Polar bear–grizzly bear interactions during the autumn open-water period in Alaska

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Reduction of summer sea ice extent has led some polar bear (*Ursus maritimus*) populations to increase their use of land during the summer/autumn open-water period. While terrestrial food resources are generally not sufficient to compensate for lost hunting opportunities on the sea ice, marine mammal carcasses, where available, could help reduce the energetic cost of longer periods of land use. Subsistence-harvested bowhead whale (*Balaena mysticetus*) remains are available annually near local communities along the Alaskan portion of the Beaufort Sea coast to bears that come to shore. Relatively large numbers of polar bears and some grizzly bears (*U. arctos*) use these resources, creating a competitive environment among species and social classes. We documented competitive interactions among polar bears and between polar and grizzly bears for bowhead whale remains adjacent to a small community in northeastern Alaska in September 2005–2007. We observed temporal partitioning of the resource by bears, with lone adult polar bears and grizzly bears primarily feeding at night, and higher use by polar bear family groups and subadults during dawn and dusk. Interspecific interactions were less frequently aggressive than intraspecific interactions, but polar bears were more likely to be displaced from the feeding site by grizzly bears than by conspecifics. Female polar bears with cubs were more likely to display aggressive behavior than other social classes during intra- and interspecific aggressive interactions. Our results indicate that grizzly bears are socially dominant during interspecific competition with polar bears for marine mammal carcasses during autumn.

Key words: Alaska, behavior, climate change, competition, dominance, feeding, grizzly bear, interspecific, polar bear, sea ice

Summer sea ice conditions in the Arctic have changed dramatically over the past few decades with the minimum extent of summer sea ice decreasing 30% since the late 1970s (Stroeve et al. 2012) and a decline in summer minimum sea ice extent of 9.4–13.6% per decade (Intergovernmental Panel on Climate Change 2013). Additionally, record low annual sea ice extents have been recorded regularly over the past decade (Stroeve et al. 2012). Recent models suggest sea ice loss will continue in the coming decades and that the Arctic Ocean could be nearly ice-free by mid-century (Overland and Wang 2013). This reduction in the summer sea ice extent could be especially problematic for polar bears (*Ursus maritimus*) that rely on sea ice to hunt their primary prey, ringed seals (*Phoca hispida*) in the prey-rich shallow waters over the continental shelf (Stirling et al. 1977), and that tend to minimize time spent over deeper, less-productive waters (Wilson et al. 2014). Shorter periods of the year when sea ice is over the continental shelf reduces the amount of time bears can hunt and has already been shown to have negative population-level effects (Regehr et al. 2010;

Rode et al. 2010a; 2014). In addition to reducing the amount of time polar bears are able to hunt over the continental shelf, lower summer sea ice extent has led to bears increasingly using land in the summer and autumn (Stirling et al. 1999; Schliebe et al. 2008; Gleason and Rode 2009; Cherry et al. 2013). In areas, such as Hudson Bay, Canada, where seasonal ice melts completely, polar bears that are forced to summer on land spend the majority of their time fasting as they wait for ice to reform in autumn (Knudsen 1978; Derocher et al. 1993; Atkinson and Ramsay 1995). Although polar bears display limited activity during this period (Ferguson et al. 1997), energy expenditure is much higher than that observed for hibernating bears (Robbins et al. 2012). Thus, any increase in the time polar bears spend on land could lead to longer periods of fasting and increased nutritional stress.

Although studies have reported that polar bears feed on terrestrial food resources (Russell 1975; Gormezano and Rockwell 2013; Stempniewicz et al. 2014), the overall contribution of terrestrial food sources to a polar bear's energy budget is thought

to be low (Ramsay and Hobson 1991; Hobson et al. 2009; Rode et al. 2010b). However, an energetic benefit may be obtained from feeding on marine mammal carcasses that wash up on shore. For example, Bentzen et al. (2007) demonstrated that polar bears in the southern Beaufort Sea population derived up to 26% of their nutrition from bowhead whale carcasses. Bowhead whales can reach a body length of 19 m and have thicker blubber than any other cetacean, constituting up to 50% of their body mass (George 2009). Given the continued loss of sea ice and the potential for this to increase nutritional stress (Molnár et al. 2010), polar bears can be expected to aggregate in large numbers on ephemeral resources such as marine mammal carcasses, when available. Indeed, large aggregations of polar bears (e.g., ≤ 30) have been observed throughout the Arctic feeding on beached whale carcasses (e.g., Taylor et al. 1985; Treacy 1993; Hansen 2004).

In the southern Beaufort Sea, polar bears have been increasing their use of land during the open-water period since the 1990s (Gleason and Rode 2009). When on land, these bears have the opportunity to feed on bowhead whale carcasses that are harvested by indigenous communities for subsistence purposes. Each year, the community of Kaktovik, Alaska (Fig. 1) harvests up to 3 bowhead whales and the remains are deposited near town, drawing large numbers of polar bears and a few grizzly bears (*Ursus arctos*) to feed (Miller et al. 2006). To the best of our knowledge, this annual gathering of polar and grizzly bears is unique and has not been documented elsewhere. This provides a unique opportunity to observe both intra- and interspecific competition between polar and grizzly bears for limited food resources during a period when polar bears are restricted to land. This resource may be particularly important to polar bears in the southern Beaufort Sea which have shown signs of nutritional stress associated with sea ice loss (Cherry et al. 2009; Regehr et al. 2010; Rode et al. 2010a; Bromaghin et al. 2015).
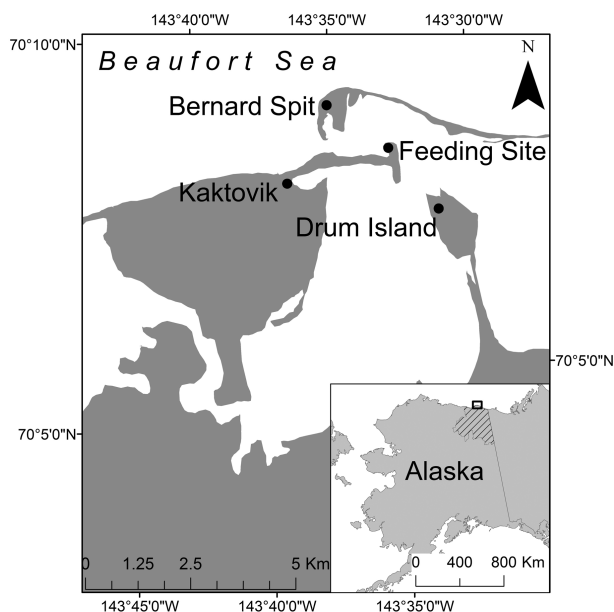
The potential importance of bowhead whale carcasses to polar bears in the southern Beaufort Sea may depend on the sex and age classes that have access to and use those resources. Little is known, however, about competition for food resources among polar bears. Most studies documenting polar bear interactions while on land occur in the near-absence of food (Latour 1981; Derocher and Stirling 1990). While larger bears have been documented being dominant when on the sea ice (Stirling 1974), polar bear competition for food while on land could be different, given different social and ecological conditions (Ramsay and Stirling 1988). Large aggregations of polar bears around concentrated food resources while on land could lead to significant competition and conflict between bears. For example, adult females with dependent cubs were socially dominant for resources found at a dump in summer (Lunn and Stirling 1985). Additionally, numerous studies have documented intraspecific predation by polar bears, often directed at young (< 1 year) bears (Taylor et al. 1985; Derocher and Wiig 1999; Amstrup et al. 2006). Amstrup et al. (2006) speculated that some intraspecific predation could be the result of nutritional stress.

No previous research has been done on interspecific competition between polar bears and grizzly bears given the difficulties of observing interactions in the wild. Documenting competitive interactions between the 2 species, however, is important for understanding which might be most successful in competing for limited terrestrial food resources as polar bears spend increasingly longer periods on land. When polar bears hunt on the sea ice, they generally do not face interspecific competition for prey, so it is unknown how they would interact with another apex predator. Although the potential for increased interactions with grizzly bears to lead to hybridization has been highlighted (Kelly et al. 2010), no studies have considered how competition with grizzly bears might limit the use of onshore resources by polar bears.

Our goal for this study was to document competitive interactions between polar bears and grizzly bears at remains of subsistence-harvested bowhead whales during the autumn open-water period, 2005–2007. Specifically, our objectives were to quantify intra- and interspecific use patterns of the whale remains, identify which species and social classes were socially dominant in competitive interactions, determine the frequency of aggression in interactions, and record the outcomes (i.e., temporary or permanent displacement from the feeding site) of intra- and interspecific competitive interactions.

Fig. 1.—Location of study area and feeding site for observing competitive interactions among polar (*Ursus maritimus*) and grizzly (*U. arctos*) bears during the autumn open-water period, in northeastern Alaska, 2005–2007. Kaktovik, Alaska, is located on Barter Island within the Arctic National Wildlife Refuge (hashed lines on inset map).

MATERIALS AND METHODS

Study area.—Kaktovik, Alaska is a small community of approximately 300 residents located within the Arctic National Wildlife Refuge on Barter Island, along the coast of the Beaufort Sea (Fig. 1). The village harvests bowhead whales each autumn for subsistence purposes; whalers recover the

skin, blubber, muscle, and some organ tissues and deposit the whale remains on a spit approximately 2 km northeast of the village (hereafter, the feeding site) where they are readily accessible to both polar and grizzly bears (Fig. 1). Bowhead whales have been harvested in autumn since at least 1964, with 2–4 whales harvested almost annually since 1989 (Koski et al. 2005). Polar bears were reported to feed on whale carcasses at Barter Island as early as 1986 (Amstrup et al. 1986), whereas grizzly bears were first observed feeding on whale carcasses in 2001 (Kalxdorff 2001). Polar bears most frequently access the feeding site by swimming in from offshore barrier islands which they use for resting (Miller et al. 2006), whereas grizzly bears primarily access the feeding site from the mainland, or by swimming to the site from Drum Island (Fig. 1). Use of the barrier islands by polar bears allows for individual recognition of conspecifics, including assessment of potential competitors. In contrast, grizzly bears have not been observed using barrier islands; therefore, opportunities for polar bear–grizzly bear interactions or individual recognition are likely quite rare—except during sympatric use of the mainland or Drum Island.

Data collection.—Once whale remains were deposited at the feeding site in September (2005–2007), we conducted direct observations of polar and grizzly bear use patterns and competitive behavior. Three people observed bears from a pickup truck using a Sony TRV-900 digital video recorder (Sony of Canada Ltd., Toronto, Ontario, Canada), a 20–60× Leica APO Televid 77 spotting scope (Leica Camera Inc., Northvale, New Jersey), Leitz 10×42 binoculars (Leica Camera Inc.), and a Garrity high beam spotlight (Garrity Industries, Inc., Brampton, Ontario, Canada). We divided the hours between 1800 and 0900 h into 3-h sampling sessions and classified them into the following time periods: dusk (1800–2100 h), night (2100–0000, 0000–0300, and 0300–0600 h), and dawn (0600–0900 h). To avoid observer fatigue, we systematically sampled alternate 3-h sessions until all 5 time periods were sampled, resulting in all sessions being sampled once every 2 days. We did not sample behavior during daylight hours (0900–1800 h) because we did not observe bear activity at the feeding site during that time period in previous years (Miller et al. 2006). However, each day we conducted a visual count of all polar bears visible on Barter and Drum islands and Bernard Spit (offshore barrier island, hereafter, the study area) to estimate overall polar bear abundance in the study area (Fig. 1). Because grizzly bears were not visible during day, we could only estimate their abundance based on observations at the feeding site.

During each observation session, we parked at the same location and avoided re-positioning the truck or using the engine or lights unless we could do so without eliciting a response from bears, or when it was necessary to haze curious bears that approached the truck. If bears became vigilant upon our arrival, we waited until they resumed their behavior before initiating sampling. While we could not control for other vehicles that approached the study area while bears were feeding, polar bears appeared habituated to vehicle approaches and did not typically flee if approached slowly and quietly, even when headlights were focused on them. Grizzly bears were more likely to respond to light by being displaced (e.g., moving behind whale remains or occasionally leaving the area).

Bear use patterns of the feeding site.—We used scan sampling (Altmann 1974) at 30-min intervals to determine the number and age/sex composition of polar and grizzly bears using the feeding site. The total number of bears observed per session was divided by the number of scans per session to estimate the average number of bears/scan for each session. Session data were then pooled by time period and year. When possible, we classified bears into 7 social classes reflecting a combination of sex, age, and reproductive status (Table 1). Males were distinguished from females via observation of body size, genitalia, penile hairs, and/or urination. Age classes (adult, subadult, yearling cub, or cub-of-the-year) were determined based on body size and shape. Cub classes were later pooled for analysis. Reproductive status was classified as "lone" or "family group," as determined by the presence or absence of cubs. In cases where individual bears lacked distinguishing physical features or visibility was restricted, individuals were classified as "unknown."

Competitive interactions.—Through direct visual observation and video recordings, we used all-occurrence sampling (Altmann 1974) to record competitive interactions that involved overt aggressive or submissive behavior by the initiator and/or recipient bear. We defined overt aggressive behavior as a physical display by a bear that included a directed charge, physical contact, vocalization, or a combination of these behaviors that resulted in physical displacement and/or disruption of feeding. We defined overt submissive behavior as a physical display by a bear that involved backing up, walking, and/or running away in response to another bear, resulting in physical displacement and/or disruption of feeding (Table 1). We classified interactions as either aggressive or nonaggressive. Aggressive interactions included the following scenarios: 1) both an initiator and recipient bear displayed aggressive behavior; 2) a bear initiated aggressive behavior and the recipient responded with submissive behavior; 3) a bear initiated aggressive behavior and the recipient remained neutral (i.e., displayed neither aggressive nor submissive response behavior); or 4) a bear initiated with neutral behavior and the recipient responded with aggressive behavior. All other interactions were considered nonaggressive and consisted of neutral approaches by an initiating bear that resulted in a submissive response (Table 1). Interactions involving more subtle aggressive behaviors such as salivation or stares were not recorded (unless accompanied by a charge, physical contact, or vocalization) because conditions limited our ability to sample all occurrences of them. We did not consider interactions involving light sniffing and mouthing as a competitive interaction unless the contact was paired with aggressive or submissive behavior that displaced a bear and prevented it from feeding. For each interaction, we documented whether the losing bear was displaced from the feeding site during the observation session, and if they were displaced, whether they were temporarily (i.e., physically moved but remained at the feeding site) or permanently (i.e., left the feeding site) displaced (Table 1). If more than one interaction occurred simultaneously,

Table 1.—Description of variables recorded during observation sessions of polar bears (*Ursus maritimus*) and grizzly bears (*U. arctos*) feeding on bowhead whale (*Balaena mysticetus*) carcasses on Barter Island, Alaska, 2005–2007. Behavioral definitions are modified from Stonorov and Stokes (1972) and are provided below, along with categories of each of the variables recorded during each observation session.

Variable	Definition
Social class	
Adult male	Lone male > 5 years old
Adult female	Lone female > 5 years old
Adult unknown	Lone bear of unknown gender > 5 years old
Subadult male	Lone male > 2.5 and < 5 years old
Subadult female	Lone female > 2.5 and < 5 years old
Subadult unknown	Lone bear of unknown gender > 2.5 and < 5 years old
Family group	Adult female accompanied by dependent cubs up to 2.5 years old. Cub-of-the-year: dependent cub < 1 year old. Yearling cub: dependent cub 1–2.5 years old.
Behavior	
Overt aggressive	Behavior between bears that included a directed charge, physical contact (e.g., swiping with forearms or mouthing accompanied by vocalizations and/or locked jaws), vocalization, or a combination of these behaviors that resulted in physical displacement and/or a disruption of feeding. Vocalization: roaring, huffing, hissing, and/or jaw popping.
Overt submissive	Behavior between bears that included backing up, walking away, and/or running away and resulted in physical displacement and/or a disruption of feeding.
Neutral	Nonaggressive, nonsubmissive movement of an initiator toward a recipient bear, or a response that involved "standing one's ground" (i.e., recipient bear did not move away from approaching bear).
Interaction type	
Overt aggressive	Initiator aggressive + recipient aggressive
	Initiator aggressive + recipient neutral
	Initiator aggressive + recipient submissive
	Initiator neutral + recipient aggressive
Nonaggressive	Initiator neutral + opponent submissive
Displacement	
Temporary	Bear(s) stopped feeding and physically walked or ran away from food source, but stayed at the feeding site
Permanent	Bear(s) stopped feeding and physically walked or ran away from feeding site and did not return during the sample session

a 2nd observer would assist the primary observer in recording interactions; the 3rd observer conducting scan sampling also assisted with all-occurrence sampling between scans.

Data analysis.—We determined the minimum, maximum, and average number of polar bears in the study area by consolidating daily counts for each year. Similarly, we determined the average number and composition (age, sex, and species) of bears at the feeding site during each time period (dusk, night, and dawn) by consolidating scan sampling data across all years of the study. Additionally, we used chi-square tests (Zar 1999) to determine whether there were differences in the frequency of presence/absence of polar bear family groups when adult male polar bears or grizzly bears (of any social class) were present/absent.

For competitive interactions, social class data were pooled by species and we used chi-square tests (Zar 1999) to determine if the frequencies of aggressive interactions between polar and grizzly bears, and between polar bears were different from expected. We also tested for differences in the frequency of aggressive and submissive behavior between polar bear social class (i.e., subadults, lone adult males, lone adult females, adult females with dependent cubs) in inter- and intraspecific interactions. Finally, we pooled social class data by species to determine whether the frequency of temporary or permanent displacements from the feeding site was different

than expected for inter- and intraspecific interactions. Because bears were not individually marked, we could not control for the number of observations obtained for each individual. Thus, some individuals might be overrepresented in the dataset. This study followed the American Society of Mammalogists guidelines on the research of live animals (Sikes et al. 2011) and was conducted under Federal Fish and Wildlife Permit MA046081.

RESULTS

Feeding site use patterns.—We observed bears during 121 monitoring sessions resulting in 363 h of observation (Table 2). We observed polar bears more frequently ($\bar{X} \pm SD$; 2.61 ± 3.34 polar bears/scan) than grizzly bears (0.29 ± 0.56 grizzly bears/scan). Numbers of polar and grizzly bears per scan at the feeding site ranged from 0 to 20 and 0 to 3, respectively. The average number of polar bears and grizzly bears per scan using the feeding site was higher at night (polar bear: 3.8 ± 2.9; grizzly bear: 0.5 ± 0.5) than dawn (polar bear: 0.6 ± 0.6; grizzly bear: 0.0 ± 0.1) or dusk (polar bear: 1.3 ± 1.3; grizzly bear 0.0 ± 0.0). From our daily counts, we determined that an average of 17, 13, and 28 polar bears were present in the Barter Island area in 2005, 2006, and 2007, respectively. We estimated that a minimum of 3, 2, and 3 grizzlies were present around Barter Island in 2005, 2006, 2007, respectively.

Table 2.—The average number ($\overline{X} \pm SD$) of polar bears (*Ursus maritimus*) and grizzly bears (*U. arctos*) observed during sampling sessions conducted during dusk (1800–2100h), night (2100–0000, 0000–0300, 0300–0600h), and dawn (0600–0900h) at the feeding site on Barter Island, 2005–2007. Averages are derived from scan sampling consolidated for each time period (total number of bears/total number of scans); n = the number of sampling sessions. We made observations between 5–25 September 2005, 8–28 September 2006, and 7–27 September 2007.

Year	Time period								
	Dusk			Night			Dawn		
	n	Polar bears	Grizzly bears	n	Polar bears	Grizzly bears	n	Polar bears	Grizzly bears
2005	8	0.7±0.6	0.0±0.0	24	2.8±1.8	0.5±0.4	8	0.4±0.5	0.0±0.1
2006	9	1.2±1.7	0.0±0.0	23	2.9±1.9	0.4±0.4	8	0.9±0.6	0.0±0.1
2007	9	1.9±1.3	0.0±0.0	24	5.6±3.7	0.6±0.6	8	0.5±0.6	0.1±0.1

Table 3.—Frequency of overt aggressive and submissive behavior displayed by polar bears (*Ursus maritimus*) of different social classes during competitive interactions at a feeding site on Barter Island Alaska, 2005–2007. Family group: adult female accompanied by dependent cub(s) up to 2.5 years old. Overt aggressive behavior: a directed charge, physical contact, vocalization, or a combination of these behaviors between bears that resulted in physical displacement and/or a disruption of feeding. Overt submissive behavior: backing up, walking away, and/or running away, resulting in physical displacement and/or a disruption of feeding.

Polar bear class	Competitive interaction			
	Polar bear–polar bear		Polar bear–grizzly bear	
	Aggressive (n)	Submissive (n)	Aggressive (n)	Submissive (n)
Lone adult male	19	76	1	61
Lone adult female	10	17	0	9
Family group	41	19	4	15
Subadult	6	26	0	8

For the 88% ($n = 1,892$) of polar bear observations where social class could be determined, 60% ($n = 1,138$) were lone adults (79% male, $n = 672$; 21%, female $n = 156$), 12% were adult females accompanied by dependent cubs ($n = 225$), 17% ($n = 323$) were dependent cubs (70% cubs-of-the-year, $n = 226$; 30% yearlings, $n = 97$), and 11% were subadults ($n = 206$). The proportion of polar bear family groups using the feeding site was higher during dawn (63%, $n = 55$) and dusk (42%, $n = 91$) than at night (25%, $n = 402$). Subadult use was higher during dusk (26%, $n = 56$) than during dawn (5%, $n = 4$) and night (9%, $n = 146$). Conversely, the proportion of lone adult polar bears was highest at night (66%, $n = 1,040$), compared to dawn (33%, $n = 29$) or dusk (32%, $n = 69$).

Of the 97% ($n = 226$) of grizzly bear observations for which a social class could be determined, 94% were lone adults ($n = 213$) with subadults comprising the remaining 6% ($n = 13$). We observed no grizzly bear family groups during the study, although they were observed in previous years. The sex ratio of lone adult grizzly bears was 38% male ($n = 29$) and 62% female ($n = 48$). Grizzly bears fed almost exclusively (98%, $n = 229$) at night with no observations of grizzly bears during dusk and only a few (2%; $n = 5$) during dawn. During dawn, the proportion of adults ($n = 2$) and subadults ($n = 2$) was 50%, respectively. During night, however, the proportion of adults ($n = 211$) was 95% compared to 5% subadults ($n = 11$).

In regard to whether polar bear females with dependent cubs were potentially avoiding the feeding site at night due to the presence of either grizzly bears or adult male polar bears, polar bear family groups were more likely to be present during night scans when adult male polar bears were absent (62.1%,

$n = 133$), versus when grizzly bears were absent (43.8%, $n = 133$; $\chi^2_1 = 16.3$; $P < 0.001$).

Competitive interactions.—We observed 137 interactions between polar bears and grizzly bears, 137 between polar bears, and 16 between grizzly bears. During interspecific interactions, the most common (71%, $n = 97$) scenario involved a nonaggressive approach by a grizzly bear that resulted in a submissive response by a polar bear (or multiple polar bears) present at the feeding site. We observed aggressive interspecific interactions ($n = 32$ aggressive, $n = 105$ nonaggressive) less frequently than expected ($\chi^2_1 = 38.9$; $P < 0.001$) regardless of who the aggressor was. We rarely observed aggressive behavior by polar bears towards grizzly bears ($n = 5$ aggressive, $n = 132$ nonaggressive; $\chi^2_1 = 117.7$; $P < 0.001$). Conversely, we observed aggressive intraspecific interactions ($n = 90$ aggressive, $n = 47$ nonaggressive) more frequently than expected ($\chi^2_1 = 13.5$; $P < 0.001$), regardless of who the aggressor was. Between grizzly bears, aggressive interactions appeared to occur with equal frequency to nonaggressive interactions ($n = 10$ aggressive, $n = 6$ nonaggressive).

We found significant differences across polar bear social classes in their likelihood of being aggressive during an interaction with a grizzly bear ($\chi^2_3 = 12.5$; $P = 0.006$; Table 3). Females with cubs displayed aggression towards grizzly bears in 21% of encounters compared to 2% for lone adult males, and 0% for subadults and lone adult females (Table 3). In intraspecific interactions between polar bears, we also observed differences across social classes in their likelihood of being aggressive during an interaction ($\chi^2_3 = 42.2$; $P < 0.001$; Table 3). Similar to interspecific interactions, females with cubs displayed more

frequent aggression (68%; Table 3) during intraspecific interactions than other social classes (19–37%; Table 3).

Polar bears involved in interspecific interactions were more likely to be displaced than not from the feeding site ($\chi_1^2 = 89.9$; $P < 0.001$; Table 4). Similarly, during intraspecific interactions, subordinate polar bears were more likely to be displaced than not ($\chi_1^2 = 103.4$; $P < 0.001$; Table 4). We observed different patterns in whether polar bears were permanently or temporarily displaced from the feeding site, however, depending on if the interaction was intra or interspecific. In interspecific interactions, grizzly bears permanently displaced polar bears from the feeding site at equal frequencies as temporary displacements ($\chi_1^2 = 0.5$; $P = 0.473$; Table 4). Conversely, in intraspecific interactions, temporary displacement was more frequent than permanent displacement ($\chi_1^2 = 75.0$; $P < 0.001$; Table 4). In intraspecific interactions between grizzly bears, only 12.5% of interactions resulted in permanent displacement (Table 4).

DISCUSSION

Our results indicate that grizzly bears are the dominant competitor during interspecific interactions with polar bears at the feeding site, frequently displacing polar bears without displaying aggression. We rarely observed polar bears acting aggressively towards grizzly bears; if an individual acted aggressively in interspecific interactions, it was usually the grizzly bear. Conversely, in interactions among polar bears, aggressive interactions were more frequent. These results imply that polar bears attempted to minimize conflict with grizzly bears. Additionally, grizzly bears permanently displaced polar bears from the feeding site approximately 50% of the time during interactions. This is striking when one considers that losers in interactions between polar bears were only permanently displaced from the feeding site approximately 10% of the time.

While our results suggest that polar bears, overall, were subordinate to grizzly bears, there were differences among social classes in their responses to grizzly bears. Females with cubs

Table 4.—Frequency of polar bear (*Ursus maritimus*) and grizzly bear (*U. arctos*) displacement responses during interactions at a bowhead whale (*Balaena mysticetus*) carcass feeding site on Barter Island, Alaska, 2005–2007. In polar bear–grizzly bear interactions, displacement is of the polar bear. Permanent displacement occurred when a bear left the feeding site and did not return within the 3-h sampling session; temporary displacement occurred when a bear physically moved or was interrupted from feeding but remained at the feeding site.

Interaction type	Displacement from feeding site		
	Permanent	Temporary	None
	n	*n*	*n*
Polar bear–polar bear	15	113	9
Polar bear–grizzly bear	66	58	13
Grizzly bear–grizzly bear	2	6	8

tended to avoid the feeding site during periods when grizzly bears were most likely to be there; however, this was confounded by the possibility that females with cubs may have been avoiding potential interactions with adult male polar bears as well. Regardless of which bears they may have been avoiding, if females with dependent cubs encountered a grizzly bear they were more likely to act aggressively than other social classes. Lunn and Stirling (1985) demonstrated that nearly all aggressive interactions observed between polar bears at a dump during summer were initiated by females with cubs, and family groups were the most dominant; similarly, Stirling (1974) observed that females with cubs were not subordinate to any other sex or age class of polar bear when they were threatened.

The aggressive behavior displayed by females with cubs at the feeding site was likely in defense of cubs and not to compete for food. This is supported by our observation that females with cubs frequently used the feeding site when the presence of grizzly bears and adult male polar bears was less likely. Similarly, avoidance behavior by females with cubs has been observed elsewhere. For example, Pilfold et al. (2014) found that females with cubs used lower quality habitat than other social classes. Previous research has also shown that females with cubs tend to be segregated from other social classes while on land during the ice-free period (Derocher and Stirling 1990; Ferguson et al. 1997). Females with cubs are likely less willing to risk the loss of their cubs to utilize ephemeral resources (e.g., Derocher and Wiig 1999). Thus, beach-cast marine mammal carcasses might not be as readily available to females with cubs.

It is interesting that grizzly bears were socially dominant over polar bears given that dominance hierarchies among polar bears (Stirling 1974) and grizzly bears (Stonorov and Stokes 1972) are generally based on size differences between competitors. Grizzly bears along the northern coast of Alaska are much smaller (males: ~180 kg, females: ~110 kg—Hilderbrand et al. 1999) than polar bears in the same region (males; ~375 kg, females: ~195 kg—Rode et al. 2014), thus it is surprising that polar bears were frequently subordinate to grizzly bears. There are several hypotheses, however, that may explain this asymmetry.

First, grizzly bears in low-quality habitat such as the northern coast of Alaska (Ferguson and McLoughlin 2000) may be more motivated to engage in competitive interactions with other bears to obtain access to high-quality food resources (Smith et al. 2005) such as a marine mammal carcass. As an omnivorous species, grizzly bears are also more likely to defend an energetically rich food source (Boertje et al. 1988) when it is available, since low prey density and the rate at which they capture prey makes the availability of an energetically rich food source such as a marine mammal carcass a relatively rare event (Stirling and Derocher 1990). By contrast, polar bears have access to energy rich marine mammals (Stirling 1974; Stirling and McEwan 1975; Stirling and Archibald 1977) throughout most of the year.

Second, the 2 species have different energetic requirements at the time of year when whale remains are present. Grizzly bears begin their period of winter dormancy in autumn and are hyperphagic during late summer and autumn (Nelson et al. 1983).

Conversely, polar bears are hyperphagic during spring rather than autumn (Ramsay and Stirling 1988). Polar bears in the southern Beaufort Sea are at or near their minimum body mass for the year in late March (Cherry et al. 2009). Hyperphagic behavior in spring allows polar bears to increase their mass when food availability (e.g., ice seal pups) is highest (Stirling and Øritsland 1995). When polar bears are onshore in summer and autumn, reduced prey availability can result in the onset of a fasting physiological state similar to hibernation in other bear species (Nelson et al. 1983; Derocher and Stirling 1990; Cherry et al. 2009). Polar bears in good nutritional condition may therefore be unwilling to expend the energy required to outcompete grizzly bears during this time of year. Conversely, grizzly bears den in autumn and must acquire adequate fat reserves prior to hibernation (Nelson et al. 1983; Lunn and Stirling 1985). Grizzly bears may, therefore, be more likely to compete for food sources in autumn in an effort to maximize the amount of stored fat reserves that they build up before denning.

Another explanation for why grizzly bears were dominant to polar bears may be related to their evolution. Throughout their evolution, the presence of large Pleistocene predators such as wolves, large cats, and other bears (e.g., Matheus 1995; Leonard et al. 2007) resulted in natural selection for aggression in grizzly bears which foraged in open, nonforested habitats (Herrero 1972; 1985). Polar bears, having evolved to exploit a specialized sea ice niche, did so largely in the absence of competitive influences from the suite of terrestrial Pleistocene predators that influenced brown bear evolution.

Lastly, the consequences of fighting an unknown competitor and risking injury may be a factor influencing brown bear social dominance over polar bears. While all North American bears generally exhibit risk-averse behavior and rarely engage in actual combat unless the reward is high, e.g., during breeding (Herrero 1985), the risk of injury to polar bears may have more severe consequences than to grizzlies because they are obligate carnivores and depend on their ability to hunt for survival. Polar bears may be less willing to invest in aggressive behavior against an unknown grizzly bear competitor because, if a polar bear is seriously injured, its ability to hunt will be severely limited. Conversely, grizzly bears are omnivorous and could possibly sustain a serious injury more readily, given their ability to utilize vegetative food resources. Additionally, polar bears are likely more aware of each other's competitive status, given the "risk-free" social play that occurs while on land in summer (Latour 1981). For example, in our study area, polar bears aggregated on a nearby barrier island during the day where they had opportunities to interact with each other. We often observed groups of adult male polar bears resting in very close proximity to one another in "bachelor groups" on barrier islands during the day. These individuals displayed strikingly benign behaviors, such as licking each other's mouths and sleeping adjacent to each other. Similar behavior by grizzly bears has not been reported, perhaps because their evolutionary history has selected for aggression to defend resources (Herrero 1985), and their low population density in high latitudes minimizes social interactions (Smith et al. 2005). During our study, polar bears only encountered grizzly bears at the feeding site, thus they were unable to assess grizzly bear competitive abilities in a "risk-free" environment. We do not know, however, whether previous encounters with grizzly bears may have affected polar bears' responses to grizzly bears, i.e., whether past experience led to avoidance behaviors that served to prevent potential injury.

While the feeding site on Barter Island provided a unique opportunity to observe interactions between grizzly and polar bears, it is unclear how frequently they would encounter each other at "natural" marine mammal carcasses that wash up on shore. The presence of whale remains on Barter Island is a predicable event whereas washed up carcasses would be highly unpredictable. Additionally, given the large ranges of grizzly bears (McLoughlin et al. 2000; Shideler and Hechtel 2000), they might be less likely to encounter a washed up carcass than at a location where whale remains are annually deposited by humans. However, because grizzly bears may be more human-averse (MacHutchon et al. 1998; Nevin and Gilbert 2005) than polar bears, it is likely that they would pose an even greater obstacle to polar bear use of the resource in remote areas that lack a human presence. In our study, grizzlies visited the feeding site most frequently at times when humans were least likely to be present (i.e., between midnight and 0600 h). If humans were not present, grizzly bears might completely dominate a beached carcass, further restricting polar bear access to the resource.

Our research only presented information on the competitive interactions of polar bears, but it should be noted that the majority of polar bears using the feeding site appeared quite tolerant of each other and their presence did not typically result in overt competitive interactions. For example, aggregations of up to 20 polar bears of mixed social classes were repeatedly observed feeding together with no injurious interactions observed. The arrival of a grizzly bear, however, significantly affected polar bear behavior, including their ability to feed. While it is clear that grizzly bears were the dominant competitor in our study, it is unclear what the energetic costs are to polar bears that lose foraging opportunities during the open-water period due to displacement by grizzly bears. It is also unclear if polar bears can habituate to the presence of grizzly bears, ultimately allowing polar bears greater access to the ephemeral resources at terrestrial feeding sites. Thus, future research should attempt to quantify how much energy is lost to polar bears, especially females with cubs, due to displacement (e.g., Nevin and Gilbert 2005), and the ability of polar bears to habituate to the presence of grizzly bears over time. Additionally, research should be conducted to determine if polar bears displaced from the feeding site adjacent to Kaktovik are more likely to travel into the community looking for food resources. In the interim, interspecific competition could potentially be reduced by dividing the whale carcasses into several feeding sites to disperse bears.

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