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Attendance and nursing patterns of harp seals in the harsh environment of the northwest Atlantic

Elizabeth A. Perry[1] · Garry B. Stenson[2] · Alejandro D. Buren[2]

Abstract Harp seals are capital breeders who give birth to single pups and nurse them with fat-rich milk for 12 days on pack ice in the North Atlantic under harsh environmental conditions. Our objective was to examine female attendance and nursing patterns under varying environmental conditions to determine whether these patterns change in response to changing weather conditions. The behaviour of 158 harp seal females and pups off northeastern Newfoundland was recorded every 3 min during daylight hours. Air and water temperature, and wind speed were recorded at the beginning of each observation session. We constructed GAMM models to examine the importance of these variables in predicting attendance and nursing patterns. The best model for predicting attendance included time of day, air temperature, wind speed, and the interaction between wind and air temperature. The best model for predicting nursing included wind speed, air temperature and time of day. Females were more likely to attend their pups during the afternoon when solar radiation appeared to be high, but reduced attendance during high winds and/or low temperatures. The likelihood of attending females nursing during these poor weather conditions was greater than when conditions were better. Thus, females were less likely to be present when weather conditions were poor but when present, they were more likely to be provisioning their pups. This strategy may help these females defray the thermoregulatory demands on their limited resources while ensuring that their young attain weights that are likely to increase post-weaning survival and hence maternal fitness.

Keywords Attendance patterns · Nursing · Energy conservation · Parental care · *Pagophilus groenlandicus* · Lactation · Weather conditions

Introduction

Parental care in mammals is varied in form and duration, depending on developmental and environmental constraints (see Clutton-Brock 1991; Royle et al. 2012). This is most obvious during lactation which is the most energetically costly component of reproduction for mammalian females (Gittleman and Thompson 1988). Females must produce nutrient-rich milk for their offspring while meeting their own metabolic demands. Although there is a continuum, mammals can generally be classified as income or capital breeders; capital breeders rely on resources stored in advance of the reproductive period while income breeders replenish stores by foraging during the breeding period (Jönsson 1997).

Phocid, or true, seals have short lactation periods during which females provide high-fat-content milk and pups grow rapidly (see reviews in Oftedal et al. 1987; Boness and Bowen 1996). Most phocid seals are capital breeders in which females fast (or consume little) during the lactation period, relying on energy stored as subcutaneous fat (blubber) acquired prior to parturition to produce milk for their young while meeting their own metabolic demands. In

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addition to the high cost of lactation, many phocid females give birth in climatically harsh and unpredictable environments where metabolic demands associated with thermoregulation may increase energetic requirements during this short, energetically demanding period.

Each March, harp seals (*Pagophilus groenlandicus*) gather for pupping on pack ice in the northwest Atlantic where they encounter a variety of harsh environmental conditions including snow storms, freezing rain and air temperatures that can be below −20 °C. During their 10–12 day lactation period (Kovacs 1987), females may lose approximately 39 kg of blubber (Kovacs et al. 1991), which is in the order of 28 % of their total body mass. Therefore, while females are meeting the nutritional requirements of their pups, they are also depleting their insulative layer of blubber (Chabot et al. 1996). Unlike pups that remain on the ice during this nursing period, females do not remain in constant attendance of their pups on the ice (Kovacs 1987, 1995). Harp seals are considered to essentially fast during lactation, which suggests that their absences from the ice are due to factors other than foraging.

The haul-out behaviour of many seal species has been shown to be correlated with environmental conditions which some authors have proposed could be due to energetic constraints including the cost of thermoregulation (e.g. Findley 1979; Stewart 1983; Watts 1992; Lydersen et al. 1994; Watts 1996; Chambert et al. 2015). However, many of these species pup in isolated areas and it has been difficult to test the hypothesis that females are responding to environmental conditions because of the difficulties inherent in observing seals under a range of weather conditions, particularly when poor. However, the presence of a ship based within the harp seal whelping patch off southern Labrador provided us with the opportunity to observe the animals under a variety of environmental conditions. The objective of this study was to determine whether nursing harp seals will show behavioural changes associated with environmental conditions. We hypothesize that female harp seals will alter their attendance patterns in relation to weather conditions. In contrast, we do not expect nursing behaviour to be similarly influenced by weather conditions due to the need to provision pups.

Methods

Harp seal pups were observed on pack ice at the whelping (pupping) concentration off north-eastern Newfoundland (approximately 52°N 55°W), over 8 days between 12 and 21 March. Continuous observations, with the aid of 10 × 40 binoculars, were made from the bridge of an icebreaker as it drifted with the ice during daylight hours

(0700 to 1830 hours). All observations were carried out by two (2) observers who standardized their classifications of behaviour to ensure consistency.

At the beginning of observations, a subsample of at least 10 pups was selected for observation such that they were readily visible, close to each other (i.e. sharing ice pans or on neighbouring ice pans). To reduce the likelihood of behaviour being affected by the presence of the ship, all pups were a minimum of 50 m from the ship. Observations of focal animals continued until they drifted from view or the ship started its engines to move position. Because of differential drift between the ice and the ship, the number of seals visible varied. Ice drift data confirmed that no seals were observed on more than 1 day.

Whenever possible, the relative age of pups was recorded. Based upon their pelage, pups were assigned to age classes: newborn (<1 day), yellow coat (1–2 days), thin white (2–6 days) or fat white (6–10 days) (Stewart and Lavigne 1980).

Attendance, defined as the presence of females within 2 body lengths of their pups, and the occurrence of nursing were noted for each mother–pup pair every three minutes (less than half of the duration of a nursing episode (Stewart 1987)), using scan sampling. Weather parameters, including air and water temperatures, and wind speed were recorded at the beginning of every observation session and updated hourly throughout the observation period. All measurements were obtained from the deck of the ship (i.e. approximately 6 m above the ice surface).

The effects of pup age, time of day, environmental variables (air temperature and wind speed) and their interaction on the probability of attending a pup were assessed with generalized additive mixed models (GAMM; Wood 2006), using mother–pup pair ID as a random variable, in order to account for correlation due to repeated measures (Zuur et al. 2009). We assessed the existence of collinearity among explanatory variables through visual inspection of pairwise scatterplots, and through calculating variance inflation factors (VIFs; Zuur et al. 2010). We detected correlation between air and water temperatures (Fig. 1), and thus excluded the latter from the analyses. We did not detect multicollinearity among variables. A binomial error distribution and logit link function were used. Given that the proportion of pups attended was not a monotonic function of time of day (Fig. 2), we estimated a smooth function for time of day. Thus, the GAMM used can be expressed as:

$$p_{(attend)} \sim s(\text{time of day}) + \text{wind speed} + \text{air temperature} + \text{pup age} + \text{wind speed} \times \text{air temperature}$$

where s(time of day) is an estimated smooth function of time of day. We used a penalized cubic regression spline as

Fig. 1 Environmental variables, averaged over each observation hour, as a function of time of day: mean water and air temperatures, and mean wind speed
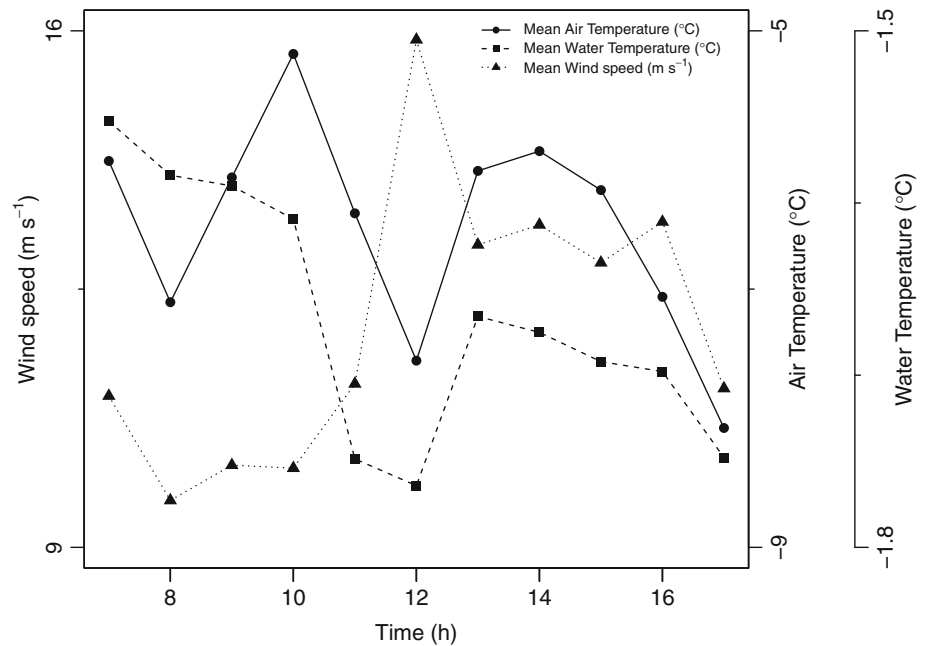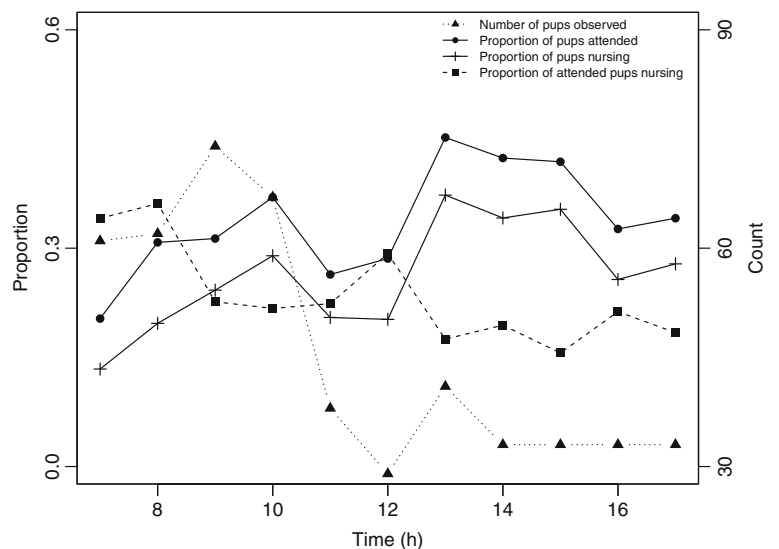

Fig. 2 Number of pups observed, and proportions of pups attended, nursing, and nursing given that they were attended, presented as a function of time of day

the smooth function, and cross-validation was used to estimate the optimal amount of smoothing.

We built all possible candidate models, and ranked and selected the best model based on the Akaike's information criterion (AIC) (Burnham and Anderson 2002) and the derived measure of evidence ratio (E_i) (Anderson 2008). Models with a ΔAIC less than 10 were considered plausible. To quantify the evidence for the importance of each explanatory variable in the set of candidate models, we calculated the relative variable importance (Burnham and Anderson 2002). The relative variable importance ($w_+(j)$)

varies between 0 and 1 and is a derived measure of ΔAIC. The larger the $w_+(j)$ the more important variable j is, relative to the other variables. Using the $w_+(j)$, all the variables can be ranked in their importance (Burnham and Anderson 2002).

The same strategy was followed to rank candidate models and assess the relative importance of the explanatory variables on the probability that a pup was nursed, given that it was attended.

All analyses were performed using the gamm4 package (Wood 2011) in R Development Core Team (2009, 2012).

Results

A total of 7567 observations were made of 178 pups over 8 days. Individual pups were observed for periods of 18 to 411 min ($\bar{x} = 127.5$ min, SD = 103.1). Nineteen pups were observed for less than 30 min and removed from the data. Since only 1 yellow pup (no newborns) was observed, this animal was not included in our analyses.

The air temperature ranged from -10 to 1.3 °C. The mean air temperature had maximum peaks during mid-morning and early afternoon; the coldest mean air temperatures were observed during noon and late afternoon (Fig. 1). The water temperature ranged from -1.9 to -1.2 °C. The mean water temperature followed the same general pattern as the mean air temperature, being coldest at midday (Fig. 1). Wind speed ranged from 5 to 18 m s^{-1}. The mean wind speed was lowest during the morning, increased to a peak at noon, and then decreased slightly and stabilized during the afternoon at higher velocities than in the morning (Fig. 1).

Overall, the number of pups observed per 1-h block ranged from 30 to 81 ($\bar{x} = 48.36$ pups, SD = 18.07). Due to differences in sighting effort and drift, the largest numbers of pups were observed during the morning with the least number of pups observed at midday. The number of observations made each hour was lower in the afternoon than in the morning (Fig. 2). The proportion of observations when pups were attended was highest during mid-morning and early afternoon, with the proportion being lowest at noon and during the late afternoon (Fig. 2). The proportion of observations during which pups were being nursing followed the same pattern as the presence of females (Fig. 2). However, the proportion of observations in which pups were nursed, given that they were attended, reached a maximum during the early morning, and continuously decreased (although at a low rate) throughout the remainder of the day, with a slight increase late in the afternoon (Fig. 2).

Attendance models were fit using 7065 observations made on 158 mother–pup pairs. Several of the attendance models had enough empirical support to be considered plausible explanations for the attendance patterns (Table 1). The best model (ΔAIC = 0) included time of day, wind speed, air temperature and the interaction between wind speed and air temperature. All top-ranked models (ΔAIC$_i$ < 10) included a term for wind speed and time of day. Air temperature, pup age and the interaction between air temperature and wind speed were present in some, but not all the top-ranked models. The best model is practically indistinguishable from the second best model ($E_{\min,i} = 1.1$) which includes only time of day and wind speed as explanatory variables (Table 1). These two models had approximately twice (or more) as much support as the rest of the models. The variables that had the largest relative importance were wind speed and time of day (both $w_+(j) = 1$), followed by air temperature ($w_+(j) = 0.61$), the interaction between air temperature and wind speed ($w_+(j) = 0.42$), and lastly pup age ($w_+(j) = 0.27$). However, the direction of the relationship between attendance and pup age was not consistent across the top-ranked models, and given the relative low importance, we did not consider pup age to be an important variable in describing attendance patterns.

The best model had a very good fit to the observed proportion of observations in which harp seal pups were attended (Fig. 3). The effect of time of day on the probability of female seals attending their pups increased until 9 h, decreased slightly in mid-morning, and then reached a maximum in the mid-afternoon (1400 hours), before dropping off prior to dusk (Fig. 4). At low air temperatures, the probability of female seals attending their pups decreases sharply with increasing wind speed (Fig. 5). The effect of wind speed at high air temperatures is not as marked. At high wind velocities, the probability of female seals attending their pups increases with increasing air temperature, while at low wind speed this effect is practically nil (Fig. 5).

Nursing models were fit using 2358 observations made on 135 mother–pup pairs. The 23 mother–pup pairs not included in this analysis had pups that were never attended during our observation periods. As with the attendance models, several of the nursing models had enough empirical support to be considered plausible explanations of nursing patterns (Table 1). The best model included wind speed, time of day and air temperature. The second best model had almost the same empirical support ($E_{\min,i} = 1.32$) and included only wind speed and time of day as explanatory variables. Wind speed had the largest relative importance ($w_+(j) = 1$), followed by time of day ($w_+(j) = 0.86$), air temperature ($w_+(j) = 0.59$), pup age ($w_+(j) = 0.35$) and lastly the interaction between air temperature and wind speed ($w_+(j) = 0.16$).

The best model captured well the patterns of variation observed in the proportion of attended pups nursed (Fig. 6). The probability of an attended pup being nursed was the highest early in the morning (Fig. 7). At any given hour, the likelihood of nursing was greatest at high wind velocities and low air temperatures (Fig. 8). Overall, the likelihood of nursing decreased with lower wind velocities. In all models that included pup age, the probability that thin white pups were nursed was consistently higher than the probability that fat white pups were nursed, although given the relatively low importance of pup age, this result should be taken cautiously.

Table 1 GAMM models describing which variables were best predictors of attendance and nursing (given that they were attended) of harp seal pups

	Model	ΔAIC	$E_{min,i}$
Attended	$p \sim$ wind + air + s(time) + wind × air	0.00	1.00
	$p \sim$ wind + s(time)	0.19	1.10
	$p \sim$ wind + s(time) + Pup age	1.32	1.93
	$p \sim$ wind + air + s(time) + Pup age + wind × air	1.43	2.05
	$p \sim$ wind + air + s(time)	1.58	2.21
	$p \sim$ wind + air + s(time) + Pup age	3.14	4.81
Nursing	$p \sim$ wind + air + s(time)	0.00	1.00
	$p \sim$ wind + s(time)	0.55	1.32
	$p \sim$ wind + s(time) + Pup age	1.20	1.82
	$p \sim$ wind + air + s(time) + Pup age	1.83	2.50
	$p \sim$ wind + air + s(time) + wind × air	1.85	2.52
	$p \sim$ wind + air + s(time) + Pup age + wind × air	3.72	6.42
	$p \sim$ wind + air	3.81	6.73
	$p \sim$ wind + Pup age	3.96	7.25
	$p \sim$ wind	4.31	8.62
	$p \sim$ wind + air + Pup age	5.05	12.51
	$p \sim$ wind + air + wind × air	5.71	17.41

Variables included wind speed (wind), air temperature (air), time of day smoothed (s(time)), pup age and the interaction term wind × air. The delta Akaike's information criterion (**Δ**AIC) and the derived measure evidence ratio (E_i) for each model are included
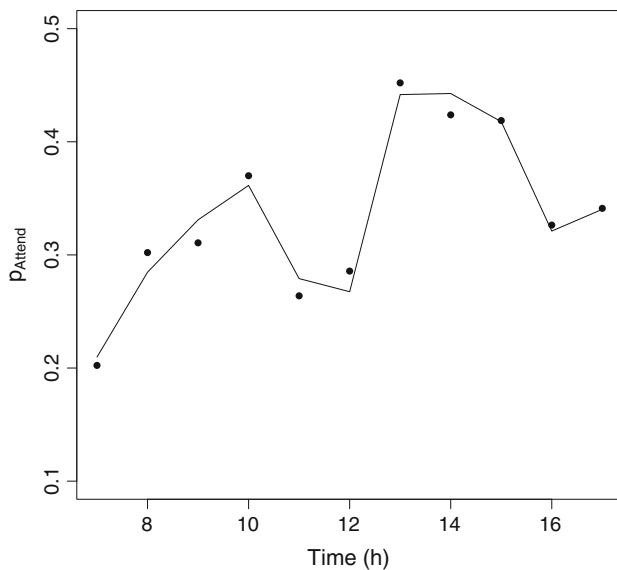
Fig. 3 Visualization of the fit of the best model to describe the proportion of pups attended ($p_{attend} \sim$ wind + air + s(time) + wind × air)
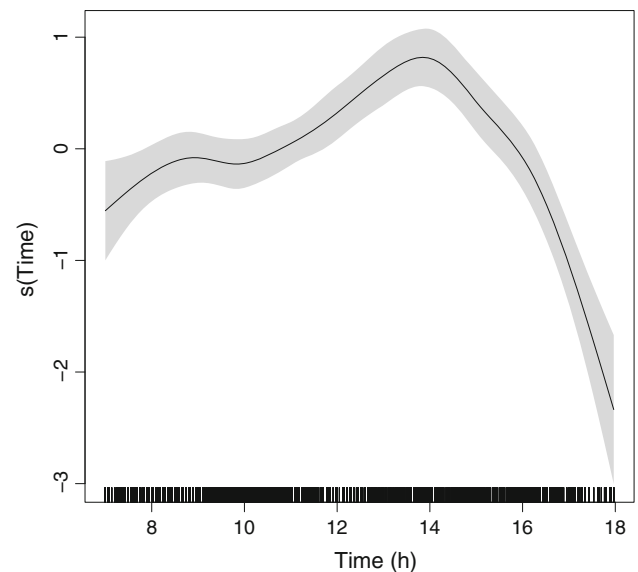
Fig. 4 Estimated effect of time of day on the probability of a harp seal females attending her pup. *Shaded areas* show the 95 % confidence intervals. *Black vertical lines* on the abscissa axis show the distribution of observations of the covariate Time of day

Discussion

Harp seals give birth and nurse their pups on the pack ice off Newfoundland under environmental conditions that can be extremely harsh. The weather conditions we observed from the ship during this study were typical of the region based upon 1971–2000 data for the nearest weather station (St. Anthony, NL 51.4°N 56.1°W, http://climate.weath eroffice.gc.ca/climate_normals). In this area, the average March temperature is −7.1 °C (ranging from −31.6 to +9.8 °C), with sustained wind speed up to 27 m s^{-1}, and gusts of 41 m s^{-1}, resulting in an extreme wind chill (representing the relative temperature on human skin) of
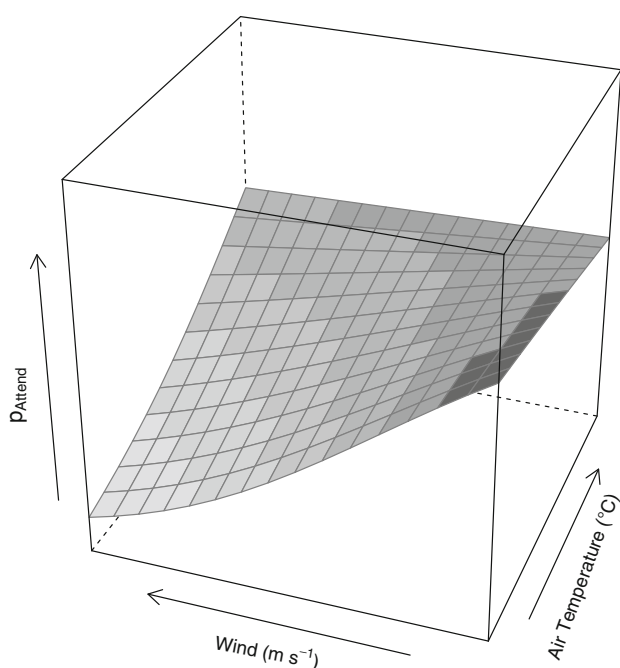
Fig. 5 Estimated effect of wind speed and air temperature on the probability of a harp seal female attending her pup. *Shading* gradient represents probability: *lighter shading* represents lower probabilities while *darker shading* represents higher probabilities. The parameters that describe the relationship between wind speed, air temperature and the likelihood of females attending pups are constant throughout the day although the probability varies among hours. For ease of visualization, the surface at the time when the probability of attending is maximal is shown (13 h, see Fig. 4)
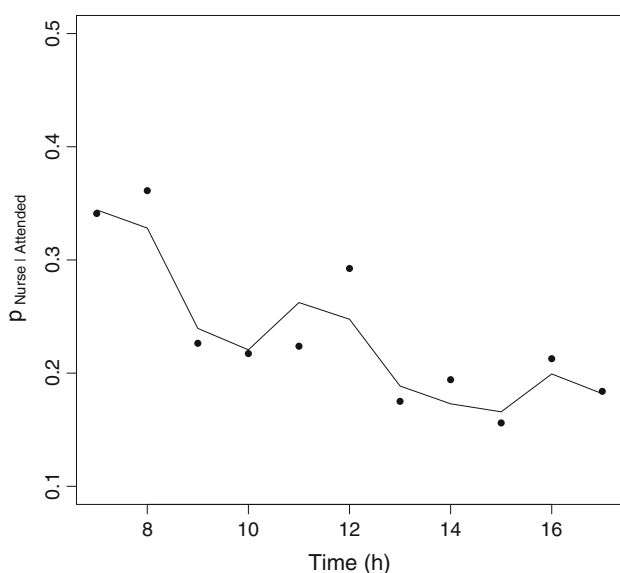

Fig. 6 Visualization of the fit of the best model to describe the proportion of nursing pups, given that it was attended ($p_{nurse|attended} \sim$ wind + air + s(time))

Fig. 7 Estimated effect of time of day on the probability of an attended pup being nursed. *Shaded areas* show the 95 % confidence intervals. *Black vertical lines* on the abscissa axis show the distribution of observations of the covariate Time of day
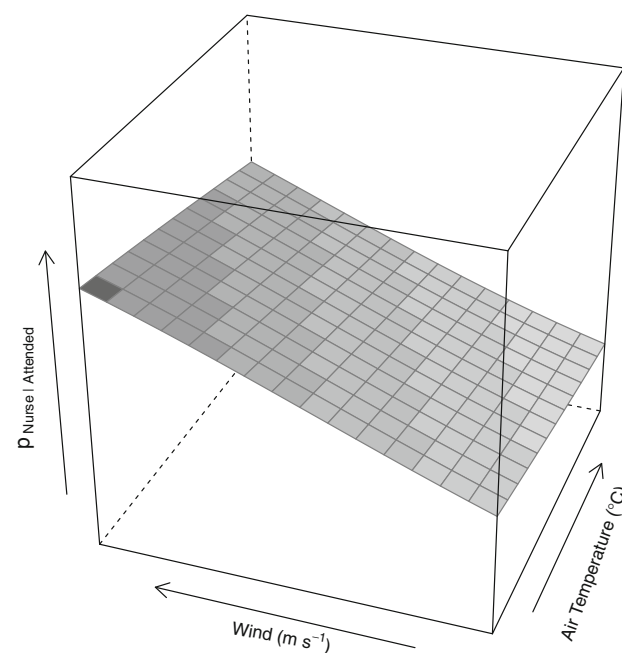
Fig. 8 Estimated effects of wind speed and air temperature on the probability of an attended pup being nursed. *Shading* gradient represents probability: *lighter shading* represents lower probabilities while *darker shading* represents higher probabilities. The parameters that describe the relationship between wind speed, air temperature and the likelihood of nursing are constant throughout the day although the probability varies among hours. For ease of visualization, the surface at the time when the probability of nursing is maximal is shown (7 h, see Fig. 7)

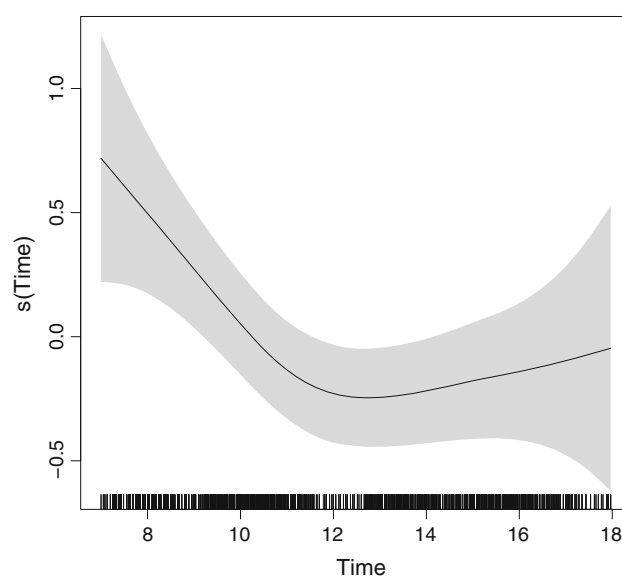−48.5 °C. There is an average monthly snowfall of 83.9 cm accumulated over at least 20 days. We found that harp seal females respond to these weather conditions by adjusting the amount of time they spend on the ice attending their pup, as well as the likelihood of nursing when on the ice.

Although harp seals require ice for whelping and nursing, they use areas where they can maintain access to water. Most commonly, they utilize areas that are 60–90 % ice covered or maintain open holes if the ice sheets freeze together (Sergeant 1991, Stenson personal observations). Females leave their young to go into the water on a regular basis, and although they can feed during lactation (e.g. Lydersen and Kovacs 1993), stomachs are usually empty or contain only small amounts of food (Stewart and Murie 1986; Sergeant 1991). Even when in the water, females spend much of their time near the surface (Lydersen and Kovacs 1993) and appear to maintain contact with their pups (Stewart 1987). This suggests that harp seals are not entering the water simply to feed.

Polar bears (*Ursus maritimus*) feed upon harp seals off the coast of Newfoundland (Sergeant 1991), and it has been suggested that seals go into the water to avoid predation. However, while bear kills are seen, they are not common (Stenson personal observations) given the large number of pups present, raising the question of how much selective pressure is actually being applied. Harp seals show similar behaviours and remain close to water in other areas such as the Gulf of St. Lawrence (e.g. Lydersen and Kovacs 1993) and the White Sea (Popov 1966, cited in Sergeant 1991) where bears do not occur. Also, going into the water would increase exposure to other potential predators such as killer whales (*Orcinus orca*) and sharks (Sergeant 1991). Therefore, it seems unlikely that harp seals are accessing water to avoid predation.

We found that female attendance varies with time of day. A low proportion of females were observed on the ice with their pups in the early morning and at noon, while attendance was higher during mid-morning and peaked in the early afternoon, just after solar noon (Fig. 2). Many of the females we observed spent a considerable proportion of the day in the water. Changes in the number of females present on the ice over the daylight hours were also reported among nursing harp seals in other whelping areas although the patterns varied considerably; Kovacs (1987) found that in the Gulf of St. Lawrence, the highest numbers of females were present on the ice early in the morning and late in the afternoon. Also in the Gulf, Stewart (1987) observed that, in general, females tended to be on the ice with their pups most from mid-morning to late afternoon, but the pattern varied considerably among the three years of his study. Popov (1966, cited in Sergeant 1991) found that females in the White Sea were rarely on the ice in the morning but were hauled out on the ice in the middle of the day and evening. Using a contingency analysis of time together and nursing by hour and age, Stewart (1987) found that the hours of sunlight explained the greatest amount of variation in hourly differences in attendance and suggested that females may take advantage of the higher solar radiation and air temperatures that usually occur during the midday and afternoon to haul out on the ice. Similarly, Lavigne (1982) reported that young harp seals haul out when the sun is shining and may utilize solar radiation as an external source of heat. In fact, Øritsland and Ronald (1978) estimated that harp seal pups may exhibit hyperthermia if solar radiance is high. Siniff et al. (1971) also found that the period of peak inactivity or haul-out in Weddell seals corresponds to the time of the highest elevation of the sun, suggesting that they may be taking advantage of increase solar radiation. Although we do not have data on the amount of sunshine present during the study, the peak attendance we observed occurred shortly after solar noon when solar radiation would be greatest and therefore may have provided some thermoregulatory advantage.

By carrying out an analysis that simultaneously considers the effects of multiple variables on the probability of attending, we found that, in addition to time of day, attendance patterns of female harp seals were strongly influenced by wind speed and temperature; as wind speed increased and temperature decreased, more females were in the water. This is in contrast to Stewart (1987) who observed a similar hourly pattern in attendance, but concluded that wind speed and cold were not important factors influencing the presence of females on the ice. However, Stewart (1987) studied harp seals in the southern Gulf of St. Lawrence where ice and environmental conditions were very different from those in our study area; during the years of his study, the ice was generally composed of large flat pans with less access to the water. Also, being further south, the weather conditions are, on average, milder than in our study area (Environment Canada, http://climate.weatheroffice.gc.ca/climate_normals). Therefore, Stewart (1987) may not have encountered the harsh conditions we observed which allowed us to identify the importance of the interaction between wind and temperature.

Like Kovacs (1987), we found that the number of females nursing their pups showed the same pattern as the number of females present on the ice (i.e. attendance). However, when we restricted our analysis to pups that were attended, we observed that attended pups were much more likely to be nursed early in the morning than at any other time of the day and that the likelihood of being nursed was influenced by weather. Stewart (1987) found a significant relationship between weather patterns and attendance, but not with nursing in harp seals. In contrast, we found that when wind speed was higher and/or air temperature was lower, there was a greater likelihood that the females that were present on the ice were, in fact, nursing. This suggests that under these conditions, females were leaving the water mainly to provision their pups.

The reason why female harp seals would exhibit these patterns of behaviour is not clear. Haul-out behaviour (reproductive and non-reproductive) of many seal species has been shown to be correlated with weather conditions leading researchers to suggest that thermoregulatory constraints are involved (Watts 1996; Twiss et al. 2002; Paterson et al. 2012). In the poor weather conditions encountered in this study, we found a relationship between wind conditions, air temperatures and attendance similar to haul-out patterns described for walruses (Wartzok and Ray 1980), Weddell seals (Siniff et al. 1971; Thomas and DeMaster 1983; Andrews-Goff et al. 2010) and leopard seals (Rogers and Bryden 1997). Ice-breeding grey seal females also spend a substantial portion of the nursing period in the water, if they have easy access, and it has been suggested that this behaviour could help with thermoregulation (Lydersen et al. 1994).

While air temperatures ranged between −10 and 1.3 °C in this study, water temperatures varied little, ranging from −1.9 to −1.2 °C. Examining the metabolic rates of seals in cold water, Irving and Hart (1957) found that although harbour seals increase metabolism in waters less than 10 °C, harp seals showed no increase in metabolism in waters as low as −1 °C. Similarly, Gallivan and Ronald (1979) found that the core body temperature of adult harp seals was independent of water temperature, showing no change in temperatures ranging from 1.8 to 28.2 °C. They concluded that harp seals in water have a wide thermoneutral zone (>28 °C) and that the lower critical temperature is below 0 °C, primarily due to the role of the blubber layer in the reduction in heat loss. Lavigne (1982) also felt that there is no evidence that healthy adult harp seals have difficulties thermoregulating in cold water, although lean seals may have to increase metabolism to meet thermoregulatory demands. The blubber thickness of female harp seals will decline as the energy is transferred to the pup but neither we, nor Stewart (1987), found any relationship between female attendance behaviour and pup age at the whitecoat pup stages present during our study. Harp seals lose core mass as well as blubber during the nursing period which may allow the seal to maintain blubber thickness, presumably for thermoregulation (Chabot et al. 1996).

The metabolic responses of seals to changes in air temperature while on the ice are less clear. A number of studies have shown that the skin temperature of harp seals will decline with decreasing air temperature (e.g. Øritsland and Ronald 1973; Øritsland et al. 1978; Folkow and Blix 1989) although it has been estimated that the blubber layer will provide sufficient insulation to withstand extremely cold air temperatures (e.g. −71 °C Lavigne 1982). In a study of a small number of young harp seals, however, Folkow and Blix (1989) found that metabolic rates were higher at air temperatures of −30 °C than at either −10 °C or 10 °C. They were unable to determine a lower critical temperature precisely, but felt that it was below −10 °C. Based upon in vivo measurements of radiative surface temperatures of adult harp seals, Øritsland et al. (1978) estimated the relationship between air temperature, wind speed and radiative surface temperatures to be $T_{ra} = 23.4 + 2.85T_a - 1.61V$ where T_{ra} = radiative surface temperature, T_a is ambient air temperature and V = wind speed in m s^{-1}. Based upon this relationship, the radiative surface temperature may have been as low as −34 °C at the extreme conditions we observed ($T_a = -10$ °C, $V = 18$ m s^{-1}). Frank et al. (1999) found that while metabolic responses to temperature in humans are predominately regulated by core temperatures, skin temperature is as important as core temperature in determining thermal comfort. Therefore, it is possible that seals leave the ice under unfavourable weather conditions either because remaining would result in increased metabolic rates to meet the thermoregulatory demands, or simply to reduce the likelihood that they will encounter temperatures that could require increased metabolism. The importance of behaviour cannot be overlooked when thermal balance is being examined (Lavigne 1982).

Thus, it is possible that female harp seals defray some of the thermoregulatory costs associated with caring for pups on ice by spending time in the water when the conditions are extremely cold. This may, in part, explain why harp seals are always near a water access point when hauled out. Hooded seals (Cystophora cristata) also give birth to, and care for their young, on the pack ice at the same time as harp seals, but appear to have developed a different method to address the problem of balancing energy demands. Unlike harp seals, they do not leave their pups, remaining on the ice for the full lactation period. However, because they are larger, hooded seals have a smaller surface area to volume ratio and so may have lower size-specific heat loss. Perhaps more importantly, they have an extremely short 4-day lactation period (Bowen et al. 1985) after which the females leave their pups on the ice. Not only does this contracted period of dependence ensure that nursing can be completed on unstable ice, it allows for rapid transfer of maternal stores while shortening the length of time that female hooded seals must contend with the harsh weather and drain their energy stores.

In conclusion, we found clear patterns in female harp seal pup attendance that reflected extremes in wind and temperature conditions, possibly related to thermoregulation requirements of the adult females. In addition to a daily pattern, the probability that a pup was attended decreased, while the probability that attended pups were nursed increased, in harsh weather conditions (high wind speed and low air temperatures). These findings suggest

that although fewer females come out of the water, or remain on the ice, to attend their pups in unfavourable climatic conditions, those that do are hauled out to nurse. This ensures that the pups' energetic demands especially in younger, smaller pups, are being met. This parental provisioning strategy is likely to increase fitness returns for the females in terms of offspring survival.

Compliance with ethical standards

Human and animal rights No animal care approval was required for this study. The presence of the vessel was covered under a Fisheries and Oceans, Canada Animal Care Committee approval to G. Stenson.

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