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Behavior and activity budgets of wild breeding polar bears (*Ursus maritimus*)

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Abstract

We quantify the first complete description of breeding behavior and activity budgets of an undisturbed pair of adult polar bears, observed 24 h/d for 13 d from 2 to 15 May 1997, at Radstock Bay, Devon Island, Nunavut, Canada. The male herded the female to an area of 1–2 km^2, where we observed them throughout the observation period. All behaviors were documented from when the adult female and her 2.5-yr-old cub were first observed being followed by an adult male, through separation of the cub from its mother, a week of intense interactions preceding several days with copulation, after which they parted. They mated for 51, 86, 66, and 150 min on 9–10, 12, 13, and 14 May, respectively, and parted on 14–15 May. The male deterred three challengers. The peak breeding season for polar bears runs from early April through mid-May, although additional mating behavior has been documented in June. Timing of mating and duration of copulations in the wild were similar to reports from zoos. Induced ovulation, male intrasexual competition, female fitness, the mating system, and potential consequences of climate warming are discussed with insights made possible by documentation of the reproductive behavior of wild polar bears.

Key words: polar bear, *Ursus maritimus*, breeding behavior, social system, activity budget, climate warming.

Senior Author's Introductory Comment

In 2013 I was honored to receive the Norris Award for Lifetime Achievement at the Biennial Conference in Dunedin, New Zealand. One expectation is that the recipient will publish a paper in *Marine Mammal Science*, based on the subject of their invited talk to the conference. The critical importance of quantitative natural history documentation was the major focus of my talk. For several years, I have been concerned that detailed recording of the natural history and behavior of animals in the wild seems to be downplayed, if not overlooked, in some ecological and behavioral

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research. In the worst case scenario, a person may simply analyze a data file without ever observing the animal in its natural habitat at all. An unfortunate consequence of this approach is that despite how logical the conclusions of such an analysis study may appear to be, the author may be unable to verify or reject ecological conclusions using direct observations of the study animal in its natural habitat. Consequently, this paper does not follow the usual format of a typical scientific publication. We first present an original and unique full documentation of the breeding behavior of wild polar bears. We then illustrate the value of that detailed original observational data set to interpret anecdotal observations in the wild, evaluate observations of the breeding behavior of captive bears, and give examples of the application of such data to additional ecological topics.

Introduction

Polar bears (*Ursus maritimus*) are distributed over vast remote areas of the circumpolar Arctic at low densities. Mating in the wild is reported to occur primarily from late March through May (Lønø 1970, Ramsay and Stirling 1986), a time when sea ice is at or near its maximum but still dynamic and variable in distribution between years (Ferguson *et al*. 2000, Mauritzen *et al*. 2003). Unlike terrestrial bears, polar bears do not defend territories, probably because the degree of interannual variability in the distribution and extent of the most favorable habitat is so great that it makes the location of the best areas unpredictable (Ramsay and Stirling 1986). Thus, individual bears tend to travel over large home ranges within and between years in search of both food and potential mates (*e.g*., Mauritzen *et al*. 2003). The small number of published observations of the reproductive behavior of polar bears in the wild, and reported in the literature, have been opportunistic, few, and anecdotal (Hagen 1975, Wiig *et al*. 1992, Derocher *et al*. 2010, Smith and Aars 2015).

In this paper we describe, for the first time, the complete breeding behavior of an undisturbed pair of experienced adult polar bears in the wild, through the 13 d period they were observed, beginning with the initial separation of the adult female from her 2.5-yr-old cub, through a week of intense interactions that appeared to create gradually a state of unthreatened acceptance of each other necessary to facilitate several subsequent days during which copulation occurred, after which they parted, still without any agonistic behavior. We then use observations made during this study to discuss and interpret anecdotal observations of the behavior of polar bears made in both wild and captive circumstances as well as subjects such as induced ovulation, male intrasexual competition, female fitness, the mating system of polar bears, evolution of the timing of mating, and possible negative effects of climate change.

Methods

Study Area

Radstock Bay, on southwest Devon Island, Nunavut, Canada, is approximately 30 km long and 12 km wide at the mouth (Stirling 1974, fig. 1). From late winter through early summer (March to early July) both the bay and much of Barrow Strait, to the immediate south, are usually frozen over. The sea ice is covered with drifted snow, especially along pressure ridges. At that time of year, bears of all age and sex

classes hunt ringed seals *(Pusa hispida)* along pressure ridges that run parallel to the south coast of Devon Island, in the fast ice of Barrow Strait, across the mouths of bays and, to a limited extent, into the bays themselves (Stirling and Archibald 1977, Stirling and Latour 1978, Smith 1980). From late March through May, adult males also search for adult females to mate with in these same areas. Mark and recapture studies have confirmed that individual bears, especially females, show a high degree of fidelity to Radstock Bay and the southwest coast of Devon Island in spring between years (Stirling *et al.* 1984*)*.

Observing and Recording Behavior

Undisturbed free-ranging bears were observed on the annual ice of Radstock Bay with 15–60× Bausch and Lomb zoom telescopes from a small observation cabin located on the edge of the cliff (300 m asl) at Cape Liddon (74°42.119′N, 91°11.646′W) from 22 April through 25 May 1997, using the focal animal approach (Altman 1974, Stirling 1974, Stirling and Latour 1978).

When possible, the sex of the bear was recorded. Large males were obvious by their size, body and head shape, and, if not too distant, sometimes by the presence of penile hairs or long guard hairs on the back of their forelegs (Derocher *et al*. 2005). It was harder to distinguish females that were not accompanied by cubs or yearlings from young adult males but a yellowish urine spot was often visible on the rump below the base of the tail if they were not too distant. If sex could not be determined with confidence, the bear in question was labeled "unclassified."

Observations of different behaviors, and the times they started and stopped, were recorded continuously in field notes. The beginning and end of behavioral activities were recorded to the nearest minute. Except during occasional brief fog patches, blowing snow, or when a bear disappeared behind an ice ridge, 24 h daylight facilitated continuous observation of polar bears at distances ranging from about 0.5 to 5.0 km from the observation hut, or the nearby cliff edge. This made detailed documentation of behaviors possible, but the distances were too great to allow for recording associated vocalizations or photography. However, opportunistic photos of breeding polar bears at other locations are included to illustrate some of the behaviors.

We use the term "still hunting" when a bear stands, lies, or sits motionless beside an exposed or subnivean breathing hole, birth lair, haul-out lair, or lead, waiting for a seal to surface there to breathe (Stirling 1974, Stirling and Latour 1978). We used the term "lie" for periods when a bear lay down for less than 60 min and "sleep" for periods exceeding 60 min during which a bear appeared to be asleep. "Walk" is self-explanatory. We defined "interactive behavior" as any activities in which one bear approached to within a few meters of another, followed by chasing, confrontation, biting, rolling, fighting, or otherwise making body contact. In this study, almost all interactive behavior observed took place between the focal breeding pair, *i.e.*, the adult male and female under continuous observation, but there were also brief interactions between the adult male and potential challengers. The term "miscellaneous" was used to include a variety of brief and infrequent behaviors that made an inconsequential contribution to the overall activity budget of the bears or to the sequence of reproductive behavior, such as scavenging, rolling, defecating, or pausing briefly to look about.

From the detail revealed by the quantitative documentation of the behavior of this mating pair, we were able to confirm that some brief observations of wild male-

female pairs made at other times and locations were also of breeding pairs, even though copulation was not observed in most instances. Additional field observations included were recorded during mark-recapture population studies of polar bears in the Canadian High Arctic in spring from 1971 to 2006 and from ecotourism ships in June 2010–2015 in the pack ice around Svalbard (Norway).

Results

Table 1 summarizes the activity budgets for the adult female and adult male, from 2 to 15 May, the time from when they were first seen until they parted company 13 d later. For comparison, Table 2 summarizes the activity budgets for adult female and adult male bears that were not involved with breeding behavior, during the total observation period from 22 April to 25 May.

First Sightings, Initial Interactions, and Separation of the 2.5-yr-old Cub from its Mother

At 0256 on 2 May, a large adult male polar bear was sighted on the open sea ice of Barrow Strait, about 5 km SE of Cape Liddon, following approximately 0.5 km behind an adult female accompanied by a 2.5-yr-old cub of unknown sex. The male was approximately double the size of the female. When first sighted, the female and cub were walking steadily northwest away from the male, lying down periodically, and appearing to hunt occasionally, though for only a few minutes at a time. Although the female periodically changed directions throughout the day, the male continued to circle back and forth behind her in order to ensure she kept traveling in a northwest direction until she was eventually within Radstock Bay, north of both Cape Liddon and the outer line of pressure ridges running roughly NE-SW across the mouth of the bay. Throughout this period, the female continued to look behind her to monitor the location of the adult male. Meanwhile, her cub kept repeatedly looking behind itself nervously and stayed so close to its mother that at times they appeared almost as a single animal. Both adults occasionally stood upright on their hind legs to look at the other, but then continued walking.

The adult male followed her for most of the day at variable distances, up to a maximum of approximately 500 m. If the female and cub lay down together, the male did

Table 1. Time and activity of activities of breeding adult female and male polar bears, 2–15 May 1997.

	Adult female		Adult male	
Activity	# minutes observed	% of total	# minutes observed	% of total
Lie <60 min	1,925	10.5	2,341	13.2
Lie >60 min	11,380	61.9	9,884	55.6
Walk	2,250	12.2	2,465	13.9
Stand/sit	163	0.9	877	4.9
Interaction	1,679	9.1	1,837	10.3
Copulation	353	1.9	353	2.0
Hunting	597	3.3	15	0.1
Miscellaneous	29	0.2	10	0.1
Total	18,376	100.0	17,782	100.0

Table 2. Amount of time spent in activities for nonbreeding adult female and male polar bears, 22 April–15 May 1997.

	Adult female		Adult male	
Activity	# minutes observed	% of total	# minutes observed	% of total
Lie <60 min	3	0.2	334	0.2
Lie >60 min	437	31.8	2,898	45.1
Walk	617	44.8	2,209	34.4
Stand/sit	5	0.4	216	3.4
Interaction	0	0.0	16	0.3
Hunting	260	18.9	347	5.4
Miscellaneous	63	3.9	400	6.2
Total	1,385	100.0	6,420	100.0

so as well, up to a few hundred meters away, with his head up, and simply watched them. After they entered an area of pressure ridges and rough ice inside the bay at about 1500, the male closed the distance to the female to about 200 m. While continuing to follow the female most of the time, whenever necessary the male ran ahead of her or parallel in order to prevent her from leaving an area roughly 1 km in diameter immediately to the north of our observation hut. At 2109, 2 May, when the male approached to within 20 m of the female, she responded by running and lunging at him but made no contact. Then all three bears ran north a short distance and stopped, at which point the male suddenly ran between the female and cub. After standing and looking at the male for about a minute, the cub ran about 20 m further away and stood watching the male and female. At this point, the female made no effort to reunite with her cub, or defend it from the male. The female then simply turned and began to walk away, followed closely by the male at a distance of 20–30 m, and by the cub at a greater distance (200+ m). The first interactions between the male and female, which involved biting around the neck and shoulders (though not drawing blood), standing up on their hind legs, and open mouth displays, began 42 min after the male separated the female from her cub. For almost two more days, the cub continued to follow the male-female pair, stopping and lying when they did, and walking when they moved, but remaining several hundred meters away. It was last seen at 1553, 4 May, walking NW away from the other bears. From the time the male first herded the female and her cub to the relatively small area of sea ice north of our observation cabin, to when the male and female separated almost 13 d later, they remained about 0.5–2.0 km away in view.

Pattern of Interactions

For several days, immediately following the separation of the female from her cub, but before copulation occurred, the interactions between the male and female were intense, and often continued for several hours at a time, though the sequence of the different behaviors was both varied and unpredictable. Usually, the female continued to walk, or run briefly, ahead of the male while he followed closely (Fig. 1a) and walked or ran to keep up as necessary, at distances ranging from about 50 m up to a few hundred meters. While following the female, he often sniffed her tracks in the snow (Fig. 1b) and lifted his head up to scent the air (Fig. 1c), looked in her direction, and walked behind her.

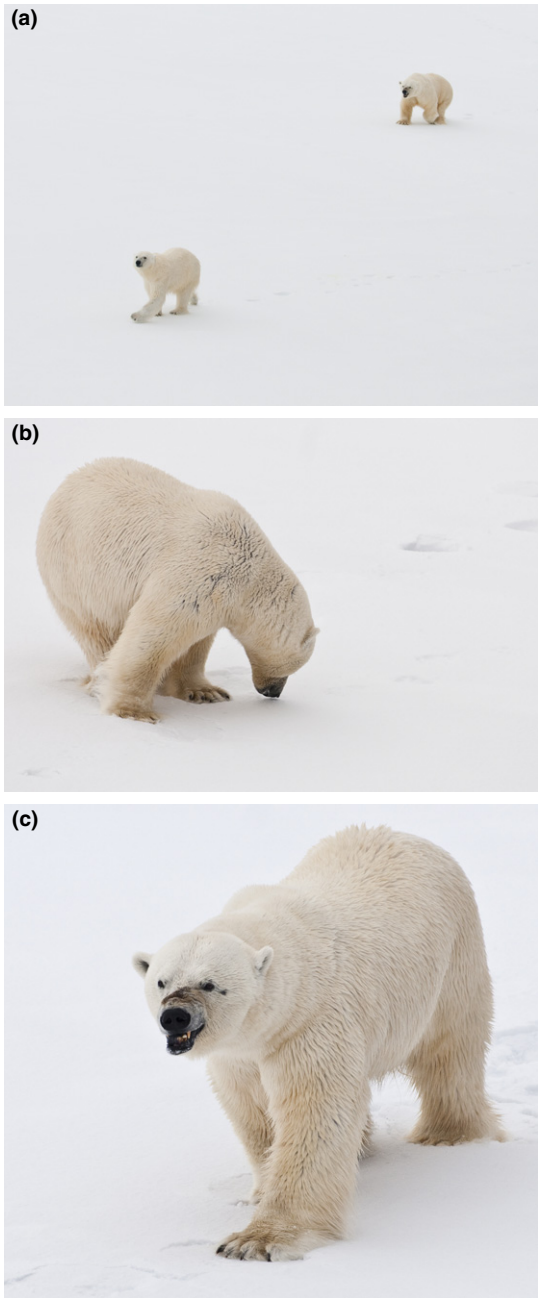

Figure 1a. Adult male polar bear following an adult female; *Figure 1b*. Adult male polar bear from Fig. 1a sniffing the adult female's tracks in the snow; *Figure 1c*. Adult male from Fig. 1a exhibiting flehmen behavior while following the female. © Rinie van Meurs.

Changes in behavior of both bears, but particularly the female, were often abrupt, intense, and unpredictable. For example, the female often ran straight at the male with her head held low but usually stopped just before reaching him. Sometimes, however, a charge might be followed by standing on her hind legs, pushing the male with a forepaw (Fig. 2) making naso-naso and interlocking jaw contact, accompanied by opened jaws and what appeared to be vocalizing, though they were too distant to be able to hear. At other times, after a chase, the female sometimes lay down, followed by the male doing the same thing or, instead she might run straight at him again but then suddenly turn and sprint away again while he ran in pursuit, usually circling ahead of her to keep her in the same area. Intense running and following sometimes ceased abruptly, followed by the bears again making naso-naso or jaw-locking contact, or simply standing and looking at each other before continuing to walk again, almost always with the female in the lead. Sometimes when charged by the female, the male responded defensively while at other times he simply stood motionless until she turned to walk or run away again.

In a typical period, lasting almost 9 h between about 1900 6 May and 0345 7 May, before they both lay down and slept for 2 h 15 min, the level of semicontinuous interaction was intense. During that period, there were a minimum of 87 individually interactions, in which the components were given in no predictable order, each lasting about 5–6 min. Between interactions, the male often sniffed her tracks in the snow as she walked ahead of him even though the female was nearby in view. Overall, the behavior of the female suggested she was not seriously trying to escape, confirming that remaining with the male and continuing to interact with him at close range was an integral part of the behavior necessary prior to copulation. Between periods of interacting, the two often lay down to sleep, side by side, but not making body contact.

During the total time they were observed, the adult female and adult male spent 9.1% and 10.3%, respectively, of their time in interactions (Table 1). The total for the male was slightly higher because he interacted briefly with other males as well as the adult female. In comparison, nonbreeding adult females accompanied by depen-

Figure 2. Adult female polar bear repelling interactive behavior of an adult male. © Paul Nicklen.

dent cubs, and males, which are normally solitary, spent 0% and 0.3% of their time interacting with other bears. All interactions by nonbreeding males were with other males.

Copulation

The first copulation began at 2342 on 9 May, following about 7 d of intense interactions as described above, interspersed with periods of resting or sleeping. When she accepted the male, the female lay on her stomach while the male mounted, using his forelimbs to pull the female toward him and control her movements. The first mounting at 2342 lasted for 3 min, followed by 1 min of separation, three more minutes mounted with some pelvic thrusting, and then by another minute apart. The female walked away, followed by the male, after which they stood facing each other before making mouth to mouth contact. The male then remounted and remained coupled with periods of pelvic thrusting, for a further 51 min, beginning at 2350 on 09 May. Although they continued to interact less intensively, rest, and sleep after copulating on 9–10 May, they did not mate again until 12 May. On 12, 13, and 14 May the male remained mounted while resting between periods of pelvic thrusting, (apart from a few momentary separations), for totals of 86, 66, and 150 min, respectively. After the initial mating, the female appeared totally submissive, aggressive interactions ceased, and unthreatening body contact initiated by the male (*e.g.*, Fig. 3) were passively accepted by the female. Prior to beginning the last and longest period of copulation, there was no preliminary behavior before the male simply mounted and began to copulate. Occasionally, particularly in the first few days, the female lay on her chest and the male, on his knees, mounted her in that position. Although the female stood during most periods of copulation, she occasionally lay down briefly and then stood again, through which time the male remained mounted. During copulation, the female sometimes swung her head from side to side, and appeared to mildly bite at the male's forelimbs. The male waved his head from side

Figure 3. Adult female polar bear showing no response while being "nuzzled" by an adult male. © Mick Brown.

to side most of the time while copulating and sometimes rested his head on her back or neck, but did not take a purchase on her neck.

While mounted, the male went through successive but brief periods of strong rapid pelvic thrusts with an average duration of 3.7 s ($n = 27$, SD $\pm$ 0.7 s, range 1.8–4.5 s), followed by brief periods during which he remained mounted but motionless. The periods of rapid thrusting were suggestive of possible ejaculation while the intervening periods between episodes of thrusting were suggestive of possible physiological refractory behavior. However, we know of no confirmation of this interpretation from any observations of either wild or captive polar bears. There was little variation in the duration of the periods of thrusting, from the first copulation to the last, but there was considerable variation in the average duration of the pauses between thrusting sessions on 10–13 May compared to those on 14 May. Although observation of the bears was continuous, because of distance, changes in light or visibility, or the angle of the bears from the viewer, the start and end of each sequence of thrusting and resting could often not be noted accurately. However, the average, SD, and minimum and maximum duration of 27 pauses between thrusting sessions that could be clearly confirmed on 10–13 May were 48.21 s, 24.57 s, and 23–102 s, respectively. When mating for the longest period observed, on 14 May, the average, SD, and minimum and maximum duration of 76 pauses between thrusting sessions, that could be clearly confirmed, were 24.87 s, 8.65 s, and 10–59 s, respectively, a duration that was significantly shorter than recorded on the earlier dates ($t = 4.95$, df = 26, $P < 0.01$).

Interactions with Other Polar Bears While Mating Pair Were Together

During the period of observation, 12 different bears approached to varying distances from the breeding pair. Seven of these (two adult males and five of unknown sex) approached to within about 50-300 m but were ignored by both bears of the breeding pair.

On 13 May a male that appeared slightly smaller than the breeding male, approached briskly. When he was about 50 m from the pair, the breeding male charged the intruder while the female ran a short distance in the opposite direction. The two males reared up, locked jaws, and began pushing each other on the chest, neck, and shoulders with their forepaws. Suddenly, the breeding male forced his opponent on to his back on the ice and stood with his jaws around the challenger's throat. The challenger lay motionless. Less than a minute later, the breeding male released his potentially lethal grip on the smaller male's throat, returned to following the female, and ignored the departure of the former challenger which had blood streaming from the side of his neck when he departed.

On 14 May a large male that appeared similar in size to the breeding male approached the breeding pair as they walked northeast within the area they occupied since their interactions began. The breeding male charged the intruder. Both stood up on their hind legs, locked jaws, and pushed each other with their bodies and forepaws. Again, within seconds, the breeding male forced his challenger onto his back on the ice with his jaws firmly around the challenger's throat. After a few seconds of lying motionless, the challenger began to move and the breeding male responded by pushing down hard with his jaws still around the throat of the challenger, who then lay still again. A few seconds later, the breeding male again pushed down hard on the challenger's throat and appeared to feint a potential bite. The challenger remained motionless and the breeding male then backed away and allowed the challenger to stand up. Once standing, the challenger immediately repeated his attack. Within

seconds, the breeding male again forced the challenger onto his back with his jaws firmly around the challenger's throat. The breeding male repeated a downward push with his jaws around the challenger's throat, while the challenger again remained motionless. A few more seconds later, the breeding male allowed the challenger to stand, after which the challenger retreated without further interactions. The breeding male then pursued the female, as she had run away a few hundred meters while the fight took place. The challenger was bleeding from the top of the base of his neck and the breeding male also had blood running from the left side of his neck. The males may have become overheated during these interactions, as the breeding male lay down, appeared to be panting, and ate snow sporadically for about seven minutes. After catching up with the female again, he stopped and ate snow again for about a minute.

About half an hour later, another large male approached the breeding pair with its head down as if it was about to attack but retreated quickly when the dominant male charged.

Separation of the Breeding Pair

The last session of copulation (150 min) ended at 1853 14 May, after which the female returned to walking about the same local area, but appeared more interested, superficially at least, in hunting than interacting further with the male, as indicated by her periodic sniffing of snow drifts, pouncing, digging, and appearing to briefly poke her head down into seal lairs beneath the snow. The male followed, watched (similar to that in Fig. 4), and initially made mild efforts to herd her back into the same area though there was no longer any charging at each other or physical contact. By about 2315, the female was headed north away from where the pair had been for most of the previous 13 d. She continued to exhibit brief bits of hunting behavior. Although the male continued to watch and follow her at distances of up to 100 m, he made no further effort to interact or influence her direction of travel. At 0200 15 May, after they had moved 7–8 km to the north, the bears entered an area of rough ice and were no longer visible.

Unpublished Observations of Reproductive Behavior in Svalbard in June

Because there has been so little detailed documentation of the behavior of mating pairs of polar bears through all the stages of breeding, few casual observers making opportunistic short-term observations have had the knowledge necessary to recognize a stage of breeding behavior if two animals were seen interacting in a variety of ways (as described above), but not actually copulating. The following six observations of breeding behavior in June were made in Svalbard by one of us (IS) or confirmed by IS from detailed descriptions and photos from experienced ecotourism guides.

23–27 June 2010, Holmiabukta, Svalbard[2]—During the period of observation, up to 14 different polar bears were observed scavenging on a fin whale carcass, including four adult males and one adult female. The identity of the female could be confirmed between observations because she was wearing a satellite radio collar. She was observed mating with two different males (identifiable from scars) on 23 and 27

[2]Personal communication from Christian Genillard, Sterne Expeditions, Petites-Buttes 18, CH-1180 Rolle, Switzerland, September 2015.

Figure 4. Adult female polar bear hunting at a ringed seal birth lair while being watched by an adult male. © Mats Forsberg.

June. On both occasions, the female approached a male that was either sleeping on the snow or feeding, initiated interactions that successively involved walking, standing on the hind legs, and swimming, after which she appeared to present herself on land, waited, and then continued to present herself again and allowed the males to mount. Copulation lasted for less than a minute. The total interaction with each male lasted approximately 30–40 min. No fighting or competition between males was observed.

16 June 2012, Brepollen Fiord, Svalbard (IS)—A large adult male and an adult female half his size were seen standing together on an ice floe 30–40 m in diameter. The female walked back and forth while the male circled and herded her to keep her on the floe. They remained together on the floe for about an hour, during which time she made no attempt to escape. She then calmly walked to the edge, dove into the water, and started to swim away from the floe. The male immediately dove in and followed. The pair appeared to be in the phase of interacting behavior before or between sessions of copulation.

18 June 2013, Seven Islands, Svalbard (IS)—A large adult male and adult female were observed standing together but not interacting at 0630. The male walked slowly away while the female laid down. Thirty minutes later, he returned to the female and nosed her head and neck. She raised her head but did not move. After standing beside the female for a further 30 min, the male walked away. The ship departed before it could be determined if the male kept walking away or returned to the female. This appeared to be a pair that were in the last stages of mating or, more likely, had recently finished and were in the process of separating.

19 June 2014, approximately 3 km west of Seven Islands, Svalbard[3] —For about 45 min, the two bears walked back and forth and occasionally came together while the male made occasional nasal contact with the upper body of the female (Fig. 3). No mating was observed. The pair appeared to be between copulations or possibly recently finished breeding behavior.

[3]Personal communication from Mick Brown, 43 Oakridge Acres, Tenby, Wales, SA70 8DB, U.K., June 2015.

25 June 2014, North end of Hinlopen Strait, Svalbard[3,4]—An adult female was observed walking on an ice floe, approaching the ship, and being closely followed by an adult male (Fig. 1a). The male often sniffed the tracks of the female in the snow (Fig. 1b). When he followed the female, he curled his upper lips, held his head up to scent the air, and exhibited flehmen behavior (Ewer 1998) while he walked (Fig. 1c). The pair appeared to be in the phase of interacting behavior before or between sessions of mating.

24 June 2015, 15 km NW Lagøya, Svalbard (IS)—An adult male was observed walking across an ice floe, 60–80 m behind an adult female. They came together, made naso contact, and the female sat while the male stood in front of her and made naso contact again. Ten minutes later, she began to walk slowly away at distances of 0.5–1.5 km for about half an hour until they disappeared in the fog, 1.25 h after they were first seen. The pair appeared to be near, or past, the end of the mating period and in the process of separating.

Hunting Behavior of the Breeding Pair

During periods of interacting with the male, the female sometimes broke away suddenly and exhibited what would normally appear to be standing still-hunting over a ringed seal birth lair or breathing hole (Stirling 1974, Stirling and Latour 1978). On several occasions, she briefly pounced, dug, and appeared to try to break into the lair, giving the superficial impression she was hunting seriously, while the male simply stood nearby and watched (similar to Fig. 4). However, such hunting behavior lasted only 1–3 min in most cases compared to periods of 20–30 min or more per standing still-hunt by an adult female accompanied by cubs-of-the-year (COY) or yearlings at Radstock Bay in other spring seasons (Stirling and Latour 1978). Although in total, the adult female and male of the breeding pair hunted for only 3.3% and 0.1% respectively of the time they were under observation (Table 1), the difference was significant ($\chi^2 = 542$, df = 1, $P < 0.01$). In comparison, nonbreeding adult females and males observed during the same time period hunted 18.9% and 5.4% of their total time respectively (Table 2), which was significantly more for each sex than for the breeding female and male ($\chi^2 = 744$, df = 1, $P < 0.01$, ($\chi^2 = 903$, df = 1, $P < 0.01$, females and males, respectively).

No kills were made by the mating pair so it was not possible to document the extent to which feeding behavior might occur if there was an opportunity. However, overall participation in hunting behavior and momentary scavenging was so small (female: 298/18,376 min = 0.016%; male: 24/17,782 min = 0.001%) that the values were simply included in miscellaneous).

Other Activities

The largest block of time spent in a single activity by the male/female pair was lying for durations >60 min, which we defined as sleeping. The female and male of the pair spent 61.9% and 55.6%, respectively, of the total time they were observed in this activity (Table 1) compared to 31.8% and 45% for females and males not involved in mating behavior which was significantly different ($\chi^2 = 440$, df = 1, $P < 0.01$, $\chi^2 = 206$, df = 1, $P < 0.01$, females and males, respectively) (Table 2).

[4]Personal communication from Rinie van Meurs, Lobzowska 57/43, 31-139 Krakow, Poland, June 2015.

The second largest activity for the male/female pair was walking, most of which resulted from the large amount of time the female walked while the male followed and herded her so that she remained within the same small area, between periods of interaction or lying. The total time spent walking was 12.2% and 13.9% respectively for the female and male (Table 1). In comparison, female and male bears not involved with mating behavior spent 44.8% and 34.4% respectively of their total time observed walking while searching over much more extensive areas for potential locations for hunting (Table 2), which was significantly greater for both sexes (χ^2 = 1,081, df = 1, $P < 0.01$, χ^2 = 2,040, df = 1, $P < 0.01$, females and males, respectively).

Discussion

Overall Pattern of Reproductive Behavior

Some components of the breeding behavior of polar bears, both in the wild and in zoos, have been described briefly elsewhere (*e.g.*, Hagen 1975, Malyov 1990, Malev *et al*. 1990, Wiig *et al*. 1992, Tumanov 2001, Derocher *et al*. 2010, Smith and Aars 2015; this study, IS, CS, and DA, unpublished observations). These predominantly anecdotal accounts include short accounts of males and females of mating pairs running at each other, physically interacting, males herding females to areas where the probability of encountering potential competitors might be reduced, males competing with other males for females, and breeding pairs (or their tracks in the snow) apparently remaining together for several days or weeks before copulation. Consequently, to date, this is the first and only description of behavioral changes through the complete mating sequence of a pair of wild adult polar bears, including an activity budget, from the time the adult male was first seen following the adult female and her 2.5-yr-old cub, the separation of the cub from its mother by the male, the days of interacting before the occurrence of multiple copulations over several days, through to the eventual separation of the pair. The large size and dominant behavior of the adult male, and that the female was initially accompanied by her 2.5-yr-old cub, may indicate that the observations reported here were representative of the overall pattern of breeding behavior for fully adult and experienced bears.

Timing of Mating and Duration of Courtship Behavior

Historically, much of our quantitative understanding of the timing and duration of the breeding season of polar bears originated from histological examination of reproductive organs collected from polar bears harvested by hunters over several years in Svalbard (Lønø 1970) and Greenland (Rosing-Asvid *et al* 2002). Rosing-Asvid *et al*. (2002) found the first *corpus luteum* on 1 April, the last ovulations in mid-May, and suggested that mating begins in March and ends in May. However, Rosing-Asvid *et al*. 2002) also reported that male polar bears in Greenland still had high concentrations of spermatozoa in June and July. On the basis of similar histological examinations of ovaries and testes from polar bears harvested in Svalbard, and anecdotal observations, Lønø (1970) concluded that mating occurred from late March to July and suggested the possibility that the peak breeding period might be as late as mid-June.

Probably because of the large number of days that are apparently necessary for breeding behavior in polar bears to be completed, there is no other full documentation of the total amount of time a male-female pair needs to remain together in the wild in order to breed successfully. However, on the basis of occasional resightings of recognizable bears while conducting mark-recapture studies, Derocher *et al* (2010) reported that a 22-yr-old female and a 12-yr-old male remained together at Hopen Is., Svalbard, for 16 d and Wiig *et al* (1992) reported a male-female pair remaining together for 18 d in Hornsund, Svalbard. These observations are consistent with our observations, suggesting that overall, an adult pair of polar bears may require up to two weeks or more in the wild to complete the full sequence of breeding behavior.

Most sightings of paired bears in the wild made by Inuit hunters, and by biologists tagging large samples of bears for population assessment, were made between mid-March and late May (Lønø 1970, Hagen 1975, Lentfer *et al*. 1980, Ramsay and Stirling 1986). Of 6 observations of mating behavior reported by Lønø (1970) 5 occurred between 10 March and 7 May and only one dated from June 20.

However, the observation of mating reported by Smith and Aars (2015), and the six previously unpublished observations of breeding behavior in Svalbard, all occurred in June. Of importance, even though copulation was not observed in five of the six brief observations of an adult male and female together on the ice, their behavior could reliably be identified as part of the normal pattern of breeding behavior when compared to documentation of the full sequence at Radstock Bay. The single most defining behavioral aspect, was that the female in a breeding pair showed no sign of fear while remaining in close proximity to the adult male for an extended period, even to the point of calmly allowing frequent physical contact (Fig. 3) not directly involving copulation. At all other times, when not actively involved in breeding behavior, adult females with or without cubs normally avoid adult males immediately, sometimes fleeing instantly at a dead run, probably because of the high risk of direct predation and cannibalism of themselves or their cubs (*e.g*., Taylor *et al*. 1985, Stirling and Ross 2011). Consequently, it appears that the function of the week-long period of semicontinuous interacting between the male and female at Radstock Bay, when it appeared that the female could escape by outrunning the slower large male if she chose to, functioned to modify their behavior sufficiently to allow them to remain together while preparing to mate, mating, and then eventually separating, without risking possible injury to, or death of, the female. Such behavior on the part of both the male and female represents the most dramatic change in behavior imaginable when compared to nonbreeding adults. The uniqueness of this change in behavior, is underlined by the fact that the male retained the ability to instantly be highly aggressive and fight with other males, while not being threatening to the female for the duration of their breeding behavior. At present, it remains unknown how long after separation from a male the female reverts to her normal pattern of fear and avoidance.

From an analysis of a large data set on the age, sex, and reproductive status of polar bears captured in spring in Lancaster Sound, Nunavut, Molnár *et al*. (2008) reported that breeding pairs were observed between 5 April and 28 May and that the peak in observations of apparent reproductive pairs was around mid-April followed by a slow decline in the proportions of paired males and females until the end of May. In April 33.8% of sampled males and 40.7% of sampled females were paired, in contrast to May, when only 15.3% of males and 17.9% of females were paired. Similarly, from an assessment of the levels of serum steroid concentrations in wild male polar bears,

(Palmer *et al*. (1988) and Howell-Skalla *et al*. (2002) suggested a mating season from early April to late May.

It is important to note there is an uncertain amount of possible bias in assessing the end of the potential mating period, based on observations of wild bears or those from the harvest, because little mark-recapture field work, or hunting has taken place after about mid- to late May in most areas for several decades. Nevertheless, the cumulative data presented above from observations of behavior in the wild, studies of histology of reproductive organs of harvested bears, and observations of breeding pairs of polar bears made during large-scale mark-recapture studies, suggest that although some polar bears are capable of mating from about late January to early July, the peak of breeding behavior is from late March through mid-May. The wide variation in possible times of mating and fertilization of ova does not skew the timing of birth because polar bears have delayed implantation (Lønø 1970) so the timing of implantation is determined by photoperiod in the autumn, regardless of when mating might have occurred (Spady *et al*. 2007).

Detection of a Potential Reproductive Female and Weaning of the Young

Anecdotally, polar bears have been reported sniffing the tracks of conspecifics in the wild and male polar bears have been observed to follow preferentially the tracks of an adult female on the sea ice that was apparently available for reproduction, after sniffing and ignoring the tracks of several other bears of various age and sex classes (Stirling and Derocher 1990). In our observations of the focal mating pair at Radstock Bay, the male often sniffed the tracks of the female in the snow (Fig. 2b) and lifted his head up to scent the air while following her (Fig. 2a, c). It is likely he was using flehmen behavior (Ewer 1998) (Fig. 3c) to enhance his olfactory sensitivity for assessing possible changes in the reproductive receptivity of the female, which in turn likely influenced changes in his own behavior toward her. In controlled experiments with captive polar bears, Owen *et al* (2014) also confirmed that males used flehmen behavior when differentiating the reproductive condition of different females, from pedal scents in tracks in snow collected from free-ranging polar bears of different sex and reproductive classes on spring sea ice in the Beaufort and Chukchi seas. Furthermore, histological examination of pedal skin collected from two adult females indicated prominent and profuse apocrine glands in the feet in association with large compound hair follicles, suggesting that they may produce scents that give off chemical signals indicating reproductive status. These results, and our observations of paired polar bears in the wild, suggest that scent from pedal glands, and possibly urine as well, in a female's tracks in the snow convey information on reproductive receptiveness to conspecifics and that chemical communication in polar bears has evolved to facilitate communication and social behavior related to reproduction between individual animals that are widely dispersed over vast areas at low densities.

In most polar bear populations, cubs are weaned at 2.5 yr of age (Ramsay and Stirling 1986) but the process of weaning has rarely been documented. Of 91 females observed with adult males in spring in the Canadian Arctic, none was accompanied by a cub (Ramsay and Stirling 1986). It has been assumed, but not reported except in this study, that the males force weaning on the 2.5-yr-oldcubs by chasing them away from the female at the beginning of their reproductive interactions. Occasionally, however, a cub may still be observed nearby while the adults are mating (*e.g*., Hagen 1975). Whether, or how often, a female and her formerly dependent cub might reunite after mating behavior ceases is unknown. However, one adult female observed

hunting for several hours with her 2.5-yr-old cub in Radstock Bay on 5 August 1973, suddenly walked briskly away, unnoticed, while the cub was lying still-hunting nearby. When the female was about a km away on the ice, the cub suddenly noticed she was gone and began to run after her. However, when the cub got close, the female turned, aggressively charged, and chased it away for several hundred meters, before turning and vanishing into the distance. The cub appeared disoriented and wandered about aimlessly on the gravel ridges near the shoreline for several hours before eventually returning to the ice to hunt. In this instance, it appeared the 2.5-yr-old had apparently either remained with the mating pair, or reunited with its mother after mating was completed, and the female eventually chased it away herself.

In an earlier observational quantitative behavior study, also conducted at Radstock Bay, it was concluded that polar bear cubs <2.5 yr of age in the Canadian High Arctic are not capable of hunting seals sufficiently successfully to be able to survive without their mothers to provide for them (Stirling and Latour 1978) with the result that all female bears accompanied by dependent cubs of any age were protected from being hunted. Since then, it has generally been assumed that females accompanied by yearlings are not available for breeding (Ramsay and Stirling 1986), and this is likely correct in most cases. However, there are two documented instances of an adult male herding an adult female that did not seriously attempt to escape, appeared to ignore their yearling cubs, and were beginning interactions characteristic of breeding behavior. On 17 May 1977 IS sighted an adult male-female pair of polar bears together near the east coast of Baillie-Hamilton Island in the Canadian High Arctic. Her two yearling cubs were about 200 m away and trying to reunite with the female but she showed no interest in them. After 30 min of watching the male herding the female and the cubs trying to approach her but being ignored or chased away, all bears were immobilized for tagging. The female was lactating but her vulva was swollen and clearly in breeding condition. The male had open wounds on his side and over one eye from fighting with other males. No subsequent observations of any of the bears were recorded.

On 20 June 2005, at the Andoyne Islands in northern Svalbard, a female bear with two yearling cubs was sighted running over the ice followed by a male.[5] All entered the water and then the cubs and their mother exited onto a small island. The cubs began to call and, initially, the female turned toward them. However, once the male reached the island, the female began to ignore the cubs and walk away, followed by the male, despite her cubs calling to her. The female then swam to another island, followed by the male. Once on the island, the male approached the female after which the pair walked back and forth and interacted. However, the female did not try to escape. A short time later, two other adult bears appeared interested and began to approach but then the first male and the female swam away together. Observations ceased at this point, after about 2.5 h. How often females accompanied by yearling cubs might abandon them, apparently to mate with an adult male as described above, or the hormonal basis for this unusual behavior, are unknown.

Documentation of Reproductive Behavior in Zoos

Dates and duration of mating behavior, though most often simply focused on copulation, are also available from zoos. Such observations are sometimes difficult to

[5]See note 4 above.

compare to our observations of wild bears because of the primary focus on copulation with limited related descriptive detail and that behavioral sequences may be interrupted by bears being moved or separated at times by keepers. Malev *et al*. (1990) reported that the duration of estrus (apparently defined as the period during which a male-female pair interacted and copulation was observed) in 104 polar bears in Russian zoos averaged 11.2 d, with a range of 1–43 d. The average is similar to the 13 d the male-female pair were observed together at Radstock Bay. Copulations were recorded by Malev *et al*. (1990) over a period lasting from 25 January to 13 June. Malyov (1990) reported that from 1978 to 1987 in the Kazan Zoological Gardens, estrus was observed from 13 March to 27 April and lasted from 8 to 13 d (sample size not given). Tumanov (2001) reported the number of cubs born as a result of copulations observed each month at the St Petersburg Zoo, Russia, from 1938 to 1988. The durations of estrus or numbers of copulations were not reported but the following summarizes the number of cubs produced by individually known females, resulting from copulations observed by month: February, 9; March, 15; April, 20; May, 4; and June, 2), suggesting a peak in breeding success in March and April, similar to the overall pattern reported above from wild polar bears.

In a study of testosterone levels in scats from 14 male polar bears in zoos, monitored for periods of 12–36 mo, testosterone levels were highest from early January through the end of May (Curry *et al*. 2012). Stoops *et al*. (2012) measured immunoreactive progesterone, progesterone metabolite (PdG), estrogen, and androgen metabolite (T) concentrations from fecal samples collected from 20 captive female bears over a 24 mo period. The fecal hormone analysis confirmed that female polar bears are seasonally polyestrous, with estrus occurring over a lengthy period from January to June. These findings supported the conclusions from previous reports that estrus and mating may occur over multiple days and, that like wild polar bears, captive females were potentially capable of reproducing over a relatively long breeding season. Taken together, these conclusions about the breeding season of polar bears based on observations of mating behavior in zoos, augmented by histological and hormonal studies, are similar to those made from wild bears, and suggest that while the breeding may occur from January through June, the peak of copulatory behavior occurs in April and May.

Duration of Copulation

The male of the mating pair we observed remained mounted and alternately copulating and resting between periods of rapid thrusting for periods of 51, 86, 66, and 150 minutes on 9–10, 12, 13, and 14 May, respectively, apart from momentary separations. Smith and Aars (2015) observed a 15 min copulation of wild polar bears. Similarly, Malyov (1990) reported that the duration of copulation in two captive bears at the Kazan Zoobotanical Garden was 25-30 min but gave no sample size or range. In one copulation, lasting 30 min, Malyov (1990) reported that the male had 20 "orgasms," lasting 2–3 s. The reported durations of these "orgasms" are similar to our documentation of the average length of "intense thrusting sessions" of 3.7 s. It seems likely that these brief periods of intense thrusting culminate with orgasm, but we know of no confirmation in the literature. The average duration of the refractory periods, declined significantly from 48.21 s through the first 3 d of observations of copulation to 24.87 s on the last day. The mean of the latter was similar to the range reported by Malyov (1990) of 18–30 s. The increased duration and intensity of the last observation of copulation in our observations suggests the possibility that the ini-

tial bouts functioned to stimulate ovulation while the last session may have been critical to maximizing the probability of fertilization.

Malyov (1990) reported that after mating, the female became aggressive toward the male, sometimes so intensively that they had to be separated. We observed nothing similar and aggressive behavior by the female to the male, postcopulation, has not been reported in other accounts of mating polar bears in the wild (Hagen 1975, Smith and Aars 2015). Similarly, no aggressive behavior was observed in the male-female pairs observed in June in Svalbard. Although there are few data on this aspect, we suggest that the observation of apparent "aggressive" behavior of females toward males, following copulation in captivity, may have been an artifact resulting from captivity.

Compared to the observations at Radstock Bay, and the other observations from Svalbard in June, the copulatory behavior described by Genillard[6] from Svalbard in 2010 differed markedly. Although the female remained in the same area with up to 13 other bears, including four adult males, her interactions with the males, and the copulations seen, were extremely brief. Her age, status, and behavior in relation to any of the other bears prior to the observations was unknown. The apparent lack of sexual interest in the female on the part of the adult males, or possible predatory behavior, may have been influenced by a decline in hormonal activity so late in the breeding season and possibly because of the male being satiated by feeding on a dead whale (see *23–27 June 2010, Holmiabukta, Svalbard* above).

Induced Ovulation, Male Intrasexual Competition, Female Fitness, and the Mating System of Polar Bears

The only ursid in which induced ovulation has been confirmed experimentally is the black bear (*Ursus americanus*) (Boone *et al*. 2003, 2004). However, because bears are distributed in a solitary manner during the breeding season, it has generally been assumed that induced ovulation occurs in most ursids (Bunnell and Tait 1981, Stirling and Derocher 1990, Spady *et al*. 2007). Certainly, the extended period through which the male and female polar bears were observed interacting in this study before copulation was initiated, followed by several more days during which copulation continued, appears to confirm that a significant amount of behavioral interaction over an extended period is required before ovulation can occur.

The need for extended behavioral interaction prior to the initiation and completion of copulatory behavior also provides a motivation for males to sequester females into areas where they are less likely to encounter competing males, if possible (*e.g*., Ramsay and Stirling 1986, Wiig *et al*. 1992, this study). Ramsay and Stirling (1986) reported that 8% (7/91) of females documented in breeding pairs were accompanied by more than one male. Wiig *et al*. (1992) reported one female being accompanied by three different males over a period of 18 d, although that may have been partly influenced by interruptions from research activities. In our study, the male and female under observation experienced 12 different bears passing within 1–300 m. Of those bears, five were potential challengers, three of which departed quickly without fighting when threatened by the male of the breeding pair. The completely dominant status of the male of the breeding pair was demonstrated by his ability to defeat both of the two largest challengers that were willing to fight, in seconds, by physically forcing them to the ice and holding them down with his jaws around their throats.

[6]See note 2 above.

Although the second male fought by the dominant male challenged him a second time after being allowed to stand up, and both had bleeding wounds when they separated, the fight was again over in seconds and there was never any doubt about which bear was dominant.

Recent genetic analyses have confirmed that it is possible for 3- and 4-yr-old males to sire offspring (Cronin *et al*. 2009, Zehl *et al*. 2009, Richardson 2014). Because, on average, adult females wean their cubs at 2.5 yr of age, they are only available to mate every 3 yr, so that the initial simplistic ratio of males to females is 3:1. However, Rosing-Asvid *et al*. (2002) found that male testis length did not reach 95% of asymptotic size until 5.8 yr of age and Derocher *et al*. (2010) found that the mean age of males paired with females (13.6 yr) was similar to the age at which males reach 97% of their asymptotic body mass (13.5 yr, Derocher and Wiig 2002), suggesting that older and larger males likely do more mating than younger ones. In the southern Beaufort Sea, the mean age of breeding males was 12.7 yr (Cronin *et al*. 2009). In Western Hudson Bay, the fathers of a total of 873 cubs were determined genetically and their mean age was 13.0 ± 4.5 yr (range: 2–25; $n = 628$) (Richardson 2014). Seventy-five percent of paternities in Western Hudson Bay were assigned to males 10–20 yr old, with a marked peak in male reproduction between 11 and 15 yr of age, and accounted for 46% of all paternities.

The intensity of the competition between males for breeding females is also indicated by the increase of damage to the teeth from intrasexual fighting as males become older (Ramsay and Stirling 1986, Derocher *et al*. 2010). Although some fights involve considerable fighting and wounding of opponents, if a male is sufficiently large and dominant, like the one we observed, it is clear that submissive behavioral interactions have evolved sufficiently to facilitate a quick conclusion to a fight so that neither animal risks significant wounding from additional, but unnecessary, fighting. Such observations emphasize the importance of large body size to the reproductive success of male polar bears and hence, the evolution of such predominant sexual dimorphism (Ramsay and Stirling 1986; Derocher *et al*. 2005, 2010). As well as ensuring that ovulation occurs while a male is present, the extended period of interactions between a male and female potentially allows time for challengers to find a breeding pair so that if intrasexual competition occurs between them, the most dominant male may be more likely to be the one that completes copulation with the female and fertilizes her ova. Although that does not appear to facilitate direct choice by the female, the combination of a high degree of sexual dimorphism, and the age-related reproductive data in Richardson (2014), suggest that with respect to the female's fitness the extended period of behavioral interaction that precedes copulation, as well as the occurrence of copulation over several days, maximizes the probability that she mates with the most dominant male(s) available at the time.

Similar observations have been made of mating pairs of the closely related brown bear (*Ursus arctos*) remaining together for extended periods during mating, and some degree of sequestering of females (*e.g.*, Hornocker 1962, Herrero and Hamer 1977, Hamer and Herrero 1990). However, in some documented cases, fighting between adult males has been significantly less than that reported from polar bears. For example, Sparrowe (1968) observed one male grizzly copulating with a female for 25 min, after which a second male then mounted the same female and attempted to copulate for a few minutes. No aggressive interactions were noted between the three bears involved in copulation or with three other bears feeding within a few meters. Hornocker (1962) observed a female brown bear that mated 10 times with four males in 2 h. Considering such observations, it is not surprising that 15%-28% of litters of

brown bears had litters with multiple paternities (Bellemain *et al*. 2006). Similarly, in two studies of black bears, 28% and 29% of litters had multiple paternities (Kovach and Powell 2003, Costello *et al*. 2009). In contrast, the percentage of multiple paternities documented in polar bears in the Barents Sea (Zeyl *et al*. 2009) and in western Hudson Bay (Richardson 2014) were 6.9% and 6.6%, respectively.

Taken together, these data demonstrate that both age and larger body size, not simply the ability to produce sperm, are the primary determinants of male reproductive success. Polar bears have the highest degree of sexual dimorphism of all bear species (Stirling and Derocher 1990), suggesting that selection for large body size and greater sexual dimorphism is linked to intense selective pressure for large size because it increases the likelihood of being able to defend reproductive exclusivity of estrous females once sequestered, as observed in this study, which in turn results in increased fitness of the larger males. Such behavior, as a consequence of marked sexual dimorphism, probably also explains the low proportion of multiple paternity litters. In addition, because of the long time period required for behavioral interaction to take place between the male and female prior to the completion of mating, it is likely that the maximum number of individual females that can be impregnated by a single male is likely about 4–6 (Richardson 2014).

The mating system of polar bears has been variably described as polygynous (DeMaster and Stirling 1981), scramble with the possibility of polyandry (Ramsay and Stirling 1986), promiscuous (Zehl *et al*. 2009), female defense polygyny, or serial monogamy (Derocher *et al*. 2010) and serial female-defense polygyny (Richardson (2014). The meaning of the last term is that once a male finds and sequesters a reproductive female to the best of his ability, he remains with her and mates until the process is completed, after which, he seeks another female with which to repeat the same process. This latter terminology appears to be the clearest and most supported by observations made in this study, as well as in other related anecdotal reports cited above.

Comparison of the Activity Budgets of Breeding Pairs of Polar Bears and Adult Male and Female Bears Not Engaged in Mating Behavior

One of the most biologically important differences in the activity budgets of paired and unpaired adult female and male polar bears in this study was in the amount of time spent hunting (Table 1, 2). The extreme brevity of the hunts undertaken by the adult female, while the male stood only a few meters away, suggests that the occurrence of such behavior during breeding functioned more as a displacement behavior than representative of serious hunting. Even though the proportion of time that the female and male of the mating pair spent hunting was a very small proportion of the time they were observed, the females hunted significantly more than did the males. Similarly, female polar bears not paired with a male also hunted significantly more than did unpaired male bears. These results suggest that even when engaged in mating behavior, females appear to retain a greater interest in hunting than do males and that they probably return to hunting and feeding more quickly and intensely once they are alone again. Meanwhile, males in spring continue to spend less time hunting than females, even when alone, possibly because they are more driven to spend their time searching for adult females to mate with at that time. These overall results are consistent with urea-creatinine ratios documented in the blood of polar bears in the Beaufort Sea in spring that indicate a higher proportion of adult males fast during spring than do females, and the proportion was significantly higher for males that

were accompanying estrous females at the time they were sampled than those not accompanying females when captured (Cherry *et al*. 2009).

The paired female and male also spent significantly more time interacting, less time walking, and more time lying than did unpaired lone adults of the same sex (Table 1, 2). Because paired bears remained in a small area as described above and did little hunting, they simply did less walking because they were not traveling in search of places to hunt. It is likely that the greater amount of time spent lying, in both the lying <60 min and lying >60 min categories, was simply related to conservation of energy during a period in which both bears were active but that neither was hunting or feeding.

In comparison, Stirling and Latour (1978) reported that adult females accompanied by COY and yearlings hunted for 18.5% and 19.6%, respectively, of the total time they were observed in spring (April–May), and 53.1% and 35.1%, respectively, of the total time they were observed in early summer (late June–July). Lone adult males hunted 24.7% and 39.9% of their time in spring and summer respectively. The proportion of time spent hunting by lone adult females in this study was similar to that spent hunting by adult females with cubs in in the Canadian High Arctic during the 1970s. However, the proportion of time Stirling and Latour (1978) observed lone adult males hunting in spring in the 1970s (24.7%) was much higher than recorded in this study. We do not have an explanation for that except that the smaller sample size of observation time of unpaired males recorded in this study may have been a factor.

Evolution of the Timing of Breeding Behavior and Possible Negative Effects of Climate Warming

Quantification of the behavioral observations described above also provides possible insight into evolution of the timing of breeding behavior of polar bears as well as two related possible negative effects of climate warming. Polar bears reach their lightest weights of the year in late winter at about the same time as the first ringed seal pups are born in early April (Smith 1987). Most pups are weaned by mid-May at about 6 wk of age by which time the proportion of their wet weight made up of fat has increased from approximately 12%–20% to about 45%–50% and they are still relatively naïve about predators, which may make them more vulnerable to predation (Stirling and McEwan 1975). This is particularly important because polar bears may accumulate up to two-thirds of their annual energy requirement during the hyperphagic period between when the pups are weaned and breakup of the sea ice in early summer, when the seals become pelagic and largely unavailable to the bears (Stirling and Øritsland 1995). Because adult bears (especially males) spend significantly less time hunting when breeding than at other times, selection may have favored evolution of a peak mating period of April to mid-May, ahead of the relatively brief but most critical feeding time of the year. If so, such a shift could reduce the overall caloric loss that might be experienced if the peak of breeding overlapped to a greater degree with the most important time of the year for accumulating the fat reserves critical to both the survival of the adults and the eventual production of cubs. In addition, occurrence of the peak period of breeding behavior in April–May ensures that weaning of most polar bear cubs, at 2.5 yr of age, occurs just prior to the best time of year for them to begin independent hunting (Stirling and Latour 1978).

Because the most dominant adult males might mate with four or more females in a single breeding season, each of which may require 12 or more days together (not

counting search time between potential reproductive females), and that those males feed little during those periods, they likely lose a substantial proportion of their stored fat reserves during the two month duration of the main breeding season. The adult male we observed in this study, separated from the female on 14 May, toward the end of what we suggest is the peak breeding season. Although we do not know what he might have eaten prior to when we first saw him, he ate nothing during the period of observation and was visibly lean by the end of it, though not yet skinny. In an area such as Western Hudson Bay, the average date of breakup is already 3 wk earlier than it was only a few decades ago because of climate warming (Stirling *et al*. 1999; Hochheim *et al*. 2010, 2011; Richardson 2014). Thus, bears of all age and sex classes are now experiencing progressively shorter periods of time during which to accumulate fat during the most important feeding time of the year, after which they must then endure ever-longer periods of fasting during the open water season. As a result, body condition of lone adult females, most of which should be pregnant, has declined significantly (Stirling *et al*. 1999, Stirling and Derocher 2012). That trend is predicted to continue as the climate continues to warm (Stirling and Derocher 2012). For adult males that have already lost much of their body condition though the breeding season, a significant shortening of the peak period for replenishing their stored fat reserves by taking advantage of hunting newly weaned ringed seal pups may negatively influence their annual survival over time.

Lastly, Owen *et al*. (2014) experimentally documented that adult male polar bears in captivity responded more to chemical snow samples collected from the footprints of reproductive females than to other categories of polar bears. They hypothesized that if breakup becomes earlier and more extensive, the resulting increase in open water could result in disruption of a chemical signal trail on the ice and could make it more difficult for adult males to track and locate potential breeding females. Our observations of wild breeding males making constant use of scent in the tracks of adult females in the snow supports their conclusions based on studies of captive animals.

Conclusion

In summary, the quantified behavioral observations reported in the first portion of this paper present a unique full documentation of the breeding behavior or wild polar bears, which adds markedly to our understanding of the natural history of this species. Of equal importance is that this unique data base, when combined with anecdotal observations as well as studies of other aspects of polar bear biology from both wild and captive animals, facilitated greater understanding of several other aspects including defining the breeding season, evaluation of the reliability of some behavioral observations made in zoos, understanding the mating system, and defining additional potential negative consequences of climate warming. These contributions to our broader understanding of the ecology of polar bears would not have been possible without the basic collection and application of quantified long-term natural history observations of wild undisturbed animals.

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