

Windscares and olfactory foraging among polar bears (*Ursus maritimus*)

by

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Abstract

Understanding strategies for maximizing foraging efficiency is central to behavioural ecology. The theoretical optimal olfactory search is crosswind, however empirical evidence of anemotaxis (orientation to wind) among carnivores is sparse. Polar bear (*Ursus maritimus*) is a sea ice dependent species that relies on olfaction to locate prey. We examined adult female polar bear movement data, corrected for sea ice drift, from Hudson Bay, Canada, in relation to modelled winds to examine olfactory search. The predicted crosswind movement was most frequent at night during winter, when most hunting occurs. Movement was predominantly downwind during fast winds (>10 m/s), which impede olfaction. Migration during freeze-up and break-up also was correlated with wind. Lack of orientation during summer, a period with few food resources, reflects energy conservation and reduced active search. We suggest windscapes be used as a habitat feature in habitat selection models by changing what is considered available habitat. The presented methods are widely applicable to olfactory predators (e.g., canids, felids, and mustelids) and prey avoiding predators. These findings represent the first known quantitative description of anemotaxis for olfactory foraging for any large carnivore.

Preface

This thesis is original work by Ron Togunov. The research uses data acquired from GPS collars deployed by Dr. A. E. Derocher and Dr. N. J. Lunn at Environment and Climate Change Canada. Both A. E. Derocher and N. J. Lunn provided subsequent feedback on the thesis content.

Animal handling protocols that were followed received research ethics approval from the University of Alberta Animal Care and Use Committee for Biosciences, Project Name “Polar bears and Climate Change: Habitat Use and Trophic Interactions”, No. AUP00000033.

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Chapter 1

Introduction

Foraging efficiency, energy acquisition per unit time, is central to an animal's fitness (Pyke *et al.* 1977), whereby natural selection favours behaviours that maximize energy intake (Lemon 1991) while minimizing foraging time (Bergman *et al.* 2001). Foraging behaviour by predators can be classified into two broad classes: ambush predation and active search predation (Higginson & Ruxton 2015). Among ambush predators, fitness is largely determined by habitat selection (Morse & Fritz 1982; Hugie & Dill 1994). For active search predation, studies have expounded the significance of duration of patch use (Charnov 1976) and prey selection (Stein 1977), however, research on optimal search strategies among large carnivores remains sparse (Austin *et al.* 2004; Sims *et al.* 2008). Search strategies are especially important for success at large scales (Sims *et al.* 2008).

Olfactory search is common for foraging among carnivores (Gittleman 1991; Hayden *et al.* 2010). Olfactory search begins by identifying the presence of prey through odour detection, followed by odour localization (Conover 2007). In the presence of wind, odour concentration is described by the Gaussian dispersion model whereby the maximum concentration is along the horizontal axis in the direction of the wind, and mean concentration follows a normal distribution laterally and vertically (Wark & Warner 1981; Murtis 1992; Conover 2007; Cablk *et al.* 2008). The probability of detection is proportional to the odour concentration (Conover 2007), thus, a predator is more likely to detect prey when positioned directly downwind.

Traveling upwind or downwind adds the traversed distance to the area perceived through olfaction. However, traveling crosswind exposes the predator to the larger area that is upwind of its path. Therefore, the most efficient method of odour detection is to travel crosswind

(Dusenbery 1989; Conover 2007). Once detected, the predator should move upwind from the location of detection to find the source. Anemotaxis, orientation relative to wind, is well documented among insects and birds that travel crosswind when searching for an odour and upwind when localizing the source (e.g., Kennedy & Marsh 1974; Weimerskirch *et al.* 2005; Nevitt *et al.* 2008; Buehlmann *et al.* 2014). However, research on foraging of terrestrial olfactory predators is sparse (Hirsch 2010).

Polar bears (*Ursus maritimus*) exhibit both ambush and active search strategies when hunting their primary prey, ringed seal (*Pusa hispida*) and bearded seal (*Erignathus barbatus*) (Stirling 1974; Stirling & Archibald 1977; Smith 1980; Pilfold *et al.* 2012). Bears actively search for subnivean seal lairs or hauled-out seals, or ambush seals surfacing through breathing holes or along the floe edge (Stirling 1974; Smith 1980; Pilfold *et al.* 2012). To be successful, bears must first locate a potential food source. Vision alone is ineffective for locating prey from a distance, because of the rough terrain of sea ice, where pressure ridges reach a mean peak height of (Strub-Klein & Sudom 2012). In addition to vision, polar bears use olfaction to locate prey as winds carry odours across the complex icescape (Smith 1980). Olfactory bulb size is correlated with home range size among carnivores (Gittleman 1991), and polar bear home ranges are disproportionately large for their body size (Tucker *et al.* 2014). Polar bears exhibit strong responses to odours and often resort to olfactory search (Stirling & Latour 1978; Cushing 1983). Additionally, olfactory predation is presumed to underlie ringed seal haul-out behaviour; ringed seals face downwind when hauling-out, enabling them to visually detect hunting bears approaching from downwind and detect upwind bears by scent (Kingsley & Stirling 1991). Olfaction is likely important in polar bear reproductive behaviour; males assess the reproductive status of females through their footprints and locate females by tracking them (Molnár *et al.*

2008; Owen *et al.* 2015). Females with cubs, may use olfaction to avoid males due to risk of infanticide (Derocher & Stirling 1990; McCall *et al.* 2014).

Crosswind movement is likely dependent on a number of factors, including season, time of day, wind speed, and prey distribution. During summer, without access to their primary prey, polar bears prioritize energy conservation over energy acquisition and minimize unnecessary movement (Derocher & Stirling 1990; Ferguson *et al.* 2001; Rode *et al.* 2015; Rozhnov *et al.* 2015). During freeze-up, bears may favour dispersion over immediate foraging to minimize interspecific competition or, for females with dependent young, minimize risk of predation on their cubs (Derocher & Stirling 1990; McCall *et al.* 2014). Winter and spring coincide with the peak in seal pupping, during which the majority of foraging takes place and bears enter hyperphagia (Stirling & McEwan 1975). During break-up, sea-ice becomes increasingly dynamic. In areas where there is a complete seasonal melt of sea ice, bears may favour travelling against the drift to maintain their relative position (Mauritzen *et al.* 2003; Auger-Méthé *et al.* 2015) or move to shore as the cost of travelling increases (Stirling *et al.* 1999; Stirling & Parkinson 2006; Cherry *et al.* 2016). With respect to time of day, olfactory search likely increases during periods of reduced visibility. For example, nocturnal moths relied more on olfaction to locate flowers than diurnal moths of the same subfamily, which relied more on visual search (Balkenius *et al.* 2006).

Wind speed affects the concentration and distribution of odour. In slow winds, there may be insufficient directionality to assess the source of an odour, thus, bears may move independently of the wind direction. Fast winds dilute the initial concentration of the odour and decrease the detectable distance of the odour plume (Nakamura 1976; Conover 2007; Cablk *et*

al. 2008). Additionally, increased turbulence at high wind speeds impedes odour localization (Sabelis & Schippers 1984).

We used adult female polar bear GPS-based telemetry location data and modelled surface windscares to examine the significance olfaction plays in movement patterns. We hypothesized that polar bears move crosswind during olfactory search, and that this would be more common during winter, at night, and under moderate wind speeds.

Methods

Hudson Bay, Canada is a large inland sea, which covers an area of $83 \times 10^4 \text{ km}^2$ (Figure 1) (Prinsenbergh 1984) and is seasonally ice-free (Saucier *et al.* 2004). From January to early May, the Bay is covered by both fast ice (connected to shore or sea bottom) and drifting pack ice (Danielson 1971). During ice break-up (early July), the motile ice drifts south following the anticlockwise gyre (Gough *et al.* 2004) and northwesterly winds (Etkin 1991).

As part of a study of the population ecology of polar bears in western Hudson Bay (e.g., Ramsay & Stirling 1988; Stirling *et al.* 1999; Regehr *et al.* 2007), polar bears were captured in summers 2004-2014. They were located and captured from helicopters (Stirling *et al.* 1989) and a sample of females with offspring were fitted with Argos® satellite-linked global positioning system (GPS) collars (Telonics, Mesa, AZ). Animal handling protocols were approved by the University of Alberta Animal Care and Use Committee for Biosciences and by the Environment Canada Prairie and Northern Region Animal Care Committee.

A total of 123 collars were deployed (9-15 per year); most (120) obtained one location every 4 hours, whereas 3 obtained locations every 30 minutes and were analyzed separately. Collars were programmed to last 2 years and had remote release mechanisms to drop them. The

latitude and longitude coordinates were converted into Universal Trans Mercator coordinate system (NAD83 Teranet Ontario Lambert, EPSG: 5321) in R version 3.2 (R Core Team 2016).

Surface wind speeds and directions were modelled by the National Center for Environmental Prediction (NCEP) and obtained from the NOAA Operational Model Archive and Distribution System (NOMADS) (<http://nomads.ncdc.noaa.gov/data/gfsanl/>) (Bowman & Lees 2015). Validating the modelled wind was not possible, because weather station observations around Hudson Bay are used to initialize the model. However, biases in the wind estimates were identified by comparing model outputs to empirical wind measured at the Churchill Airport, Manitoba (58.74° N, 94.07° W). Historical wind data at six hour intervals were obtained from Government of Canada (<http://climate.weather.gc.ca/> accessed on October 15, 2015).

NCEP generates gridded wind estimates at 6 hour intervals at 1° resolution. To maximise the fit of the wind data to the movement data, only locations ≤ 4 hours apart were used. As the times and coordinates of both wind and movement data were not synchronized, wind data were spatially and temporally interpolated to match bear locations. First, the wind was spatially interpolated to the location of the bear using inverse distance weighting both before and after the time of a bear location (Li & Heap 2011). Because wind estimates are both uniformly distributed in space (across a 1° grid) and have low resolution, the four wind estimates adjacent to the bear's location were used. Second, the two spatial estimates were linearly interpolated to match the time of the location.

While on the sea ice, a portion of a bear's absolute displacement is involuntary and driven by ice (Mauritzen *et al.* 2003; Auger-Méthé *et al.* 2015). Thus, to study voluntary movement related to wind-driven foraging, the component ice drift was subtracted from the location data following Auger-Méthé *et al.* (2015). Ice drift data (Polar Pathfinder Daily 25 km

EASE-Grid Sea Ice Motion Vectors) were acquired from the National Snow and Ice Data Center (Fowler *et al.* 2013). Ice drift was spatially interpolated using inverse distance weighting to match the polar bear locations (Li & Heap 2011). Vector decomposition, calculation of voluntary bear movement, calculations of angle between GPS displacement relative to north, and calculation of angle of voluntary polar bear movement relative to wind bearing are depicted in Figure 2.

As habitat characteristics change over the year, and likely influence optimal foraging behaviour, we followed McCall *et al.* (2014) and analyzed data separately by season: summer (on-land locations June 1 - October 31), autumn (on-land locations November 1 - 30), freeze-up (offshore locations November 1 - December 31), winter (offshore locations January 1 - June 30), and break-up (offshore locations July 1 - August 31).

As wind velocity plays a role in olfactory foraging efficiency, the data were subdivided into “slow” and “fast” wind categories. However, because we had no *a priori* threshold for wind speed at which behaviours change, we tested a moving threshold between 2 m/s and 16 m/s. To differentiate polar bear behaviours, at-rest data (< 10 m/h) were excluded, and remaining movement data were divided into “slow” and “fast” bear speeds at thresholds between 0.5 km/h and 7 km/h between successive locations. True bear velocities are greater than the mean between successive locations as any deviations from the straight line path or variable velocities between successive locations are not captured (Rowcliffe & Carbone 2012). For each season, data were grouped into one of four categories: (1) slow wind and slow bears, (2) fast wind and slow bears, (3) slow wind and fast bears, and (4) fast wind and fast bears. Because of the moving thresholds of wind and bear speeds, each movement datum was analyzed within each wind/bear speed category.

To test whether there was a diurnal behavioural pattern, sunrise and sunset times were determined for each coordinate using the ‘sunriseset’ function of ‘maptools’ package in R (Lewin-Koh & Bivand 2013). “Day” and “night” were defined by the sun being above or below the horizon, respectively, relative to each location.

Predominant bear direction relative to wind direction was assessed using χ^2 tests. Following Spear and Ainley (1997), data were binned into one of five directions: (1) tail winds ($<25^\circ$ between bear and wind bearings), (2) cross-tail winds ($\geq 25^\circ$ & $<65^\circ$), (3) cross-wind ($\geq 65^\circ$ & $<115^\circ$), (4) cross-head winds ($\geq 115^\circ$ & $<155^\circ$), (5) and head winds ($\geq 155^\circ$ & $\leq 180^\circ$). Under the null hypothesis that bear direction is random with respect to wind direction, the expected ratio among the categories would be 5:8:10:8:5, respectively. To control for multiple tests of each data point, a Bonferroni adjustment was made (statistical significance = 0.0006; based on 7 wind speed and 12 bear speed thresholds). If a set of data was statistically significant, adjusted standardized residuals were calculated to identify which directionality had disproportionately more data points.

Means of unimodal distributions were calculated using the ‘mean.circular’ function from ‘circular’ package in R. The two means of bimodal distributions were calculated using the ‘movMF’ package in R which fits two von Mises-Fisher distributions using maximum likelihood (Hornik & Grün 2014).

Results

Wind model validation

NCEP-modelled wind was a mean 10° anticlockwise to the measured wind bearing at Churchill airport, however, 58% of modelled wind was within $\pm 25^\circ$ of the bearing measured at

the airport (Figure 3). Additionally, NCEP tended to overestimate wind speeds <4.2 m/s and underestimate winds above this speed (Figure 4).

The bears were exposed to primarily northwesterly winds with mean direction of 134° (SE) (Figure 4). At the locations on ice, there was a significant association between the angles of ice drift and modelled wind bearing (Rayleigh test, $P < 0.0001$, $z = 0.45$), with ice-drift averaging 100° clockwise to the wind bearing (Figure 6).

Geographic movement

During summer, bears exhibited marginal bidirectionality with modes around -152° (SSW) and 15° (NNE) (Figure 7a). During autumn, predominant movement was 0° (N), with northward movements nearly three times more frequent than eastward, westward, or southward movements (Figure 7b). During freeze-up, predominant movement was 84° (E) (Figure 7c). Winter and break-up movement exhibited bimodal distributions with modes around -33° (NNE) and 152° (SSE) (Figure 7d and e).

Contribution of ice-drift to displacement

During freeze-up and winter, when bears were moving slowly (<2 km/h) or when wind was fast (>10 m/s), directionality was unimodal with the mean displacement 20° relative to the wind bearing (Figure 8a). Movement with the component of ice-drift removed was a mean -2° relative to the wind bearing (Figure 8b). We expected polar bears to generally travel symmetrically to the wind (i.e., not have a preference between traveling left or right of wind). As movement with ice-drift removed deviated less from symmetry than without ice-drift removed (Figure 8), all subsequent analyses were based on movement with the component of ice-drift removed.

Movement relative to wind

Predominant directionality of the bears was crosswind during summer and autumn regardless of wind or bear speeds (Table 1 and Table 2). While winds were slow (<10 m/s) and polar bear speeds were slow (<2 km/h), the two modes of summer movement were at 94° and -90° relative to the wind bearing (Figure 9a). During autumn, the two modes were at 79° and -85° relative to the wind, with the latter was more frequent (Figure 9b). Although the directionality was significantly different from the null (summer, $\chi^2 = 42.4$, $P < 0.0001$; autumn, $\chi^2 = 68.2$, $P < 0.0001$), bear directionality was more strongly associated with absolute direction than with wind bearing (Figure 7a and b vs. Figure 9).

During freeze-up, the predominant directionality of the bears relative to wind was linked to polar bear and wind speeds. Slower bear movements (<2 km/h) were predominantly tailwind (Table 3; Figure 10a, $\chi^2 = 3942$, $P < 0.0001$). Fast polar bear movements exhibit more crosswind movement than slower movements (Table 3; Figure 10b). Where polar bear speeds were fast (>2 km/h) and winds slow (<6 m/s), movements were predominantly crosswind (Figure 10b) with modes at 90° and -100° relative to the wind ($\chi^2 = 76.8$, $P < 0.0001$), however, only 8% (n = 882) of the freeze-up data fell into this group. Figure 11a; mode = -1°, $\chi^2 = 8582$, $P < 0.0001$). Fast (>4 km/h) polar bear movements while wind was slow (<10 m/s) were predominantly crosswind (Table 4; Figure 11b; mode₁ = 81°, mode₂ = -102°, $\chi^2 = 275$, $P < 0.0001$). Dividing the fast bear and slow wind data into day and night revealed a circadian pattern, with more nocturnal crosswind movement than during the day (Figure 11c and d). As with the 4-hour collars, 30-minute collars exhibited predominantly downwind movement during slow bear movement or under fast winds (Table 5; Figure 11e; mode = -3°, $\chi^2 = 649$, $P < 0.0001$), whereas fast bear movements under slow winds were predominantly crosswind (Table 5; Figure 11f; mode₁ = 90°,

mode₂ = -109°, $\chi^2 = 113$, $P < 0.0001$). For the 4-hour collars, 10% of winter data fell into the ‘slow wind and fast bear’ category, compared to 26% of the 30-minute winter data.

During ice break-up, polar bear movements were predominantly cross-tailwinds with a unimodal directionality of 34° relative to the wind, regardless of collar frequency or bear or wind speeds (Table 5; Figure 12; $\chi^2 = 89$, $P < 0.0001$).

Discussion

We observed polar bear movement patterns that were associated with season, presence of daylight, and both wind and bear speed. Seasons vary in food distribution and habitat conditions (Derocher *et al.* 1993; Gormezano & Rockwell 2013; Rode *et al.* 2015). As food abundance and distribution change and as energetic cost of foraging change, different foraging behaviours may be optimal (Derocher & Stirling 1990; Ferguson *et al.* 2001; Beyer *et al.* 2010; Sims *et al.* 2012). Within any season, wind speed can influence the effectiveness of olfactory search. Higher wind speeds decrease the concentration of odour in the air and are thus unfavourable for search (Conover 2007; Cablk *et al.* 2008). In addition, bear speed might reflect different behaviours, only some of which are wind-associated olfactory foraging (Stirling 1974). Other behaviours such as travel between patches, migration, rest, mating, or visual search likely exhibit different relationships with wind than olfactory search.

Distinguishing between different behaviours is complicated by delineating biologically significant seasons and by the resolution and accuracy of the wind model, ice drift estimation, and frequency of polar bear locations. NCEP-modelled wind is initialized using data from weather stations and the accuracy of the model cannot be directly determined. NCEP tends to overestimate low wind speeds and underestimate high wind speeds (Figure 4); however, relative

wind speed is sufficient for identifying wind speed-dependant foraging. Although the modelled wind direction was a mean 10° left of measured direction (Figure 3), it falls within the bin sizes used in the χ^2 tests ($\pm 25^\circ$ or $\pm 20^\circ$, depending on directionality). The 4-hour resolution of the location data can only capture sustained movement, masking short-term responses to wind, such as upwind localization of a detected odour. Despite the inherent challenges and limitations of studying animals with vast and remote ranges, we observed several wind- and season-associated behaviours.

In Hudson Bay, terrestrial foraging is primarily limited to berries, seaweed, vegetation, bird eggs, and animal remains (Derocher *et al.* 1993; Rockwell & Gormezano 2009; Gormezano & Rockwell 2013) but the energetic gains are minimal (Rode *et al.* 2015; Pilfold *et al.* 2016a). Because these food sources are not as energetically dense as seal fat, polar bears prioritize energy conservation over energy acquisition by reducing unnecessary movement (Derocher & Stirling 1990; Ferguson *et al.* 2001; Rozhnov *et al.* 2015). We found a weak (though significant) association between bear movement and wind during summer, suggesting that olfactory search is either reduced or absent during this season (Figure 9a). We found a similar bimodal distribution in summer movement relative to north, with bears tending to move north or south (Figure 7a). Any movement during the summer would be constrained by the shoreline, which generally extends north-south (Figure 1). Because of the predominantly northwesterly winds (Figure 5), random movement confined by the shoreline would also be roughly crosswind. Thus, the crosswind movement we observed may be an artefact of the landscape rather than a response to wind.

Freeze-up begins in the northwest of Hudson Bay (Gagnon & Gough 2005). By moving northwards during the months leading up to freeze-up, bears are able to return to the sea ice

sooner. The northward movement we observed during autumn (Figure 7b) may be an example of polar bears' migratory behaviour in anticipation of freeze-up (Derocher & Stirling 1990).

Polar bears traveled predominantly downwind during freeze-up (Figure 10a), which leads polar bears east towards the centre of the Bay (Figure 7c). If the bears were guided by celestial or global cues (such as solar position or global magnetism) (Brillinger & Stewart 1998; Mauritzen *et al.* 2003), we would expect the movement to have a stronger association relative to north than relative to wind, which did not appear to be the case (Figure 7c vs Figure 10a). In addition to following the southeastward advancing sea ice, we suggest the movement may be partly guided by wind. As intraspecific competition affects polar bear distribution (Pilfold *et al.* 2014), the focus of the bears during freeze-up may be to disperse throughout the Bay and away from conspecifics. Females avoid males due to the threat of infanticide (Stirling *et al.* 1993; McCall *et al.* 2014) so the pattern of dispersal may be specific to such risks.

We observed crosswind movement during freeze-up, however only at particularly slow winds and high bear speeds (Figure 10b). Because predominant crosswind movement during freeze-up was found only at lower wind speeds (<6 m/s) compared to winter (<10 m/s) (Table 3), it may suggest that some foraging during freeze-up might only occur if conditions are advantageous.

During winter, at high wind speeds or when polar bears were moving slowly (i.e., when olfaction is not optimal or polar bears are not engaged in active search) movement was predominantly downwind (Figure 11a). We propose several explanations for the downwind movement. First, downwind movement during winter may represent a default orientation that generally leads bears southeast further into the Bay. Second, it may be a thermoregulatory response to high wind speeds, which minimises the surface area exposed to wind and shields the

face. Thermoregulatory downwind orientation has been modelled and observed for several taxa (e.g., Skjenneberg & Slagsvold 1968; Timisjärvi *et al.* 1984; Gebremedhin 1987; DeMatteo & Harlow 1997). Third, if wind direction fluctuates more than 30° from the mean, then upwind or downwind movement would provide more information about the environment than crosswind movement, a phenomenon described as the geometric pattern of scent dispersion (Sabelis & Schippers 1984). However, the geometric pattern of scent dispersion alone cannot account for the low frequency of upwind movement observed. Fourth, behaviours apart from olfactory search, such as travel, still-hunting, and movement following habitat features, may tend to be downwind. Non-olfactory behaviours (not including travel) occupy around 60% of polar bears' time budget (Stirling 1974; Stirling & Latour 1978; Stirling *et al.* 2016). The large frequency of downwind movement, particularly under moderate wind speeds, was not predicted. Examining other populations and their response to wind could illuminate the selective advantage of downwind movement.

During winter, at low wind speeds and while polar bear speed was high, movement was predominantly crosswind (Figure 11b), matching our predicted movement for olfactory search. If the crosswind movement during freeze-up and winter is a product of olfactory search, the greater frequency at lower wind speeds aligns with findings that polar bear hunting success increases with decreasing wind speed (Pilfold *et al.* 2015). Crosswind movement was also more common at night than during the day (Figure 11c vs. d), supporting our hypothesis that movement is primarily guided by olfaction during periods of darkness, while movement during the day may rely, in part, on visual cues. Crosswind movement was also more frequent among bears wearing 30-minute collars than those wearing 4-hour collars (Figure 11b vs. f). Additionally, the proportion of 30-minute data in the slow wind and fast bear category was 2.6

times greater than among 4-hour collars, suggesting that lower resolution collars underestimate the proportion of crosswind movement, and that the behaviour is more common than we observed.

An alternative explanation for crosswind movement is that it is a response to environmental features that are associated with the predominant winds, such as pressure ridges (Parmerter & Coon 1972). However, environmental features cannot explain the association between directionality and wind speed, as exhibited during freeze-up and winter. For example, the presence of pressure ridges is independent of wind speed, while crosswind movement was dependent on wind speed.

During break-up, mean polar bear movement was 34° relative to the wind (Figure 12). With the predominant northwesterly winds, this would take the bears southeast towards shore and following the direction of the retreating ice. However, the movement relative to north shows a large component of northwestward movement (Figure 7e). As the season progresses and sea ice melts, polar bears may spend increasingly more time swimming, during which collars cannot transmit locations (Pagano *et al.* 2012; Pilfold *et al.* 2016b). As such, limiting analysis to only 4-hour collars does not capture the complete range of behaviours, especially during break-up.

We hypothesized that polar bears move crosswind during olfactory predation and predicted crosswind movement would occur most often during winter, when polar bears enter hyperphagia (Ramsay & Stirling 1988; Messier *et al.* 1992), under moderate wind speeds, when foraging is optimal (Van Eerden & Voslamber 1995; Conover 2007; Pilfold *et al.* 2015), and at night, when olfaction may be more effective to visual search (Balkenius *et al.* 2006). The observed crosswind movement during winter in the Hudson Bay population generally supports our hypotheses and predictions. Olfactory foraging may vary across populations due to patterns

of sea ice distribution. Does maintenance of relative position on drifting ice (e.g., Mauritzen *et al.* 2003; Auger-Méthé *et al.* 2015) come at the expense of prolonged olfactory search? Polar bears on more stable ice may be less active than polar bears on drifting ice (Ferguson *et al.* 2001) - what is the role of olfaction in such stable habitats? Arctic wind speeds are projected to increase due to climate change (McInnes *et al.* 2011) and could impede polar bear hunting success, which decreases with increasing wind speed (Pilfold *et al.* 2015). Further studies using higher temporal resolution location data, in combination with direct observation of active predators or kill sites, would further our understanding of olfactory predation. Additionally, given its influence on behaviour, wind could be incorporated as a habitat characteristic in habitat selection modelling of olfactory predators, as the quality of a habitat may be dependent on windscares. In practice, windscares could be used as modifiers to the “available habitat” (e.g., fast winds invoke downwind movement, while crosswind movement would be favoured under moderate winds). To our knowledge, this is the first such evidence of crosswind orientation for olfactory search for any wild non-avian carnivore. The methods presented here are widely applicable and can provide insight on olfactory search among predators across taxa and prey avoiding predators.

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Tables

The following section contains six tables presenting analysis of significant directionality among movement data divided by wind speed and bear speed at different respective velocities. Each table represents one season and is further subset into four sub-tables that represent: 1) slow wind and slow bear, 2) fast wind and slow bear, 3) slow wind and fast bear, and 4) fast wind and fast bear. Each cell represents the significant directionality of data as or more extreme than the cut-off wind and bear speeds. For example a cell in the second sub-table (fast wind and slow bear) represents the directionality of all the data faster than the wind threshold and slower than the bear threshold. Only statistically significant (alpha value = 0.0006, chi-square) cells are colour-coded and present the directionality.

To aid in understanding, it is suggested that readers note the dominant colours of the cells in each sub-table to identify key biological patterns.

Table 2. Analysis of bear directionality relative to wind sensitivity to wind and bear speed thresholds during autumn. Greatest adjusted standardized residuals identify dominant directionality: T, tailwind; CT, cross tailwind; C, crosswind; CH, cross headwind; H, headwind; NA, no data; -, not significant (alpha value = 0.0006, chi-square).

Autumn		Limit to data with wind < 'x' m/s							Limit to data with wind > 'x' m/s							
		x	3	5	7	9	11	13	15	x	3	5	7	9	11	13
Limit to data with polar bear speed < 'x' km/h	0.5	-	-	C	C	C	C	C	0.5	C	CT	-	-	-	-	-
	1	-	C	C	C	C	C	C	1	C	CT	-	CT	-	-	-
	1.5	-	C	C	C	C	C	C	1.5	C	C	C	CT	-	-	-
	2	-	C	C	C	C	C	C	2	C	C	-	CT	-	-	-
	2.5	-	C	C	C	C	C	C	2.5	C	C	-	T	-	-	-
	3	-	C	C	C	C	C	C	3	C	C	-	T	-	-	-
	3.5	-	C	C	C	C	C	C	3.5	C	C	-	T	-	-	-
	4	-	C	C	C	C	C	C	4	C	C	-	T	-	-	-
	4.5	-	C	C	C	C	C	C	4.5	C	C	-	T	-	-	-
	5	-	C	C	C	C	C	C	5	C	C	-	T	-	-	-
	5.5	-	C	C	C	C	C	C	5.5	C	C	-	T	-	-	-
6	-	C	C	C	C	C	C	6	C	C	-	T	-	-	-	
Limit to data with polar bear speed > 'x' km/h	x	3	5	7	9	11	13	15	x	3	5	7	9	11	13	15
	0.5	-	C	C	C	C	C	C	0.5	C	C	-	-	-	-	-
	1	-	-	C	C	C	C	C	1	C	C	-	-	-	-	NA
	1.5	-	-	-	-	-	-	-	1.5	-	-	-	-	-	-	NA
	2	-	-	-	-	-	-	-	2	-	-	-	-	-	-	NA
	2.5	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	NA
	3	-	-	-	-	-	-	-	3	-	-	-	-	-	-	NA
	3.5	-	-	-	-	-	-	-	3.5	-	-	-	-	NA	NA	NA
	4	NA	-	-	-	-	-	-	4	-	-	-	-	NA	NA	NA
	4.5	NA	-	-	-	-	-	-	4.5	-	-	-	-	NA	NA	NA
	5	NA	-	-	-	-	-	-	5	-	-	NA	NA	NA	NA	NA
5.5	NA	-	-	-	-	-	-	5.5	-	-	NA	NA	NA	NA	NA	
6	NA	NA	-	-	-	-	-	6	-	-	NA	NA	NA	NA	NA	

Table 3. Analysis of bear directionality relative to wind sensitivity to wind and bear speed thresholds during freeze-up. Greatest adjusted standardized residuals identify dominant directionality: T, tailwind; CT, cross tailwind; C, crosswind; CH, cross headwind; H, headwind; NA, no data; -, not significant (alpha value = 0.0006, chi-square).

Freeze-up		Limit to data with wind < 'x' m/s							Limit to data with wind > 'x' m/s							
		x	3	5	7	9	11	13	15	x	3	5	7	9	11	13
Limit to data with polar bear speed < 'x' km/h	0.5	-	T	T	T	T	T	T	0.5	T	T	T	-	-	-	-
	1	-	T	T	T	T	T	T	1	T	T	T	T	-	-	-
	1.5	-	T	T	T	T	T	T	1.5	T	T	T	T	T	-	-
	2	-	T	T	T	T	T	T	2	T	T	T	T	T	T	-
	2.5	-	T	T	T	T	T	T	2.5	T	T	T	T	T	T	-
	3	-	T	T	T	T	T	T	3	T	T	T	T	T	T	-
	3.5	-	T	T	T	T	T	T	3.5	T	T	T	T	T	T	T
	4	-	T	T	T	T	T	T	4	T	T	T	T	T	T	T
	4.5	-	T	T	T	T	T	T	4.5	T	T	T	T	T	T	T
	5	-	T	T	T	T	T	T	5	T	T	T	T	T	T	T
5.5	-	T	T	T	T	T	T	5.5	T	T	T	T	T	T	T	
6	-	T	T	T	T	T	T	6	T	T	T	T	T	T	T	
Limit to data with polar bear speed > 'x' km/h	0.5	-	T	T	T	T	T	T	0.5	T	T	T	T	T	T	T
	1	CH	C	CT	T	T	T	T	1	T	T	T	T	T	T	T
	1.5	C	C	C	T	T	T	T	1.5	T	T	T	T	T	T	T
	2	C	C	C	C	T	T	T	2	T	T	T	T	T	T	T
	2.5	-	C	C	C	CT	T	T	2.5	T	T	T	T	T	T	T
	3	-	C	C	C	CT	CT	CT	3	CT	CT	CT	T	T	T	T
	3.5	-	-	-	CT	CT	CT	CT	3.5	CT	CT	CT	CT	CT	T	T
	4	-	-	-	CT	CT	CT	CT	4	CT	CT	CT	CT	T	T	T
	4.5	-	-	-	-	CT	CT	CT	4.5	CT	CT	CT	CT	T	T	-
	5	-	-	-	-	-	-	-	5	CT	-	CT	CT	CT	-	-
5.5	-	-	-	-	-	-	-	5.5	-	-	-	-	-	-	-	
6	-	-	-	-	-	-	-	6	-	-	-	-	-	NA	NA	

Table 4. Analysis of bear directionality relative to wind sensitivity to wind and bear speed thresholds during winter. Greatest adjusted standardized residuals identify dominant directionality: T, tailwind; CT, cross tailwind; C, crosswind; CH, cross headwind; H, headwind; NA, no data; -, not significant (alpha value = 0.0006, chi-square).

Winter		Limit to data with wind < 'x' m/s							Limit to data with wind > 'x' m/s								
		x	3	5	7	9	11	13	15	x	3	5	7	9	11	13	15
Limit to data with polar bear speed < 'x' km/h	0.5		T	T	T	T	T	T	T	0.5	T	T	T	T	T	-	-
	1		CT	T	T	T	T	T	T	1	T	T	T	T	T	T	-
	1.5		CT	T	T	T	T	T	T	1.5	T	T	T	T	T	T	T
	2		-	T	T	T	T	T	T	2	T	T	T	T	T	T	T
	2.5		-	T	T	T	T	T	T	2.5	T	T	T	T	T	T	T
	3		-	T	T	T	T	T	T	3	T	T	T	T	T	T	T
	3.5		-	T	T	T	T	T	T	3.5	T	T	T	T	T	T	T
	4		-	T	T	T	T	T	T	4	T	T	T	T	T	T	T
	4.5		-	T	T	T	T	T	T	4.5	T	T	T	T	T	T	T
	5		-	T	T	T	T	T	T	5	T	T	T	T	T	T	T
5.5		-	T	T	T	T	T	T	5.5	T	T	T	T	T	T	T	
6		-	T	T	T	T	T	T	6	T	T	T	T	T	T	T	
Limit to data with polar bear speed > 'x' km/h	0.5		C	C	T	T	T	T	T	0.5	T	T	T	T	T	T	T
	1		C	C	C	C	T	T	T	1	T	T	T	T	T	T	T
	1.5		C	C	C	C	C	C	C	1.5	C	T	T	T	T	T	T
	2		CH	C	C	C	C	C	C	2	C	C	CT	T	T	T	T
	2.5		-	C	C	C	C	C	C	2.5	C	C	CT	CT	T	T	T
	3		-	-	C	C	C	C	C	3	CT	CT	CT	CT	T	T	-
	3.5		-	-	C	C	C	C	C	3.5	CT	CT	CT	T	T	T	-
	4		-	-	-	C	T	T	T	4	T	CT	T	T	T	T	-
	4.5		-	-	-	-	T	T	T	4.5	T	CT	T	T	T	-	-
	5		-	-	-	-	-	T	T	5	T	T	T	-	-	-	-
5.5		-	-	-	-	-	-	-	5.5	-	-	-	-	-	-	NA	
6		-	-	-	-	-	-	-	6	-	-	-	-	-	-	NA	

Table 5. Analysis of bear directionality relative to wind sensitivity to wind and bear speed thresholds during break-up. Greatest adjusted standardized residuals identify dominant directionality: T, tailwind; CT, cross tailwind; C, crosswind; CH, cross headwind; H, headwind; NA, no data; -, not significant (alpha value = 0.0006, chi-square).

Break-up	Limit to data with wind < 'x' m/s								Limit to data with wind > 'x' m/s							
	x	3	5	7	9	11	13	15	x	3	5	7	9	11	13	15
Limit to data with polar bear speed < 'x' km/h	0.5	-	-	-	CT	CT	CT	CT	0.5	-	CT	-	-	-	NA	NA
	1	-	-	CT	CT	CT	CT	CT	1	CT	CT	CT	-	-	-	NA
	1.5	-	-	T	CT	CT	CT	CT	1.5	CT	CT	CT	T	-	-	NA
	2	-	-	T	CT	CT	CT	CT	2	CT	CT	CT	CT	-	-	-
	2.5	-	-	T	CT	T	T	CT	2.5	CT	CT	CT	CT	-	CT	-
	3	-	-	T	CT	T	T	CT	3	CT	CT	CT	CT	-	CT	-
	3.5	-	-	T	CT	CT	CT	CT	3.5	CT	CT	CT	CT	-	CT	-
	4	-	-	T	CT	CT	CT	CT	4	CT	CT	CT	CT	-	CT	-
	4.5	-	-	T	CT	CT	CT	CT	4.5	CT	CT	CT	CT	-	CT	-
	5	-	-	T	CT	T	CT	CT	5	CT	CT	CT	CT	-	CT	-
5.5	-	-	T	CT	T	T	CT	5.5	CT	CT	CT	CT	-	CT	-	
6	-	-	T	CT	T	T	CT	6	CT	CT	CT	CT	-	CT	-	
Limit to data with polar bear speed > 'x' km/h	0.5	-	-	T	T	T	T	T	0.5	T	CT	CT	CT	CT	CT	-
	1	-	-	-	T	T	T	T	1	T	CT	CT	CT	CT	CT	-
	1.5	-	-	-	-	-	-	-	1.5	T	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-
	2.5	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	3	-	-	-	-	-	NA	NA
	3.5	-	-	-	-	-	-	-	3.5	-	-	-	-	-	NA	NA
	4	-	-	-	T	-	-	-	4	-	-	-	-	-	NA	NA
	4.5	-	-	-	-	-	-	-	4.5	-	-	-	-	-	NA	NA
	5	-	-	-	-	-	-	-	5	-	-	-	-	-	NA	NA
5.5	-	-	-	-	-	-	-	5.5	-	-	-	-	-	NA	NA	
6	-	-	-	-	-	-	-	6	-	-	-	-	-	NA	NA	

Table 6. Analysis of bear directionality relative to wind sensitivity to wind and bear speed thresholds during winter for collars transmitting at 30 minutes. Greatest adjusted standardized residuals identify dominant directionality: T, tailwind; CT, cross tailwind; C, crosswind; CH, cross headwind; H, headwind; NA, no data; -, not significant (alpha value = 0.0006, chi-square).

Winter		Limit to data with wind < 'x' m/s							Limit to data with wind > 'x' m/s							
		x	3	5	7	9	11	13	15	x	3	5	7	9	11	13
Limit to data with polar bear speed < 'x' km/h	0.5	-	T	T	T	T	T	T	0.5	T	T	T	-	-	NA	NA
	1	-	T	T	T	T	T	T	1	T	T	T	T	T	T	NA
	1.5	-	T	T	T	T	T	T	1.5	T	T	T	T	T	T	NA
	2	-	T	T	T	T	T	T	2	T	T	T	T	T	T	NA
	2.5	-	T	T	T	T	T	T	2.5	T	T	T	T	T	T	NA
	3	-	T	T	T	T	T	T	3	T	T	T	T	T	T	NA
	3.5	-	T	T	T	T	T	T	3.5	T	T	T	T	T	T	NA
	4	-	T	T	T	T	T	T	4	T	T	T	T	T	T	NA
	4.5	-	T	T	T	T	T	T	4.5	T	T	T	T	T	T	NA
	5	-	T	T	T	T	T	T	5	T	T	T	T	T	T	NA
	5.5	-	T	T	T	T	T	T	5.5	T	T	T	T	T	T	NA
	6	-	T	T	T	T	T	T	6	T	T	T	T	T	T	NA
Limit to data with polar bear speed > 'x' km/h	0.5	-	-	T	T	T	T	T	0.5	T	T	T	T	T	T	NA
	1	-	CH	C	C	C	C	C	1	C	C	T	T	T	T	NA
	1.5	-	CH	C	C	C	C	C	1.5	C	C	C	T	T	T	NA
	2	H	CH	C	C	C	C	C	2	C	C	C	T	T	T	NA
	2.5	H	C	C	C	C	C	C	2.5	C	C	C	-	T	T	NA
	3	H	CH	C	C	C	C	C	3	C	C	C	-	-	NA	NA
	3.5	H	-	C	C	C	C	C	3.5	C	C	C	-	-	NA	NA
	4	H	-	-	-	C	-	-	4	C	C	C	-	-	NA	NA
	4.5	H	-	-	-	-	-	-	4.5	-	-	-	-	-	NA	NA
	5	H	-	-	-	-	-	-	5	-	-	-	-	-	NA	NA
	5.5	H	-	-	-	-	-	-	5.5	-	-	-	-	-	NA	NA
	6	H	-	-	-	-	-	-	6	-	-	-	-	-	NA	NA

Figures

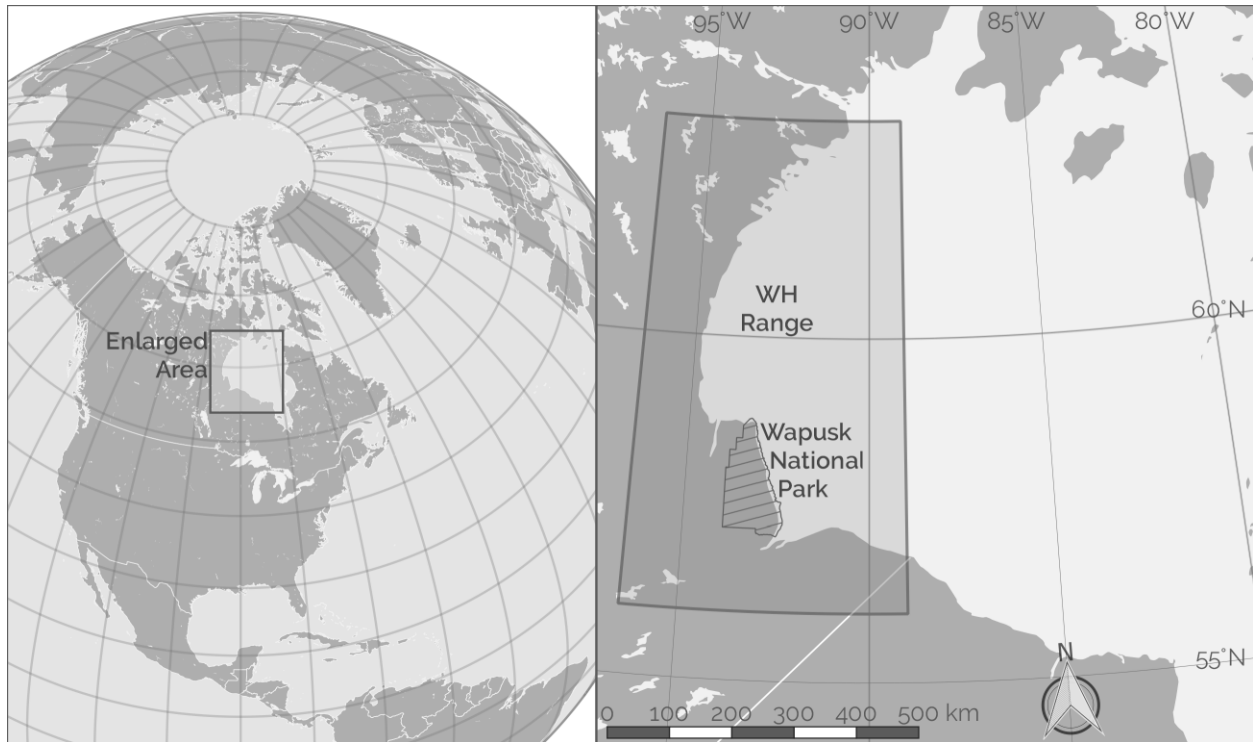


Figure 1. Study area in Hudson Bay, Canada. Shaded area represents the population boundary of western Hudson Bay (WH) polar bears.

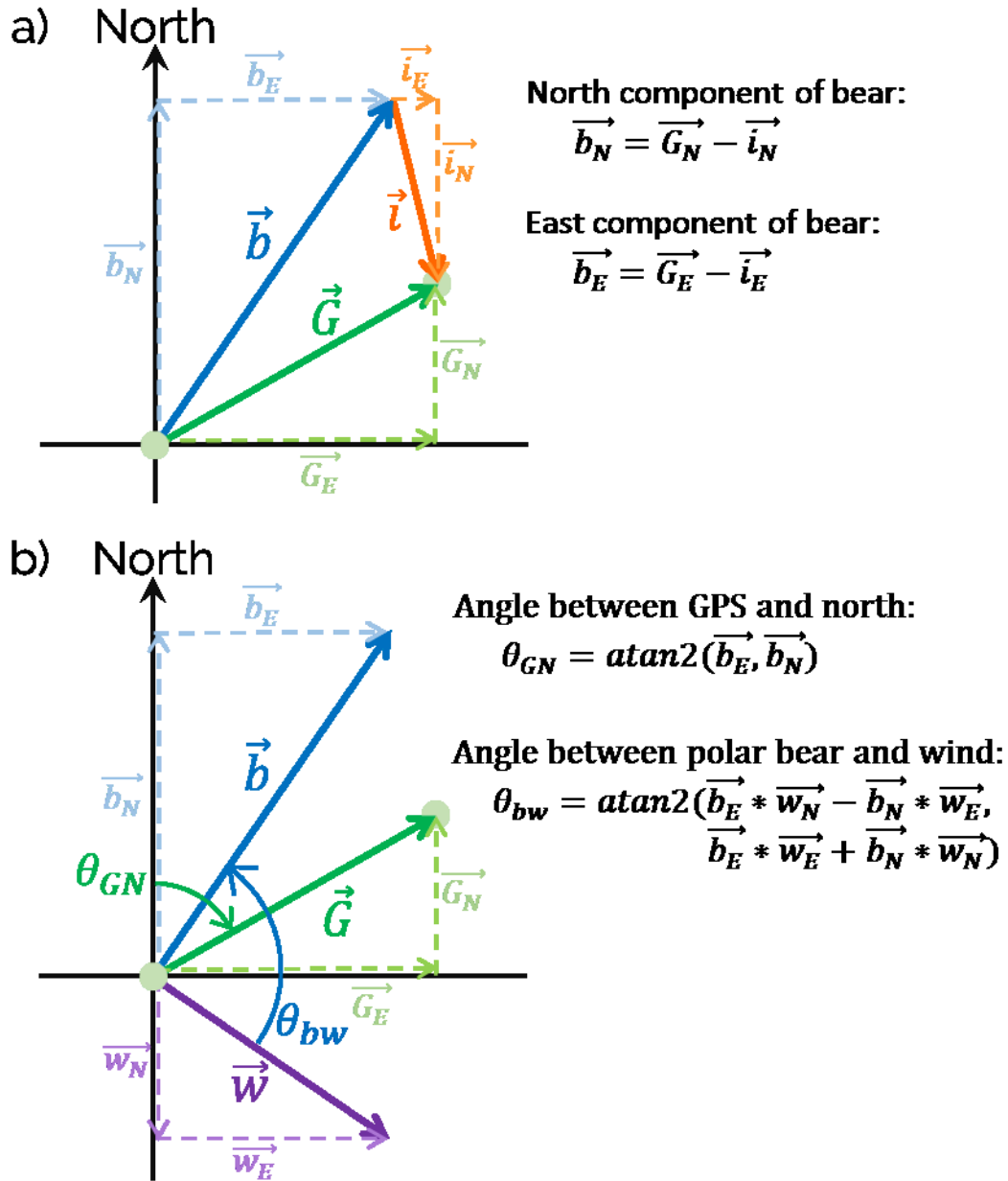


Figure 2. Schematic (a) depicts vector decomposition into easting (subscript “E”) and northing (subscript “N”), and calculation of voluntary bear movement (\vec{b}) by subtracting ice drift (\vec{i}) from GPS displacement (\vec{G}). Schematic (b) depicts calculation of angle between GPS displacement and north (θ_{GN}), and calculation of angle between voluntary bear movement and wind bearing (\vec{w} ; θ_{bw}). Note: atan2 function was performed in R version 3.2 (R Core Team 2016), other languages may take arguments in reverse order (e.g., Microsoft Excel).

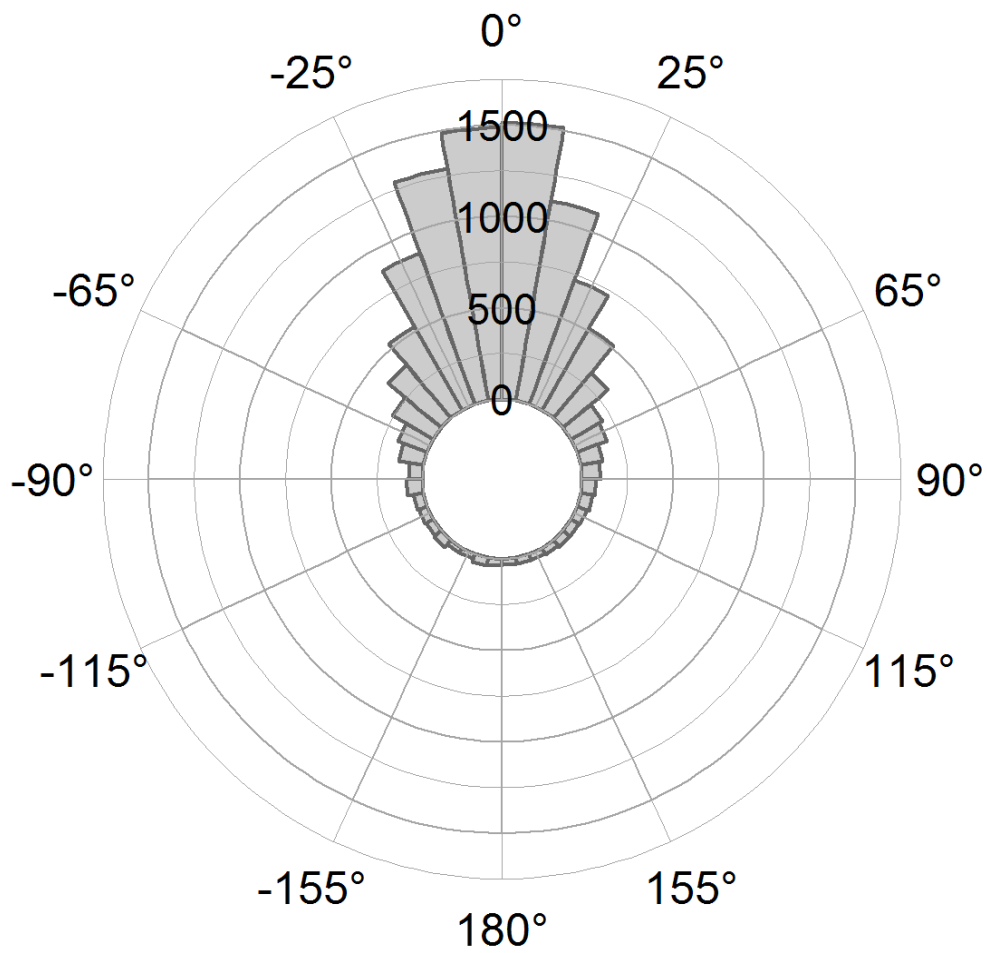


Figure 3. Frequency plot of angle between modelled wind bearings by NCEP versus measured wind vectors at Churchill airport between September 1, 2004 and April 12, 2012 (n = 11,010).

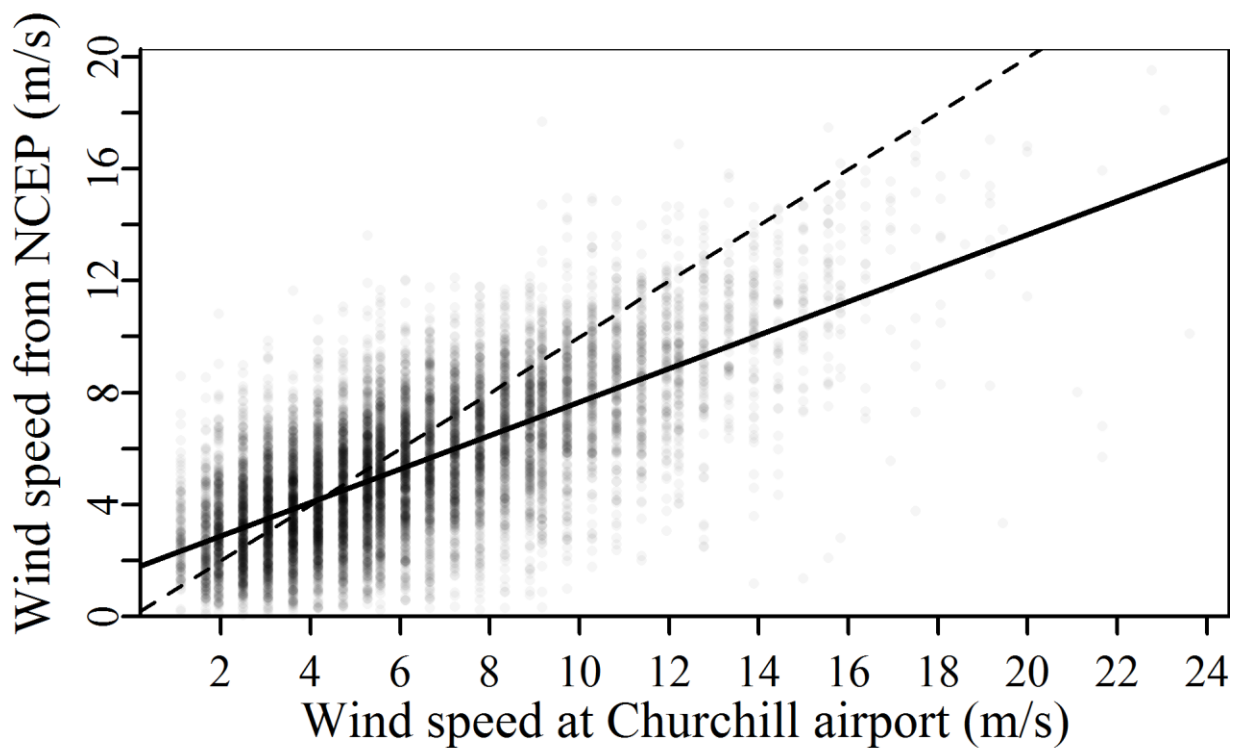


Figure 4. Regression between modelled wind speeds by NCEP versus measured wind speeds at Churchill airport, Manitoba, Canada between September 1, 2004 and April 12, 2012 ($n = 11,010$). Solid line shows line of best fit. Dashed line represents one-to-one relationship.

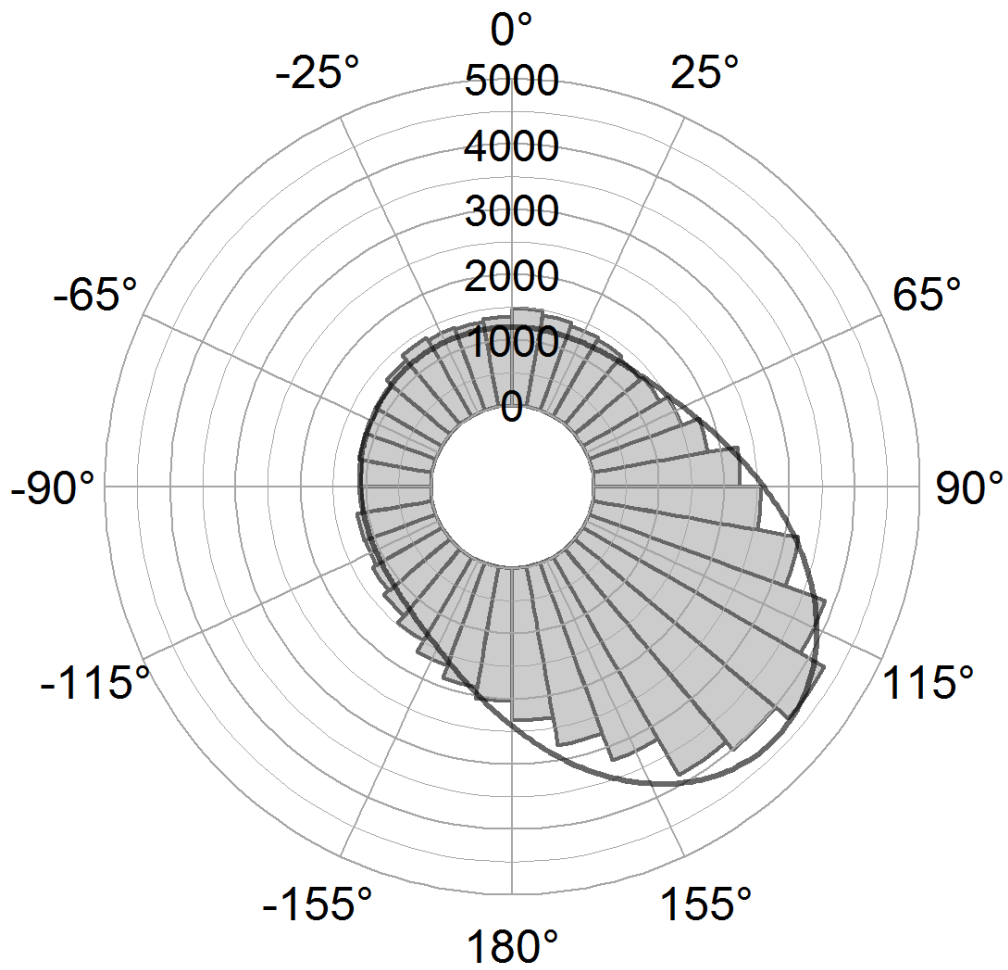


Figure 5. Frequency plot of wind bearings modelled by NCEP at all bear locations between Sept. 2004 and May 2015. Curve represents probability density function based on maximum likelihood of a mixture of two von Mises-Fisher distributions.

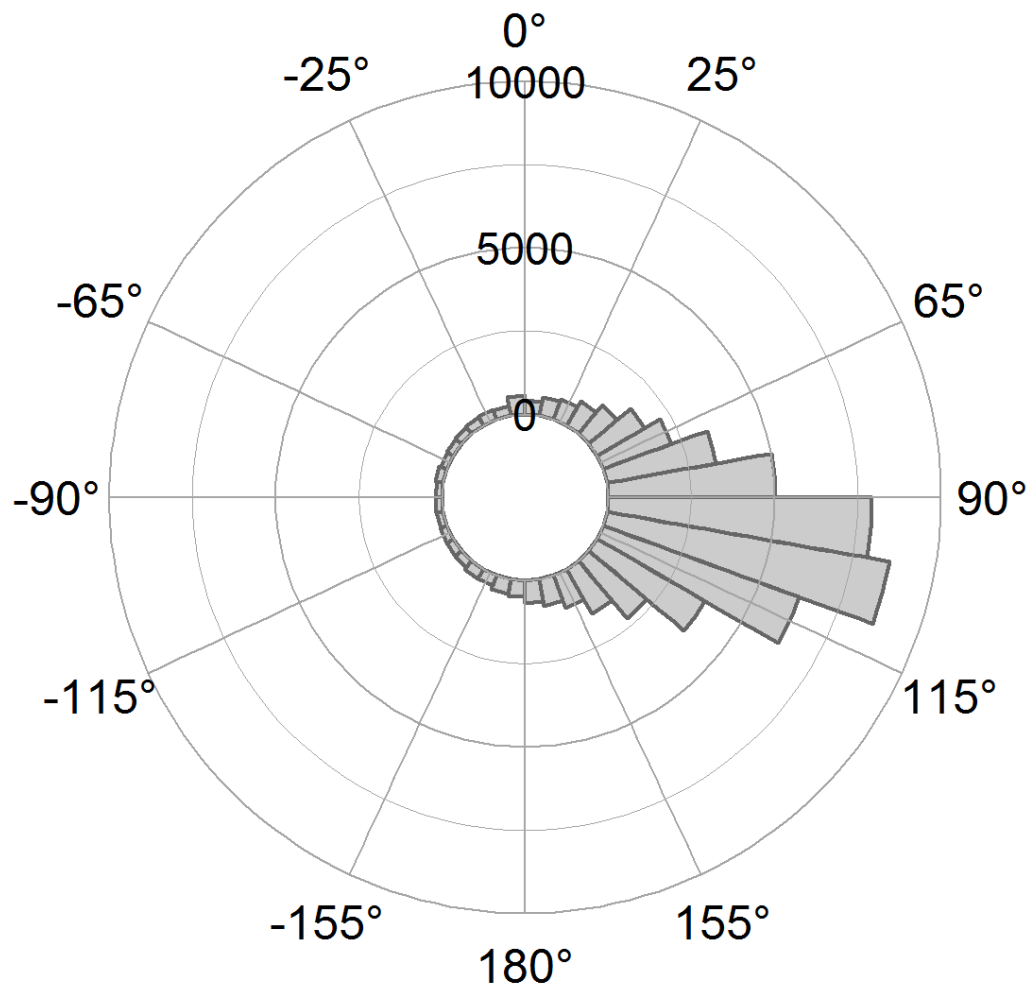


Figure 6. Frequency plot of acute angle between ice drift and modelled wind bearing at each bear location in Hudson Bay between Sep. 2004 and May 2015.

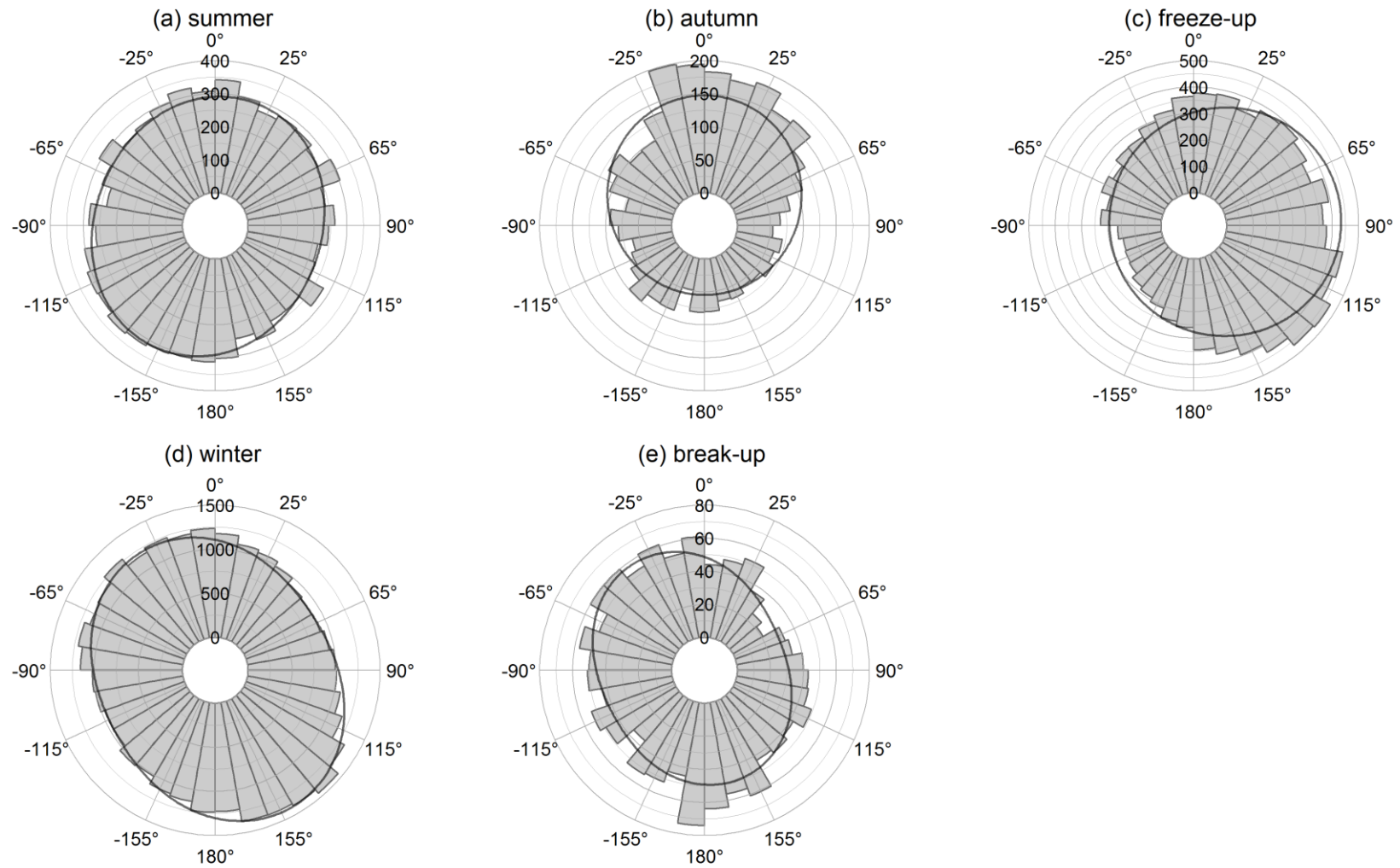


Figure 7. Frequency of polar bear bearings relative to north (0°) during (a) summer, (b) autumn, (c) freeze-up, (d) winter, and (e) break-up. Curves represents probability density functions based on maximum likelihood of a mixture of two (for a, d, and e) and a single (for b and c) von Mises-Fisher distributions.

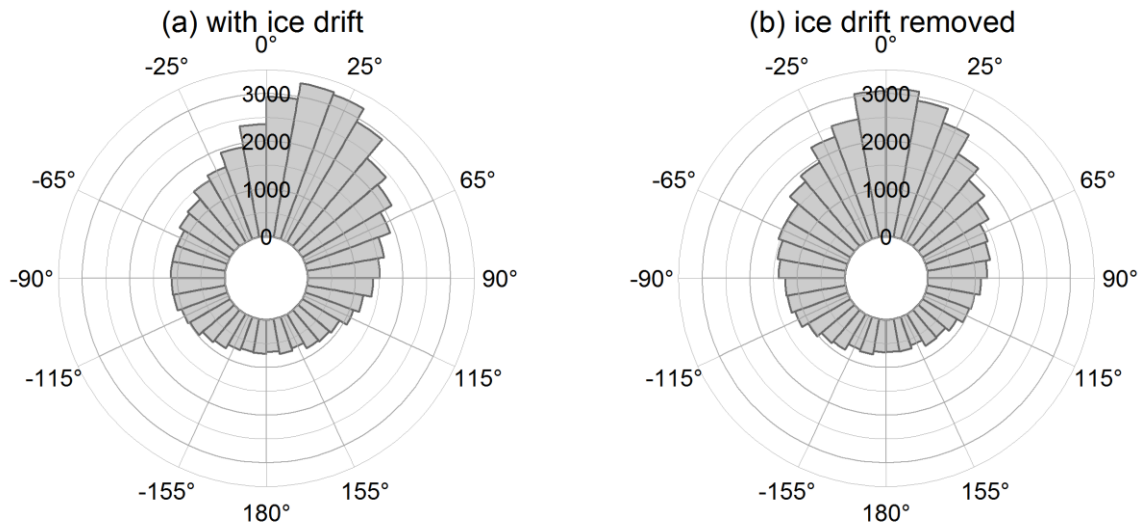


Figure 8. Frequency of (a) GPS bearing relative to wind and (b) polar bear bearing (with component of ice-drift removed) relative to wind during freeze-up and winter when wind is >10 m/s or polar bear speed is <2 km/h.

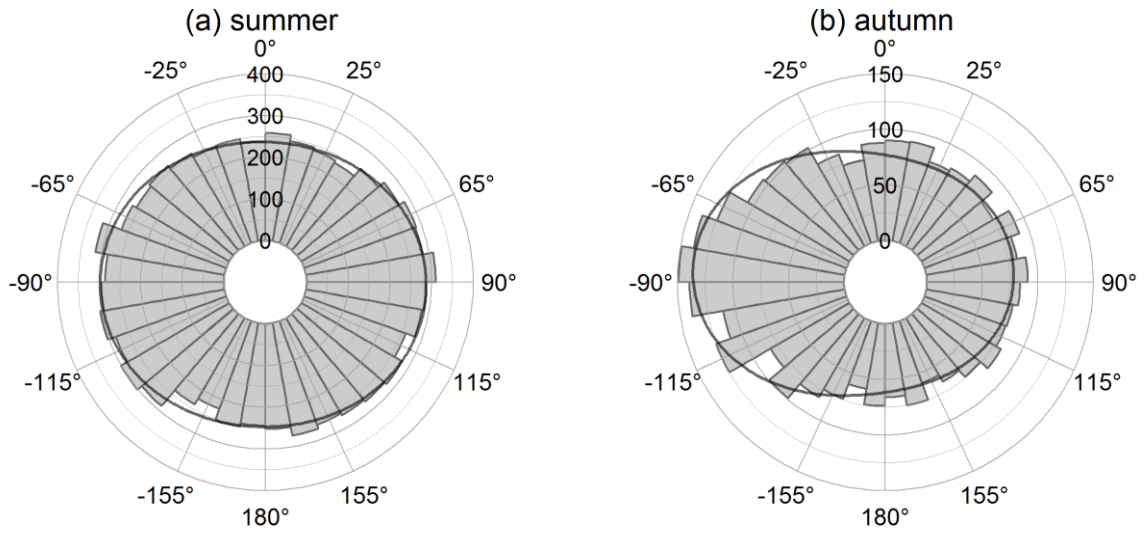


Figure 9. Frequency of polar bear bearings relative to wind during (a) summer and (b) autumn while wind speed was <10 m/s and polar bear speed was <2 km/h. Curves represents probability density function based on maximum likelihood of a mixture of two von Mises-Fisher distributions.

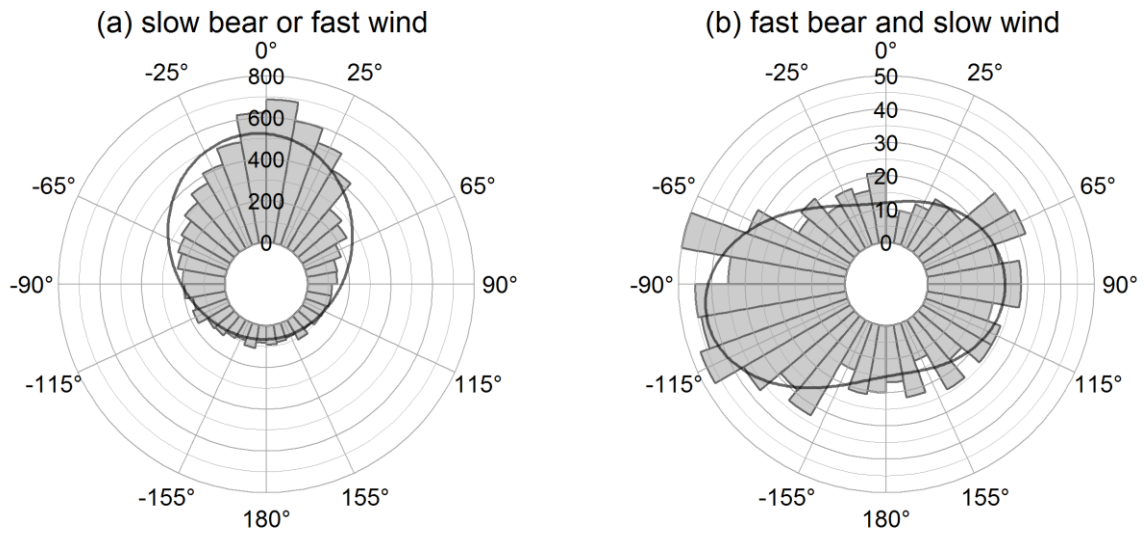


Figure 10. Frequency of polar bear bearings relative to wind during freeze-up while (a) polar bear speed was <2 km/h and (b) polar bear speed was >2 km/h and wind speed was <6 m/s. Curves represent probability density functions based on maximum likelihood of a single (for a) and a mixture of two (for b) von Mises-Fisher distributions.

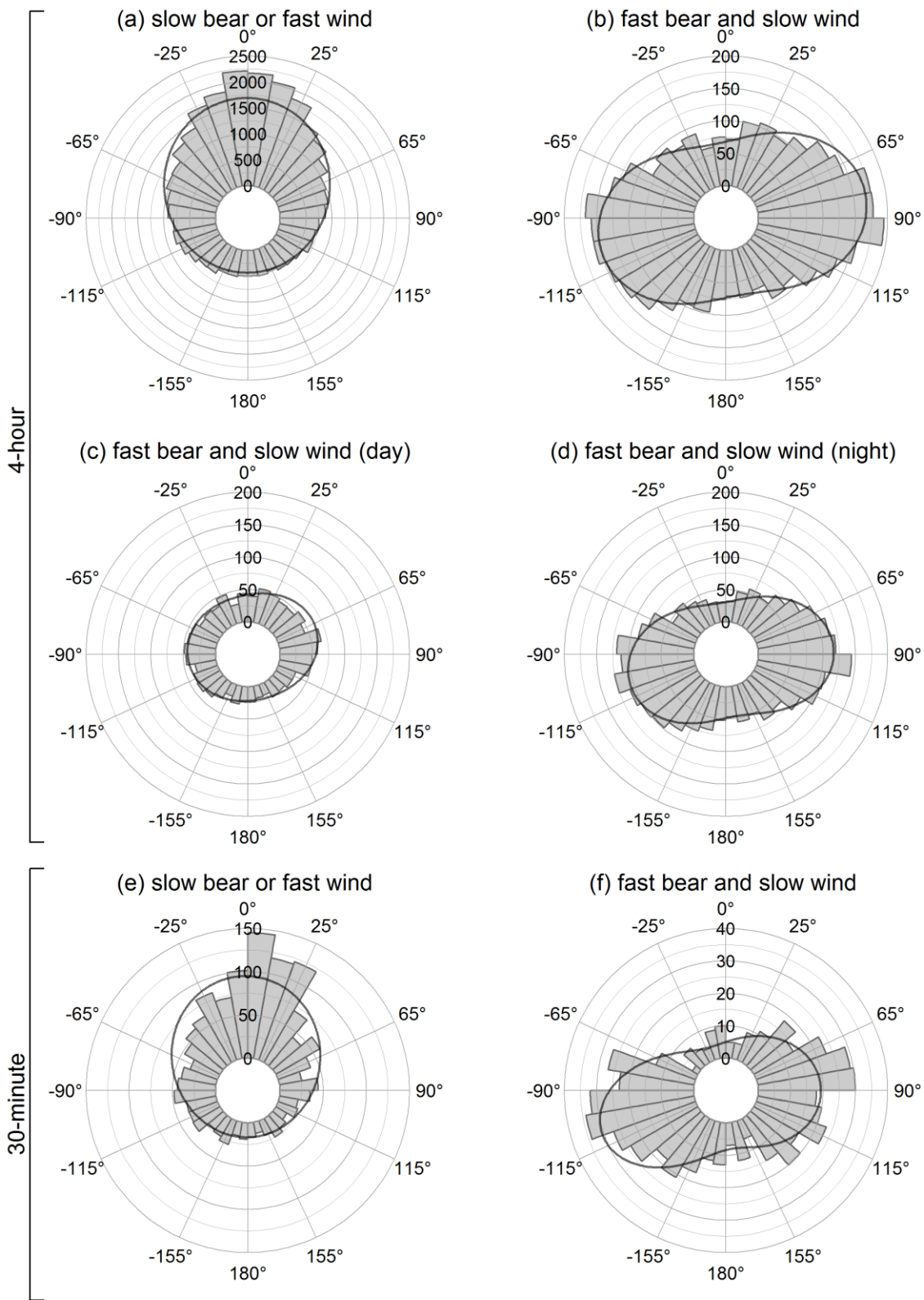


Figure 11. Frequency of polar bear bearings relative to wind during winter while polar bear speed was <2 km/h or wind speed was >10 m/s (a and e), and while polar bear speed was >2 km/h and wind speed was <10 m/s (b and f). (a) - (d) represent 4-hour collars while (e) and (f) represent 30-minute collars. (c) and (d) represent the data from (b) subset into day and night, respectively. Curves represents probability density functions based on maximum likelihood of a single (for a, and e) and a mixture of two (for b, c, d, and f) von Mises-Fisher distributions.

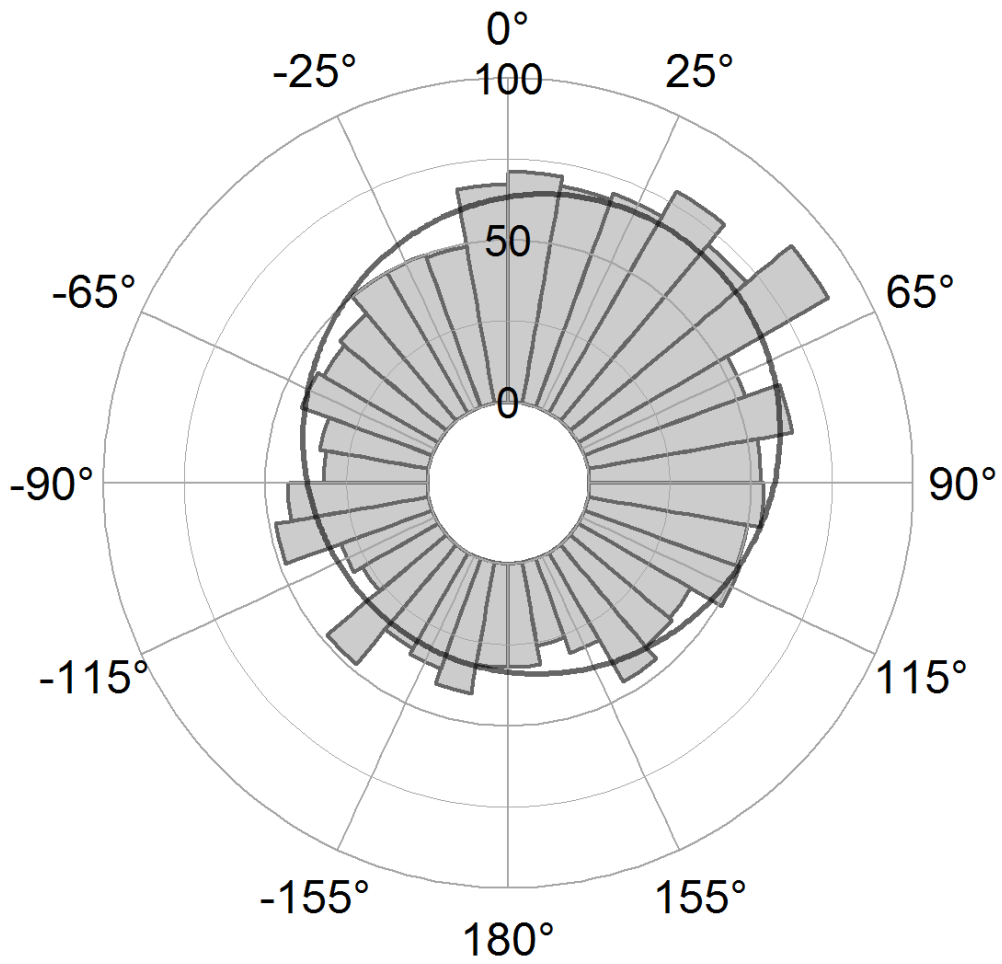


Figure 12. Frequency of polar bear bearings relative to wind bearings during break-up. Curve represents probability density function based on maximum likelihood of a von Mises-Fisher distribution.