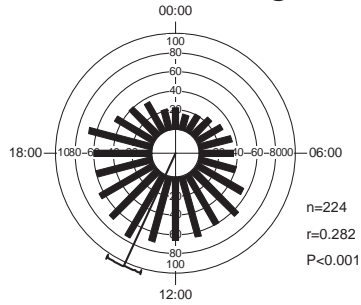
GR03 in lair



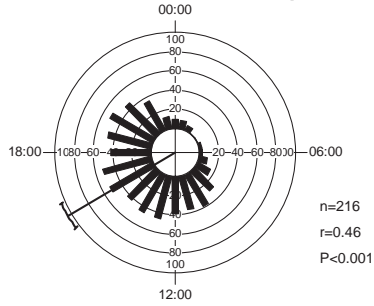
JW03 in lair



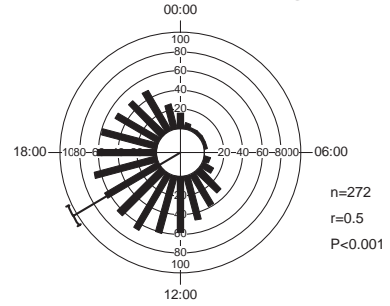
FI03 basking



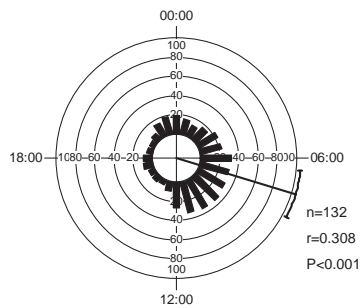
GR03 basking



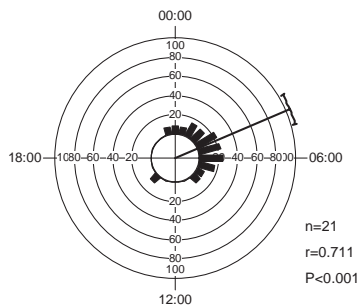
JW03 basking



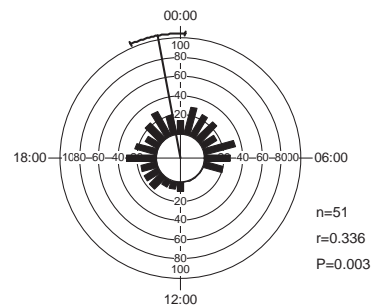
KA03 in lair



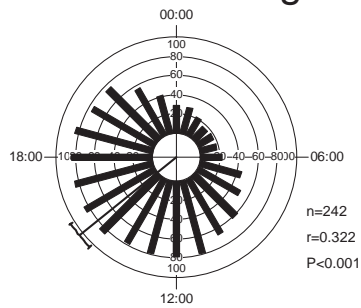
MO03 in lair



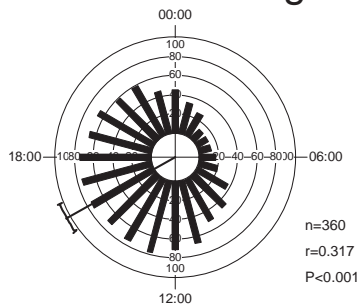
PF03 in lair



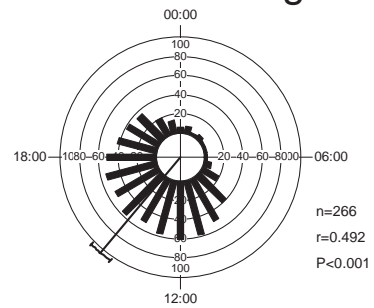
KA03 basking

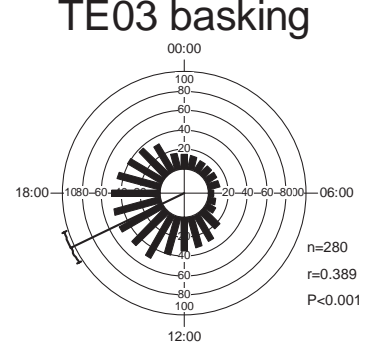
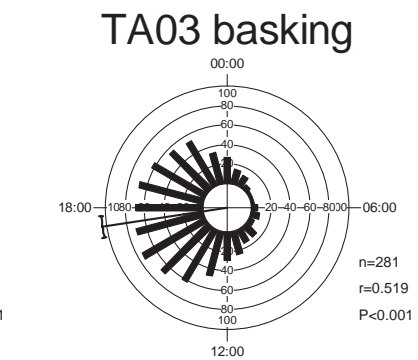
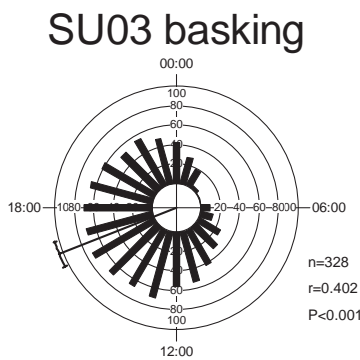
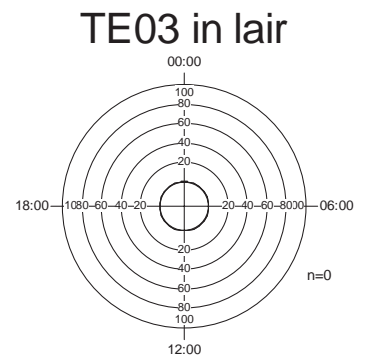
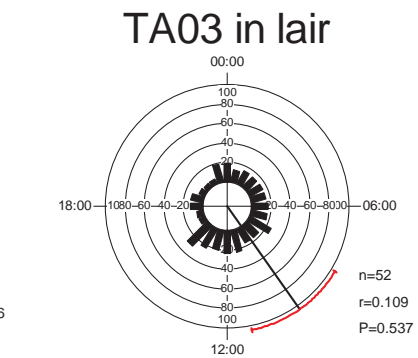
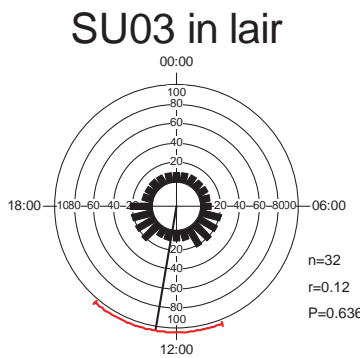
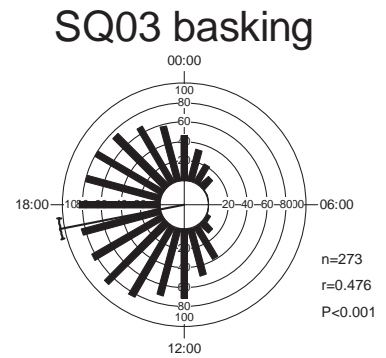
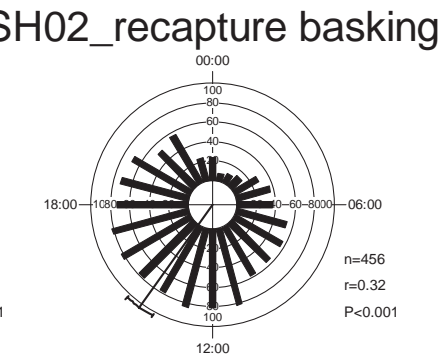
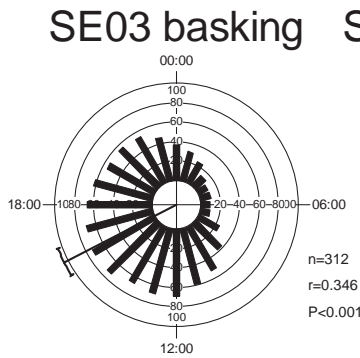
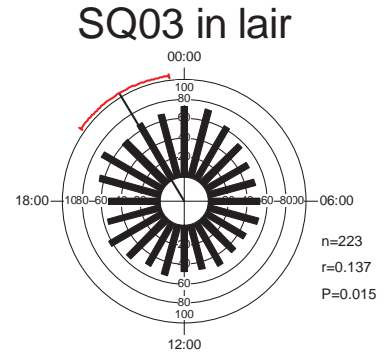
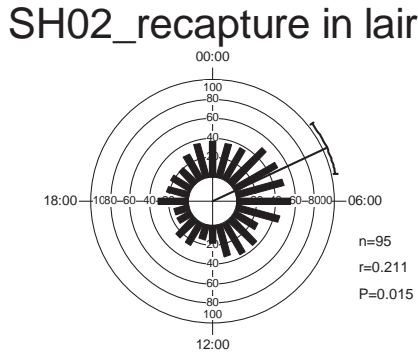
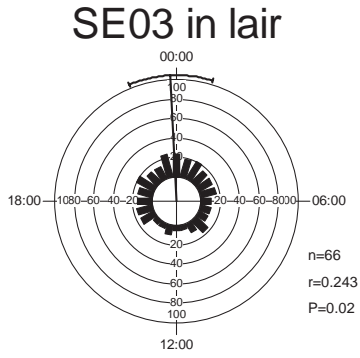


MO03 basking

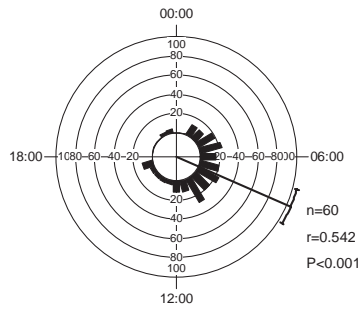


PF03 basking

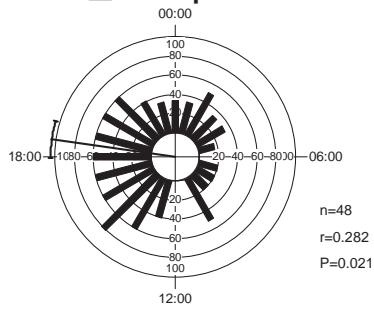




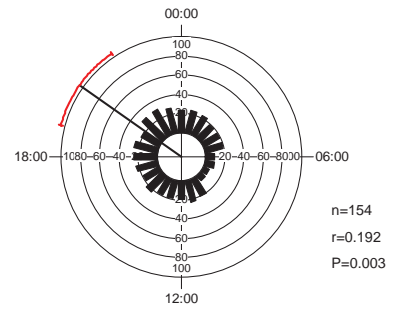
VI03 in lair



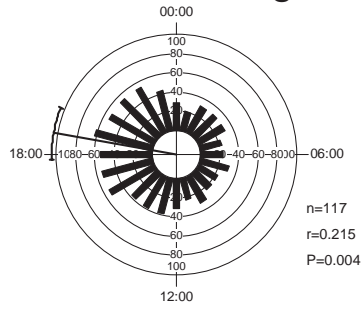
WW02_recapture in lair



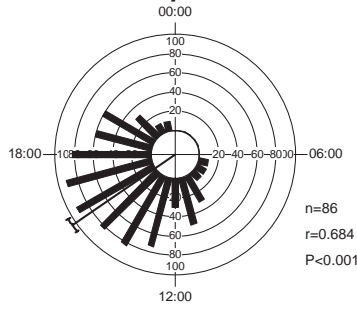
YK03 in lair



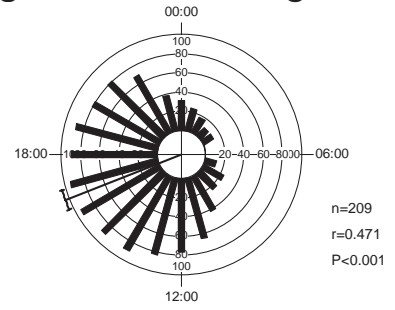
VI03 basking



WW02_recapture basking

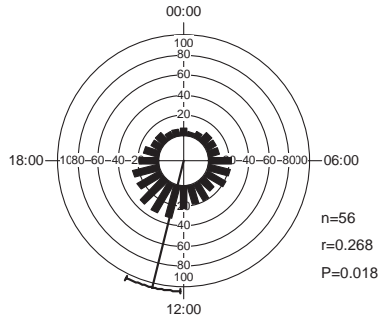


YK03 basking

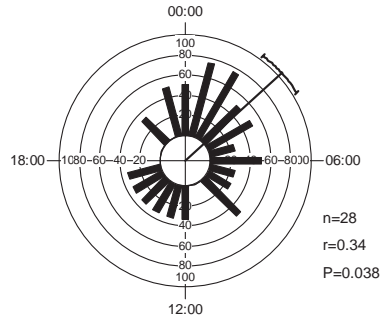


RECAPTURES

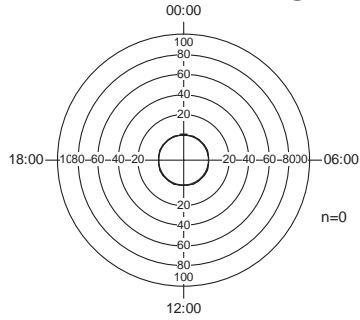
IM01 in lair



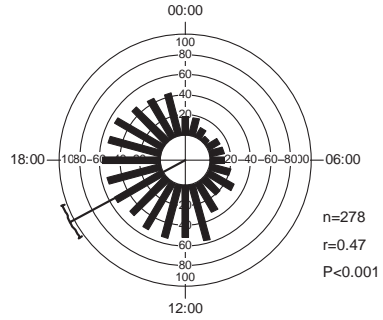
IM01_recapture in lair



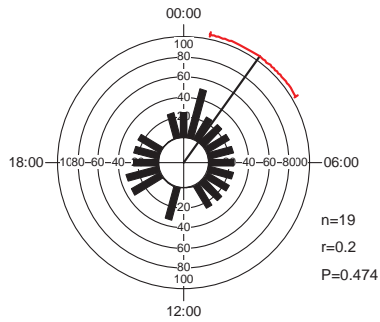
IM01 basking



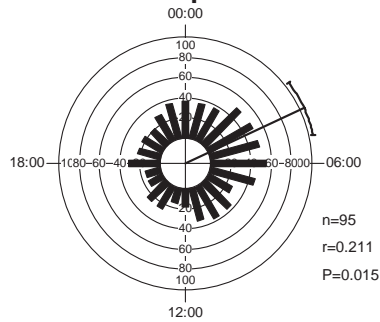
IM01_recapture basking



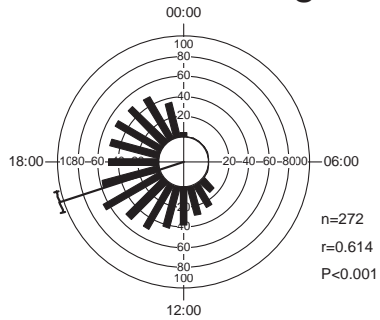
SH02 in lair



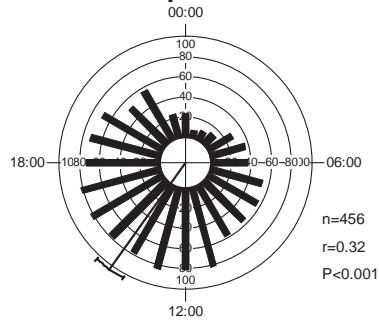
SH02_recapture in lair



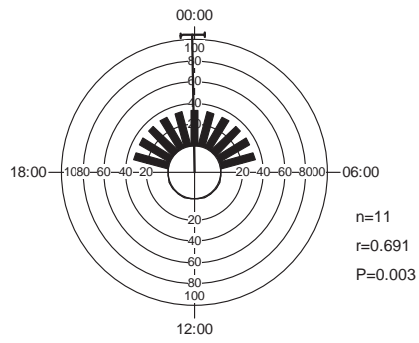
SH02 basking



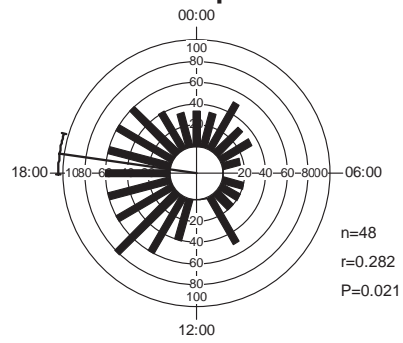
SH02_recapture basking



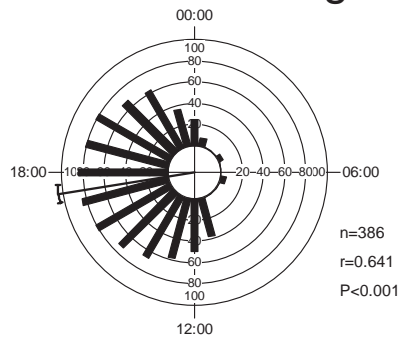
WW02 in lair



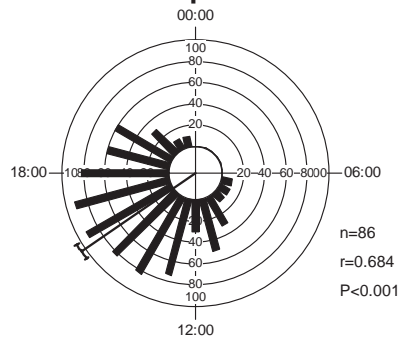
WW02_recapture in lair

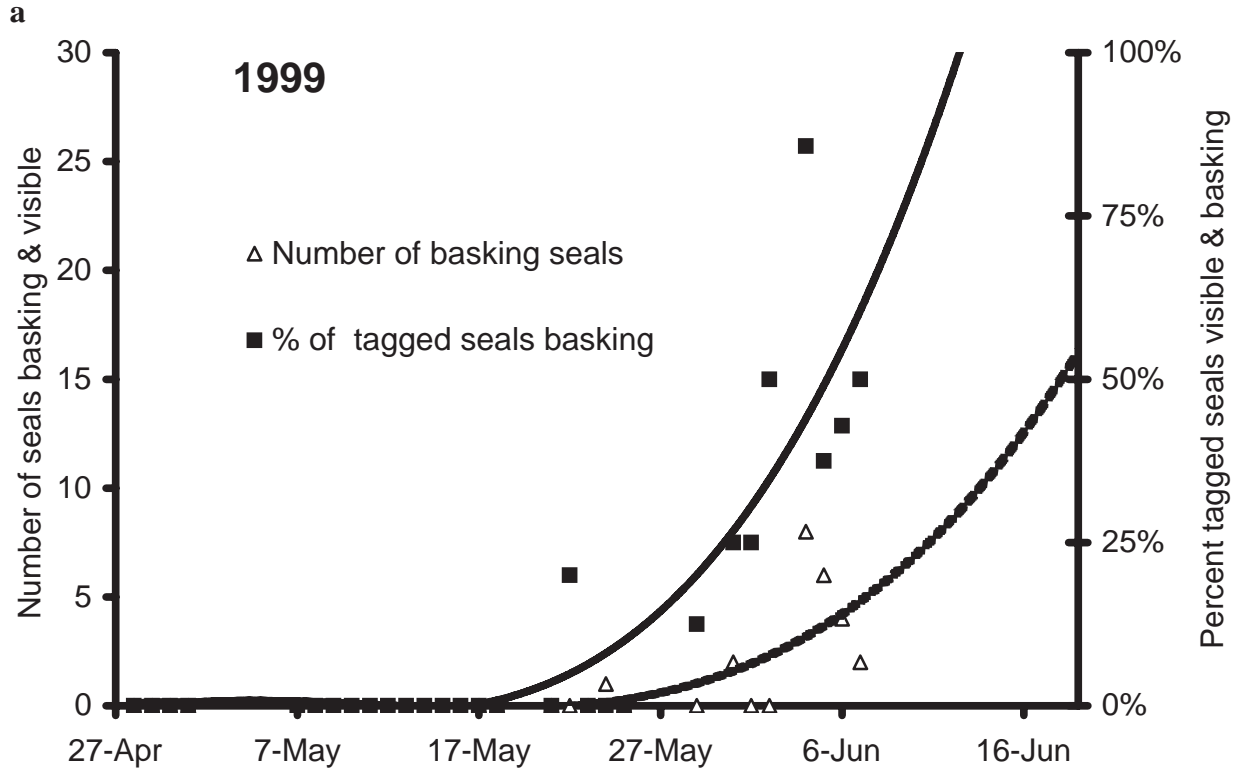


WW02 basking

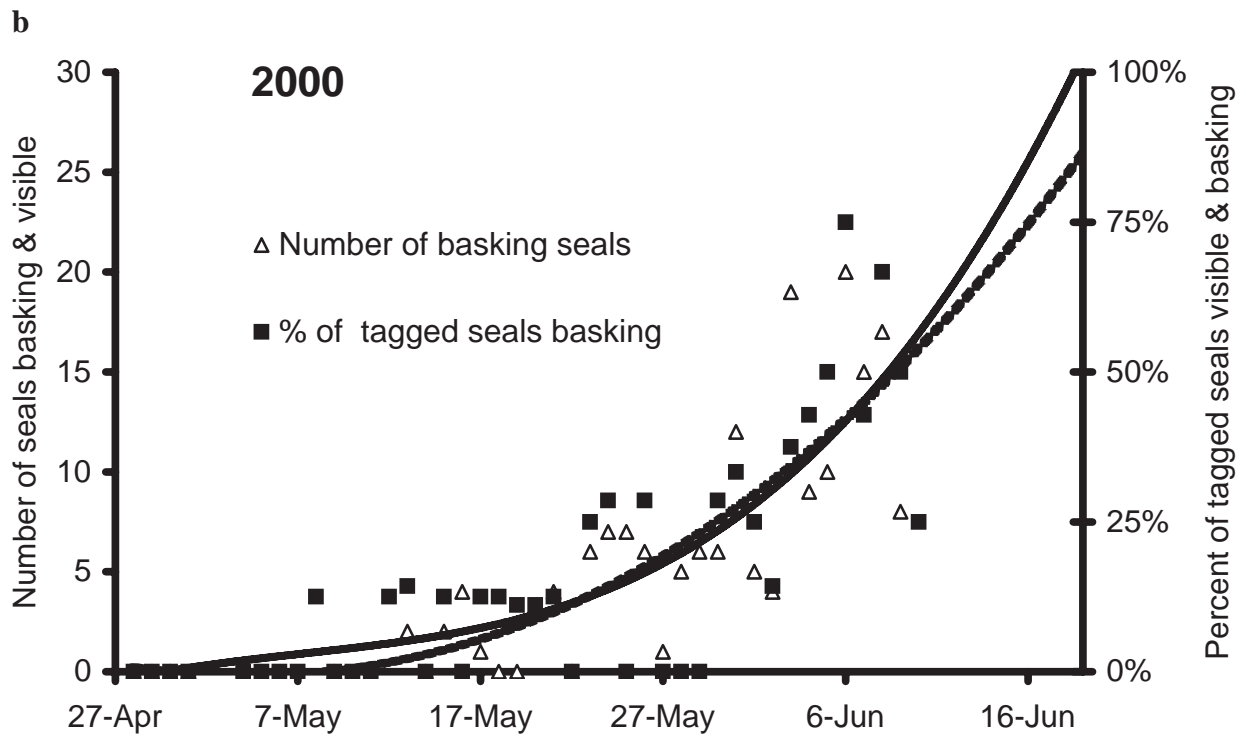


WW02_recapture basking

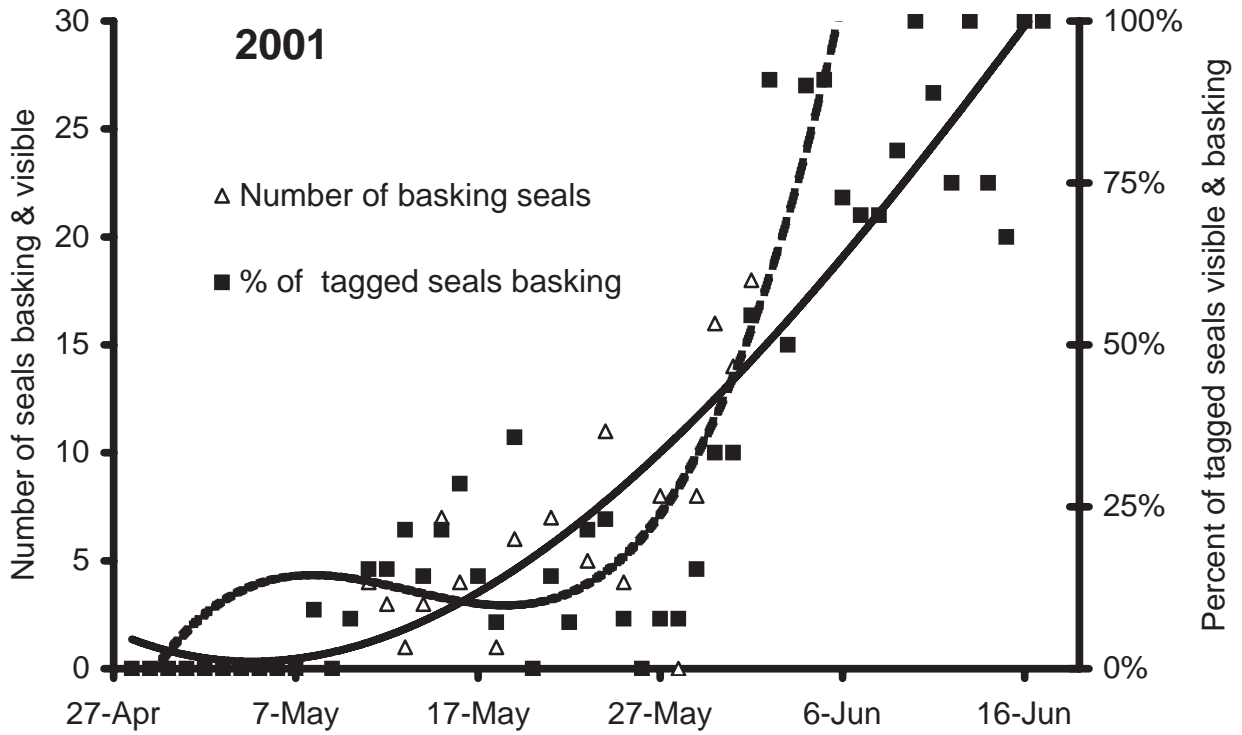




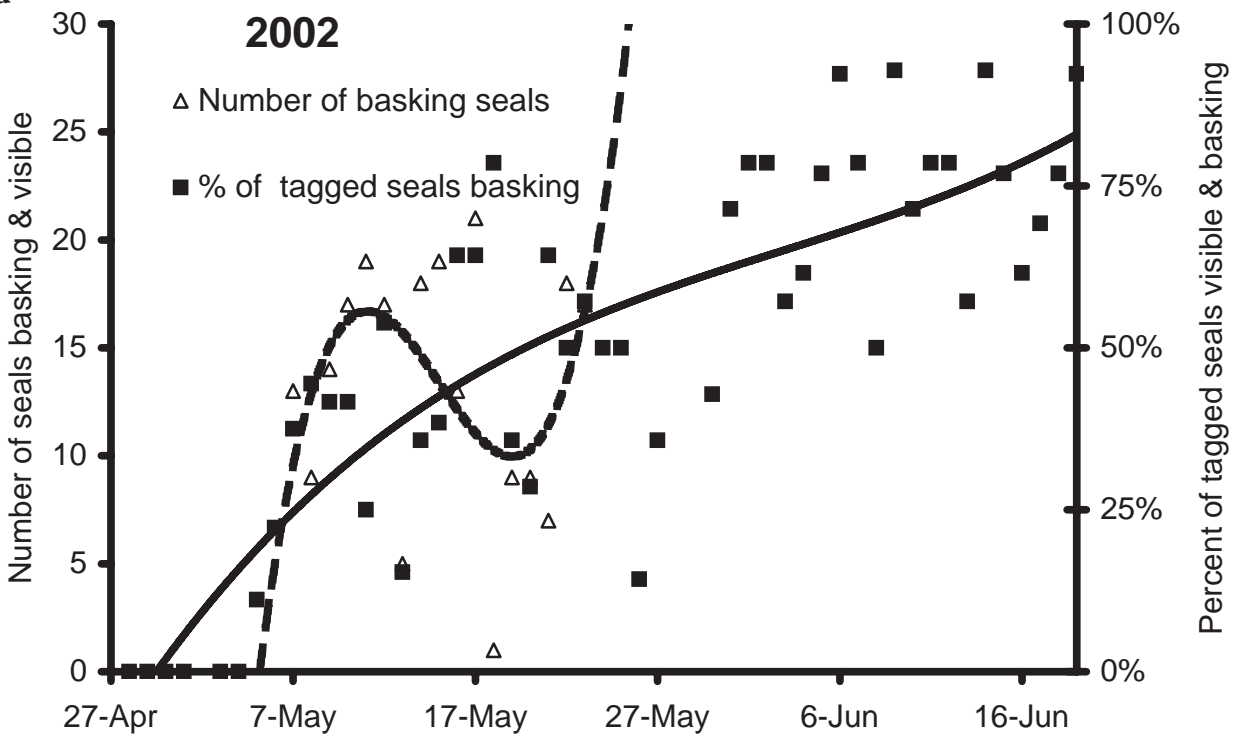
Figures 14 a through e. Total number of seals visible in the study area (dashed trend lines) and the percentage of tagged seals visible in the study area (solid trend lines) by date in 1999, 2000, 2001, 2002, and 2003.



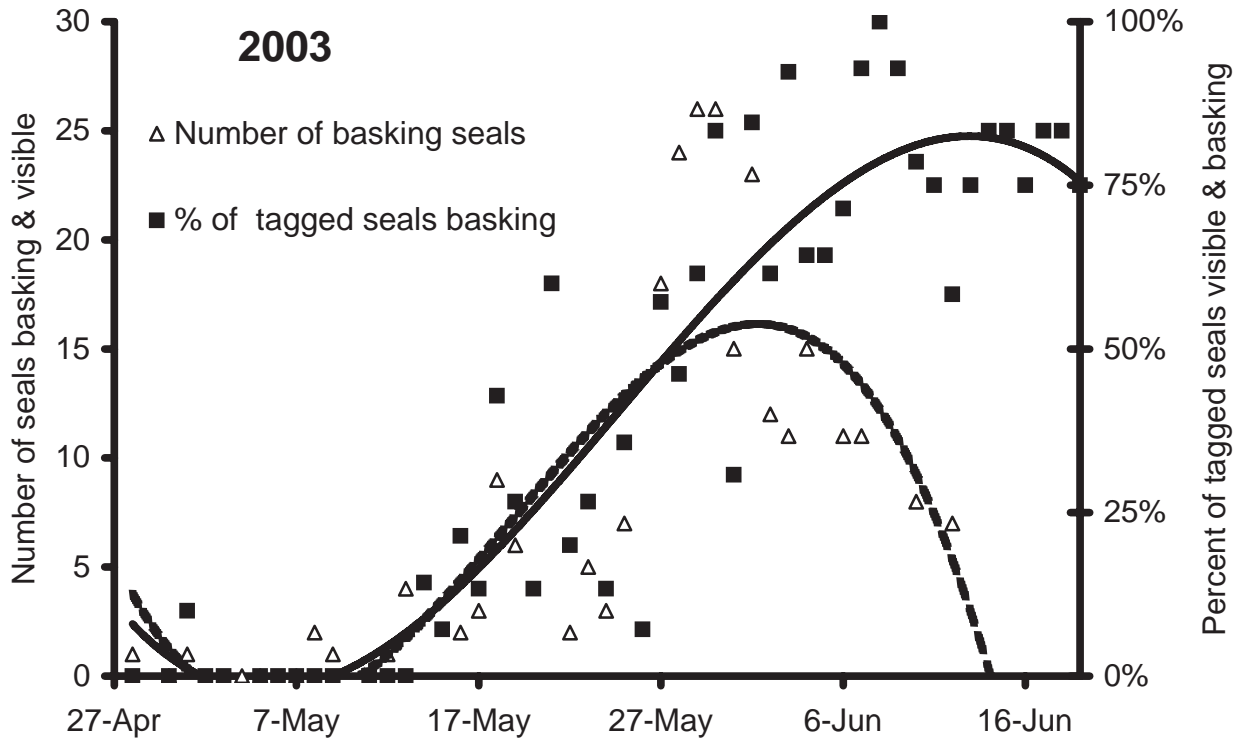
c



d



e



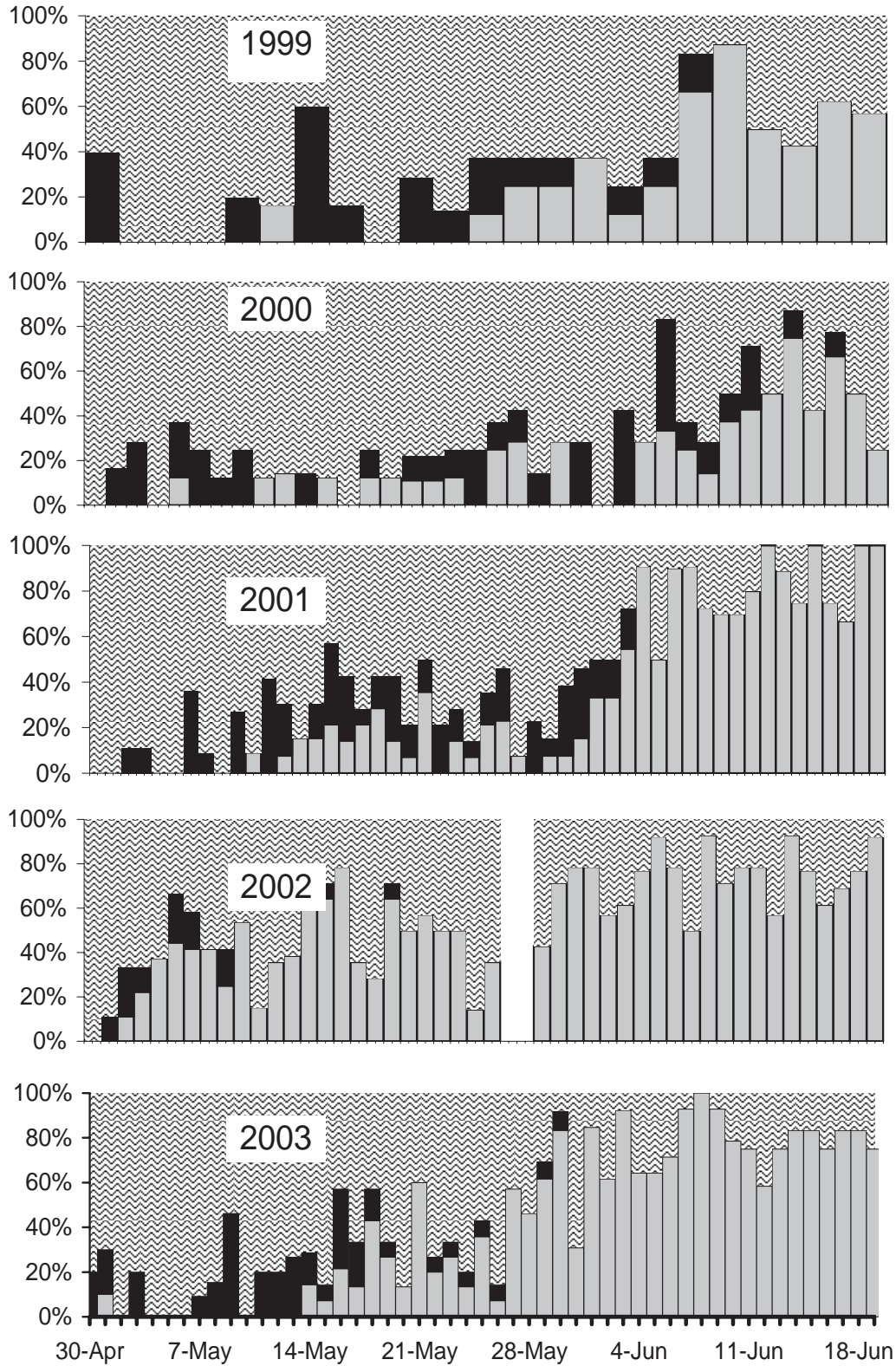


Figure 15. Percentages of radio tagged seals in the water (), in subnivean lairs () and basking on the ice () in 1999, 2000, 2001, 2002, and 2003.

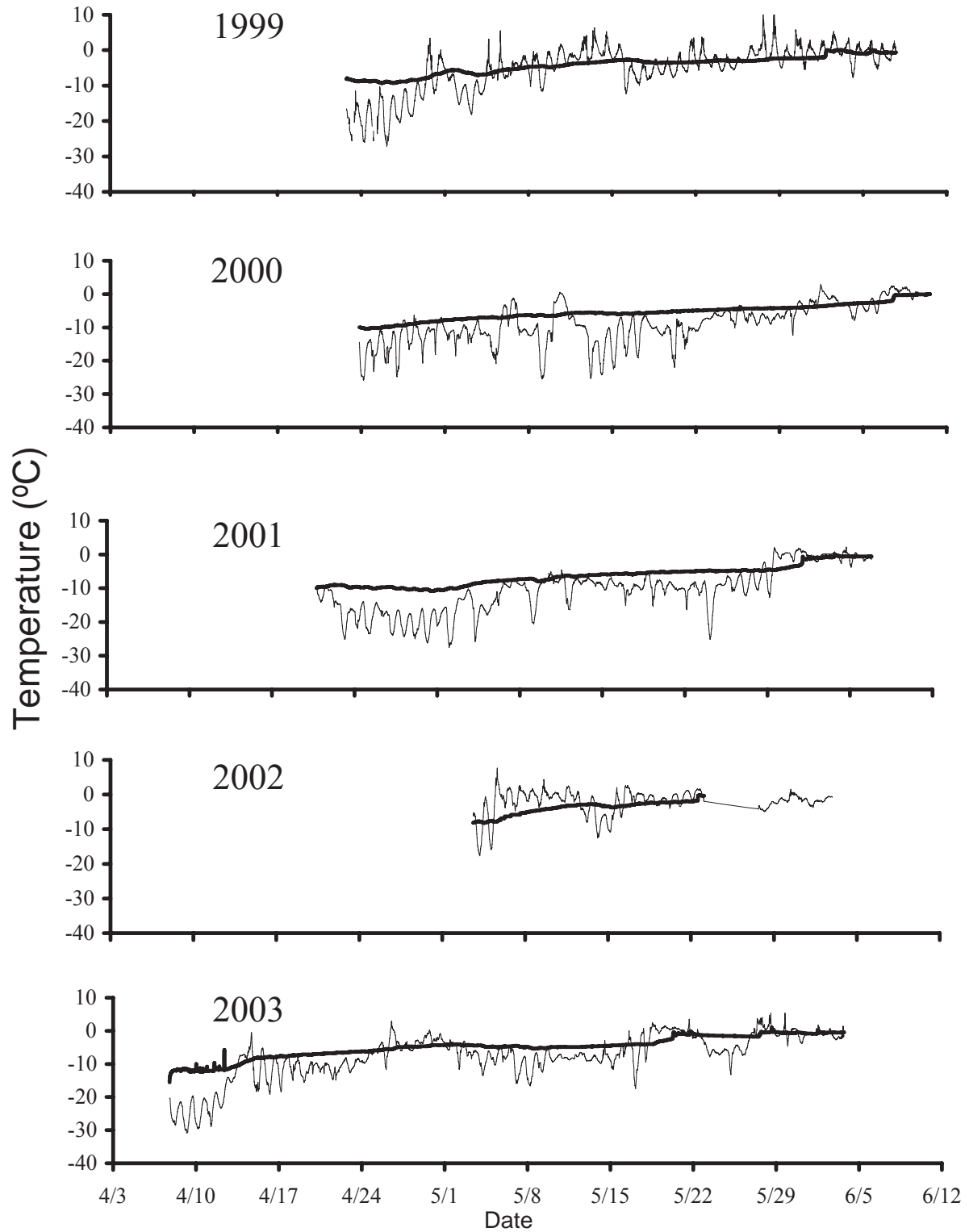


Figure 16. Air temperature (thin line) and snow temperature at the ice surface (thick line) in April, May, and June 1999–2003.

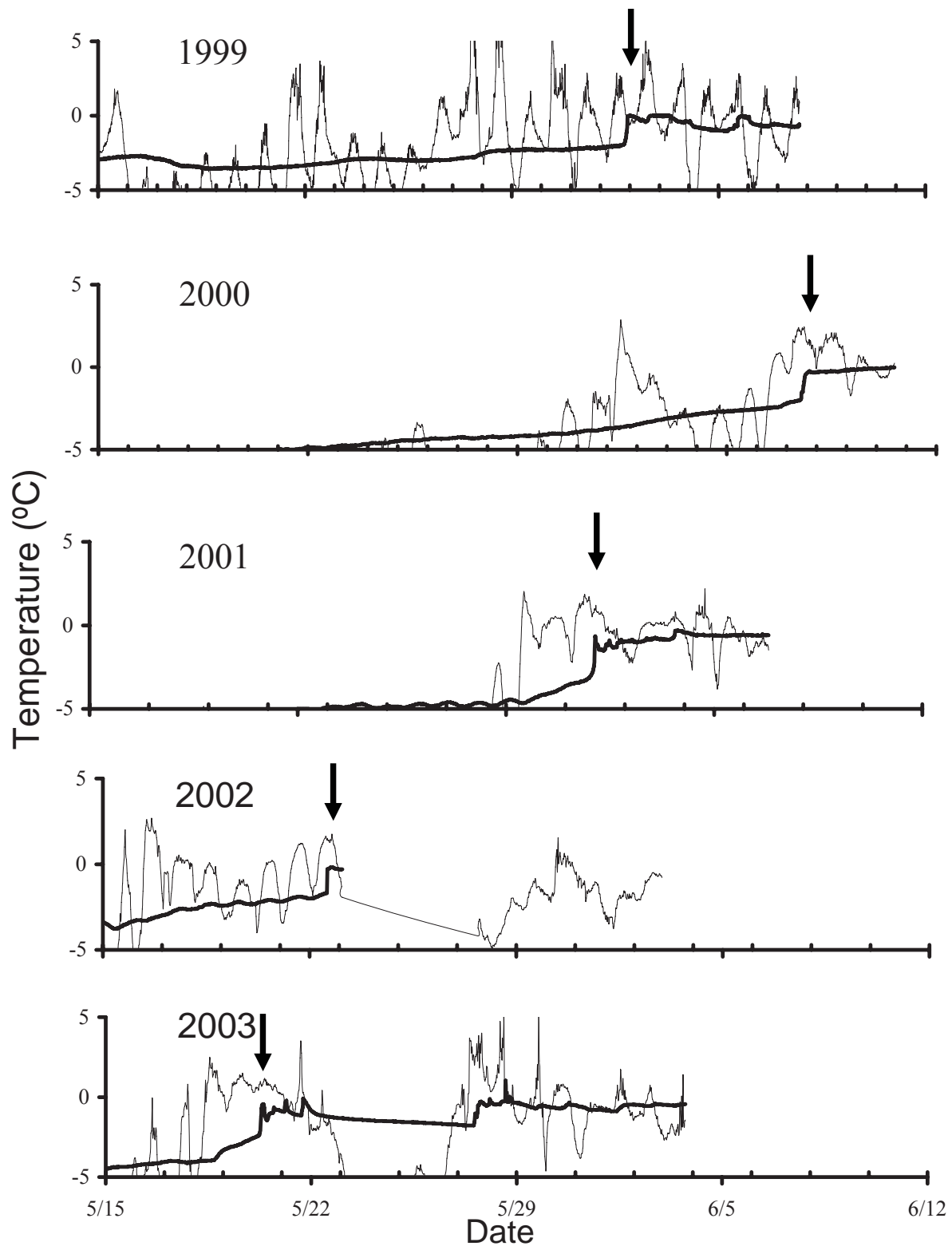


Figure 17. Close up of air temperature (thin line) and snow temperature at the ice surface (thick line) in mid May to mid June 1999, 2000, 2001, 2002, and 2003. Arrows indicate abrupt increases of snow temperatures at the ice surface from -2 to 0°C.

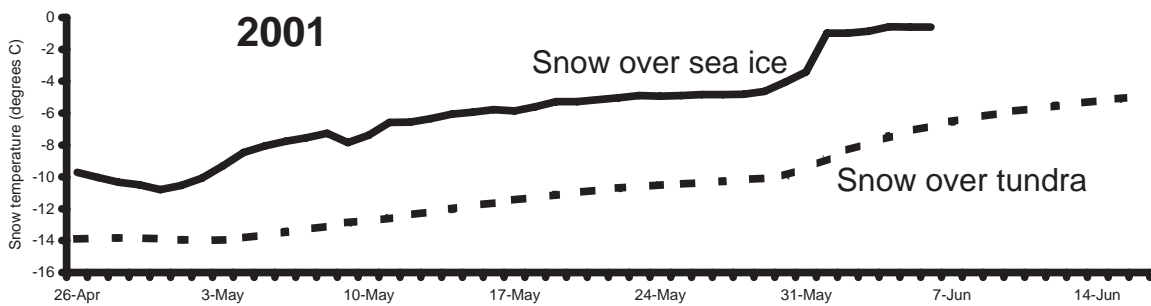
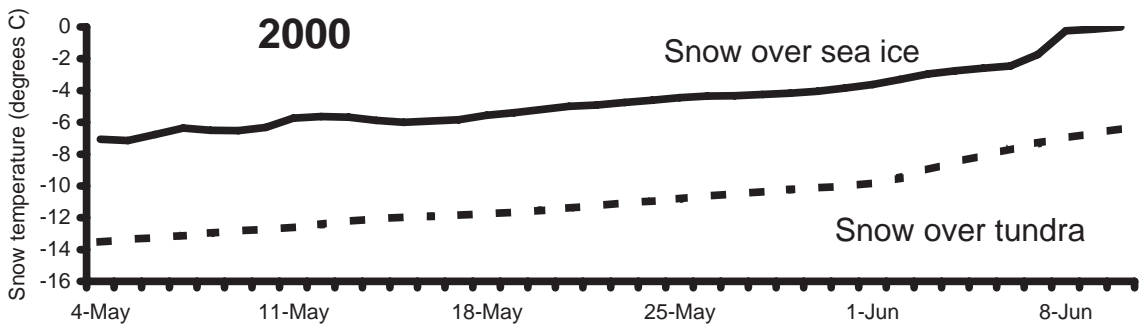
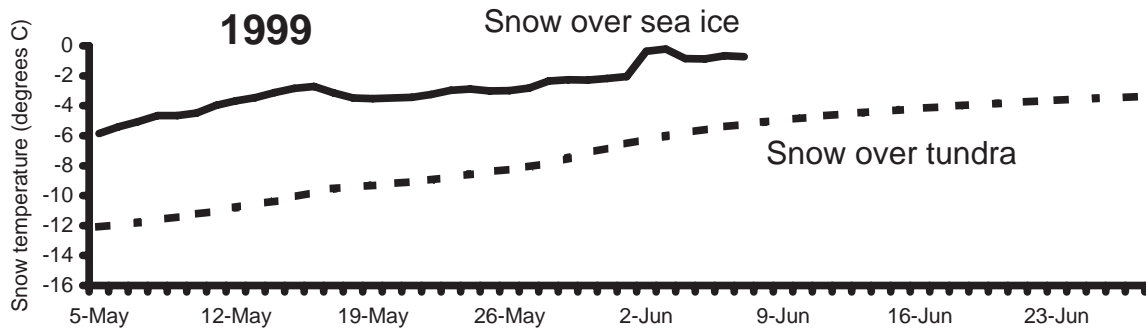


Figure 18. Snow temperatures over the sea ice in our study area and on the tundra at the West Dock, Prudhoe Bay.

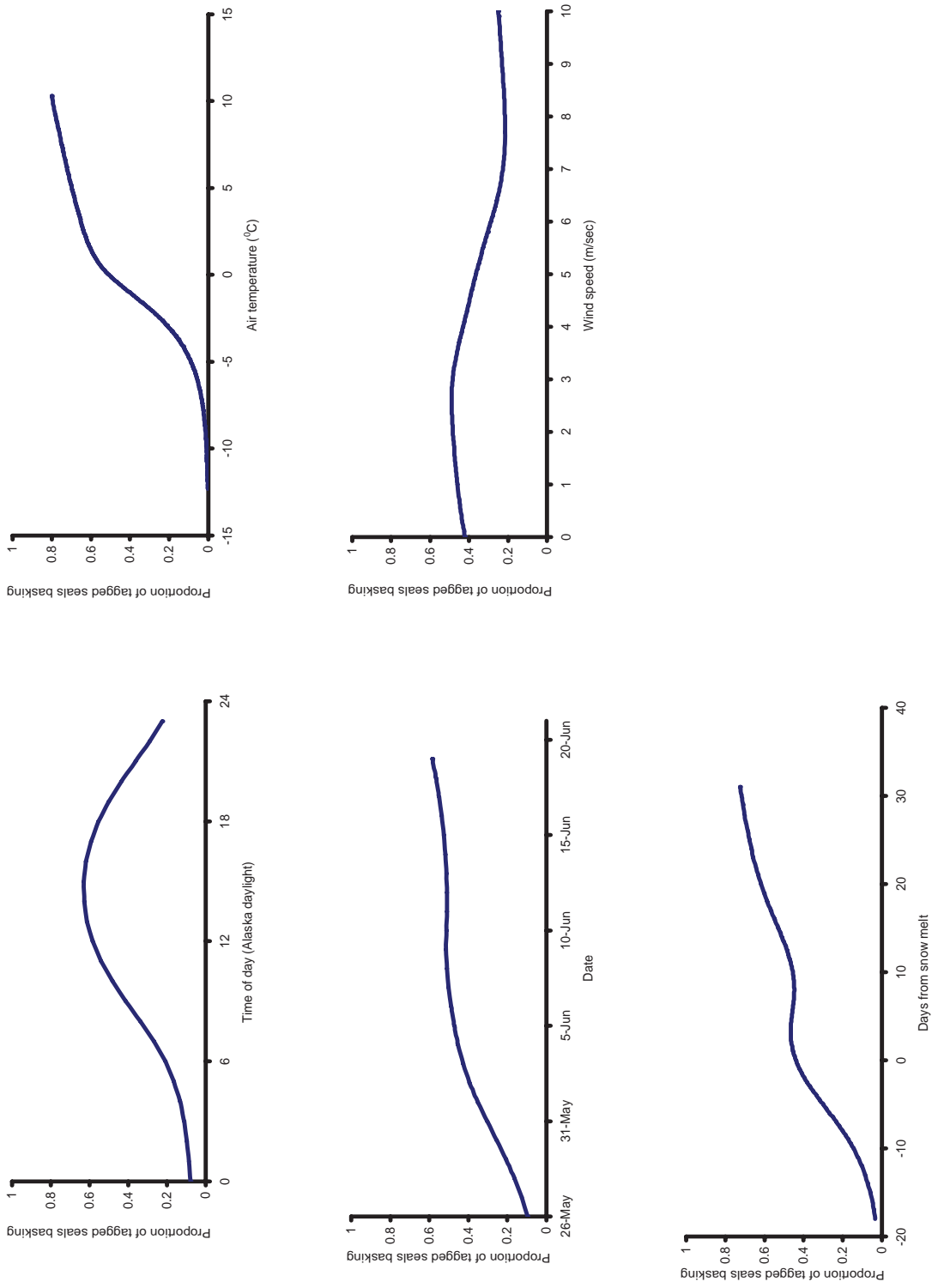


Figure 19. Influence (based on generalized additive models) of time of day, day of year, days from snow melt (estimated from passive microwave emissions), air temperature, and wind speed on the probability that radio tagged seals were visible on the ice.

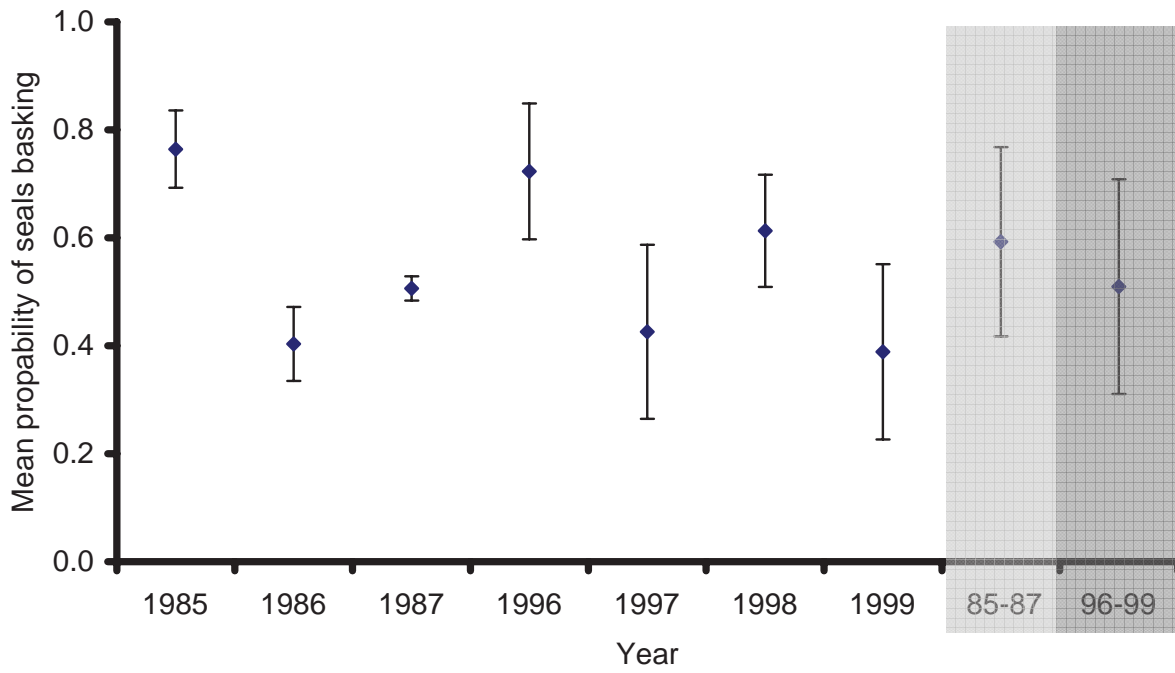


Figure 20. Probabilities (means and standard deviations) of ringed seals basking on the ice during 7 survey years (Frost et al. 2002) based on combined effects of time of day, day of year, days from snow melt, air temperature, and wind speed.

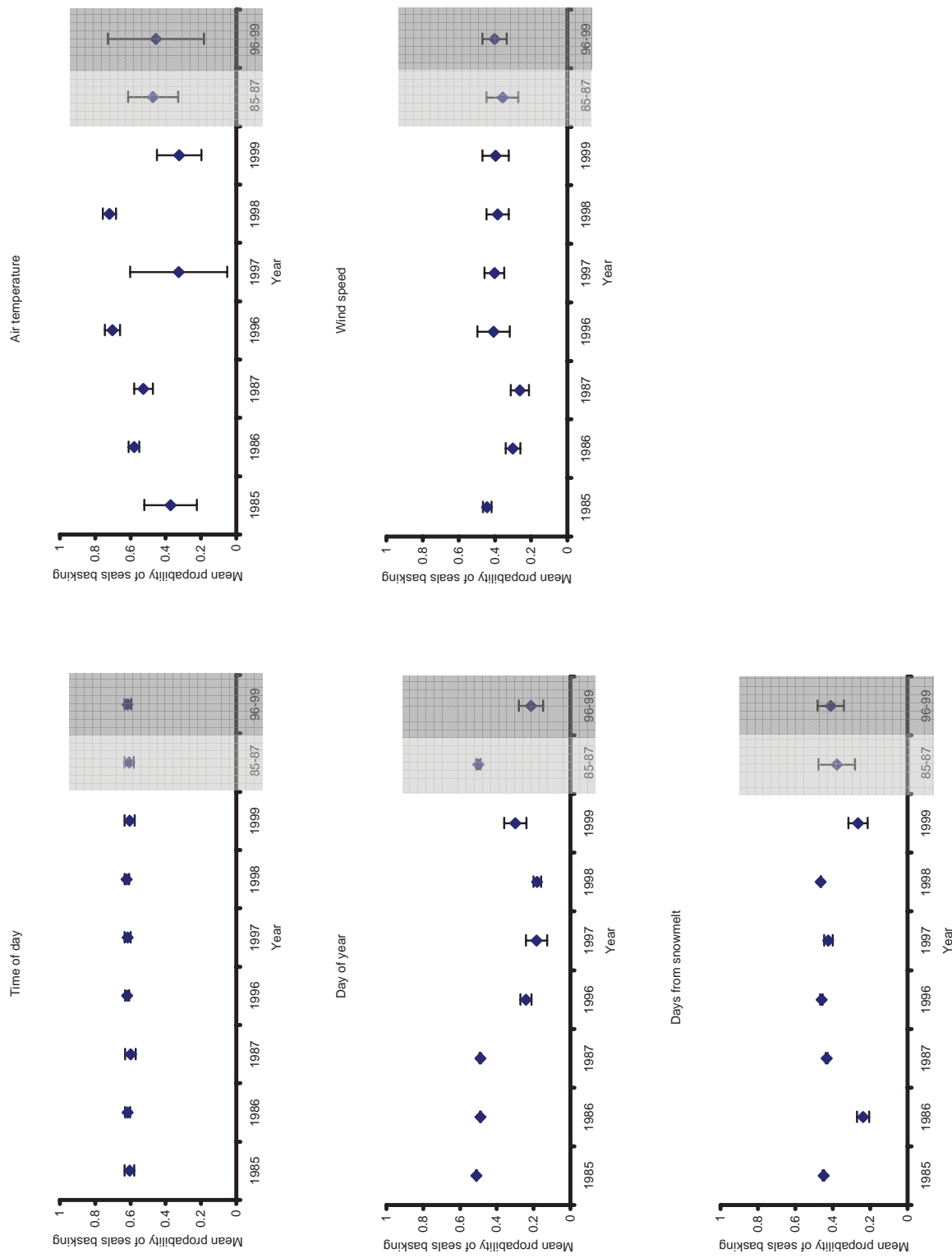


Figure 21. Predicted probabilities (means and standard deviations) of seals basking during aerial surveys conducted by Frost et. al. (2002) based on univariate models.

Table 1. Subnivean breathing holes and lairs located by trained dogs in 1999, 2000, 2001, 2002, and 2003.

Year	Breathing holes	Lairs	Birth lairs	N
1999	53%	47%	5%	120
2000	47%	53%	4%	154
2001	45%	55%	4%	108
2002	60%	40%	9%	119
2003	55%	45%	7%	110
Average	52%	48%	6%	611 (Total)

Table 2. Numbers of nets set, seal holes in which nets were set, and seals captured in 1999, 2000, 2001, 2002, and 2003.

Year	Nets set	Seal holes	Captures
1999	24	19	9
2000	41	27	15
2001	31	23	16
2002	33	26	19
2003	51	29	16
Totals	180	124	75

Table 3. Seals captured in 1999, 2000, 2001, 2002, and 2003. Minimal ages were determined from the number of annuli visible on the claws of the pectoral limbs.

Capture Date	Seal ID	Sex	Min. age	First observed out of lair
6-May-99	SW99	F	6	21-May-99
6-May-99	RI99	M	6	30-May-99
13-May-99	MA99	F	7	28-May-99
14-May-99	VR99	F	6	29-May-99
15-May-99	SM99	M	7	3-June-99
21-May-99	SP99	F	6	—
23-May-99	CH99	F	5	3-Jun-99
24-May-99	OR99	F	5	2-Jun-99
25-Apr-00	CS00	M	7	17-May-00
27-Apr-00	LM00	M	6	10-Jun-00
30-Apr-00	CC00	M	6	24-May-00
1-May-00	SL00	M	7	—
2-May-00	RA00	F	6	31-May-00
3-May-00	EL00	M	5	< 3-May-00
6-May-00	OC00	F	4	3-Jun-00
6-May-00	PU00	M	7	5-Jun-00
17-May-00	LS00	F	5	>4-June-00
18-May-00	IS00	M	7	—
15-Apr-01	PO01	M	7	24-May-01
19-Apr-01	SI01	M	7	11-May-01
20-Apr-01	TS01	M	5	3-Jun-01
21-Apr-01	IS01	M	7	12-May-01
23-Apr-01	HC01	F	7	13-May-01
23-Apr-01	JB01	M	5	15-May-01
25-Apr-01	MH01	M	8	19-May-01
25-Apr-01	MK01	M	6	1-Jun-01
29-Apr-01	KK01	F	5	2-Jun-01
1-May-01	CL01	M	6	4-May-01
1-May-01	IM01	M	7	12-May-01
8-May-01	KC01	M	5	19-May-01
9-May-01	LH01	F	5	30-May-01
13-May-01	WC01	F	8	2-Jun-01
13-Apr-02	SH02	F	6	6-May-02
16-Apr-02	EV02	F	6	10-May-02
21-Apr-02	TR02	F	8	18-May-02
25-Apr-02	WW02	M	6	5-May-02
27-Apr-02	BC02	F	7	7-May-02

Table 3, cont.

Capture Date	Seal ID	Sex	Min. age	First observed out of lair
27-Apr-02	JN02	M	5	12-May-02
28-Apr-02	HM02	F	7	9-May-02
3-May-02	NA02	F	8	8-May-02
3-May-02	RO02	F	8	6-Jun-02
7-May-02	RN02	M	7	8-May-02
7-May-02	IM01*	M	8	12-May-02
8-May-02	ND02	F	7	16-May-02
11-May-02	JU02	F	9	12-May-02
14-May-02	MW02	F	5	15-May-02
14-May-02	EF02	M	6	-
15-May-02	KK02	M	7	16-May-02
20-May-02	JJ02	F	8	(not tagged)
20-May-02	MA02	F	7	(not tagged)
9-Apr-03	YK03	M	9	2-Jun-03
13-Apr-03	KA03	F	6	1-Jun-03
16-Apr-03	SU03	F	6	18-May-03
18-Apr-03	SQ03	F	9	18-May-03
22-Apr-03	VI03	F	7	28-May-03
23-Apr-03	SH02*	F	8	14-May-03
23-Apr-03	SE03	M	6	21-May-03
25-Apr-03	JW03	M	8	18-May-03
26-Apr-03	TA03	F	7	16-May-03
26-Apr-03	TE03	M	6	28-Apr-03
29-Apr-03	PF03	F	7	13-May-03
5-May-03	MO03	M	8	20-May-03
7-May-03	WW02*	M	7	14-May-03
10-May-03	GR03	F	7	18-May-03
10-May-03	FI03	F	6	31-May-03

*Recapture

Table 4. Regression equations relating the proportions of tagged seals visible to the total number of seals visible in the study area in 1999, 2000, 2001, 2002, and 2003.

Year	Regression	r ²	F	Degrees freedom	p
1999	$7.3935x^2 + 2.3501x + 0.1298$	0.63	10.16	2, 12	0.003
2000	$26.883x^2 + 8.2731x + 2.1142$	0.72	34.12	2, 26	< 0.0001
2001	$15.563x^2 + 29.801x + 0.5151$	0.61	13.33	2, 17	0.0003
2002	$-70.34x^2 + 76.52x - 5.9268$	0.10	0.80	2, 14	0.47
2003	$-23.958x^2 + 38.163x + 0.6111$	0.63	23.86	2, 28	< 0.0001

Table 5. Dates lair abandonment was complete in 1999–2003 and possible predictors of abandonment including date the first seal abandoned a lair, date the snow at the ice surface reached 0°C, breakup date for the Kuparuk River, date that the diurnal difference in backscatter amplitude exceeded 2 dB, snow melt date indicated by the PMSTA algorithm, and snow melt date indicated by the MDSDA algorithm.

Year	Last lair abandoned	First lair abandoned	0° snow	Kup. R. breakup	Delta bcksct > 2	Microw. PMSTA	Microw. MDSDA
1999	7 June	21 May	3 June	23 May	--	2 July	6 June
2000	12 June	8 May	8 June	6 June	31 May	3 July	12 June
2001	3 June	4 May	8 June	8 June	31 May	26 June	4 June
2002	18 May	5 May	24 May	22 May	7 May	14 June	19 May
2003	2 June	29 April	27 May	--	20 May	7 July	5 June

Table 6. Comparison of generalized additive models predicting the probability of seals basking.

Covariates included in model	non parametric χ^2	non parametric degrees of freedom	p
time of day, days from snow melt, wind speed, air temperature, day of year			
time of day, days from snow melt, wind speed, air temperature	21	3	0
time of day, days from snow melt, wind speed, day of year	71	2.8	0
time of day, days from snow melt, air temperature, day of year	111	3.1	0
time of day, wind speed, air temperature, day of year	313	3.2	0
days from snow melt, wind speed, air temperature, day of year	2217	2.8	0
time of day	2452	3	0
days from snow melt	617	2.9	0
wind speed	230	3.1	0
air temperature	348	2.8	0
day of year	569	3.1	0

The χ^2 values at the 5% significance level are 5.99 for 2 degrees of freedom and 7.82 for 3 degrees of freedom.

Table 7. Proportions of tagged seals visible on the ice surface during aerial surveys conducted by LGL Ltd. in 1999–2002.

Date	1999	2000	2001	2002
28-May			0.08	
29-May			0.15	
30-May				
31-May		0.5	0.36	0.64
1-Jun		0.25		0.79
2-Jun		0.14		0.86
3-Jun	0.71	0.14		0.57
4-Jun	0.13	0.43		0.71
5-Jun	0.43	0.5		0.77
6-Jun	0.63	0.75		0.92
7-Jun	0.57	0.43		1.00
8-Jun				
9-Jun	--			
Mean	0.49	0.39	0.20	0.78
SD	0.23	0.21	0.15	0.14

Table 8. Yearly ringed seal densities (seals / km²) in the Prudhoe Bay area estimated by the Alaska Department of Fish and Game (Frost et al. 2002, 2005) and LGL Limited (Moulton et al. 2002).

Year	ADFG	LGL
1996	0.78	
1997	0.83	0.43
1998	0.89	0.39
1999	0.95	0.63
2000		0.47
2001		0.54
2002		0.83