

Comparing movement patterns of satellite-tagged male and female polar bears

S.C. Amstrup, G.M. Durner, T.L. McDonald, D.M. Mulcahy, and G.W. Garner

Abstract: Satellite radiotelemetry has provided great insights into the movements and behaviors of polar bears (*Ursus maritimus*). The diameter of the neck of adult male polar bears exceeds that of their head, however, and radio collars slip off. This has limited collection of movement information to that from radio-collared females. To overcome this difficulty and gather information about their movements, we surgically implanted satellite radio transmitters into 7 male polar bears during 1996 and 1997. We compared movements of implanted males with those of 104 adult females radio-collared between 1985 and 1995. Transmitters were implanted under the skin on the midline of the top of the neck and were equipped with percutaneous antennae. Implanted transmitters operated for up to 161 days providing 3217 satellite relocations. While transmitting, radios implanted in males provided a larger proportion of the highest quality category of position fixes than was obtained from radio-collared females. However, all implanted radios ceased transmitting before reaching their projected life-span. The abrupt termination of transmission from implanted radios suggested mechanical rather than electronic failure. Mean rates of short-term movement for males (1.18 km/h) were lower than for solitary females, females with cubs, and females with yearlings (1.70, 1.84, and 1.95 km/h, respectively). Net geographic movements from the beginning to the end of each month were comparable for males (mean = 135 km) and females (mean = 114, 152, and 168 km). Mean azimuths of these net movements also appeared to be similar. Monthly activity-area sizes for males (mean = 8541 km²) were comparable to those for females (mean = 3698, 9397, and 10 585 km²) during the time period of comparison. In contrast to the other movement measures, males traveled longer mean distances (387 km) each month than did females (217, 289, and 302 km). Movements of males, it appears, were more directed than those of females, but males confined their travels to similar-sized areas.

Résumé : La radio-télémétrie par satellite a permis d'étudier en détails les déplacements et les comportements chez l'Ours blanc (*Ursus maritimus*). Cependant, le diamètre du cou des mâles adultes est supérieur à celui de leur tête, ce qui fait que les colliers ne tiennent pas. Cette contrainte a restreint les relevés de données sur les déplacements à ceux des femelles porteuses de colliers. Pour contourner ce problème et pour enregistrer les déplacements des mâles, nous avons procédé à des greffes chirurgicales d'émetteurs radio à 7 Ours blancs mâles en 1996 et 1997. Nous avons comparé les déplacements de ces mâles à ceux de 104 femelles munies d'un émetteur entre 1985 et 1995. Les émetteurs ont été greffés sous la peau, le long de la ligne médiane du cou et équipés d'antennes percutanées. Les émetteurs greffés ont fonctionné jusqu'à 161 jours et permis 3217 repérages par satellite. Pendant la transmission, les émetteurs greffés aux mâles ont produit une plus grande proportion des repérages de la meilleure qualité que les émetteurs portés par les femelles. Cependant, tous les émetteurs ont cessé de fonctionner avant la fin de leur durée théorique de fonctionnement. L'interruption abrupte de la transmission des émetteurs greffés semble indiquer des problèmes mécaniques plutôt qu'électroniques. La vitesse moyenne des déplacements à court terme était plus faible (1,18 km/h) chez les mâles que chez les femelles solitaires, les femelles avec des petits de l'année ou les femelles avec des petits de 1 an (1,70, 1,84 et 1,95 km/h). Les déplacements géographiques nets du début à la fin de chaque mois étaient semblables chez les mâles (moyenne = 135 km) et chez les femelles (moyenne = 114, 152 et 168 km). Les azimuts moyens de ces déplacements semblaient aussi comparables. La taille des aires d'activité utilisées par les mâles en un mois (moyenne = 8541 km²) était similaire à celle des aires utilisées par les femelles (moyenne = 3698, 9397 et 10 585 km²) durant toute la période de comparaison. Contrairement aux autres mesures des déplacements, la distance parcourue en 1 mois était plus longue chez les mâles (moyenne = 387 km) que chez les femelles (moyenne = 217, 289 et 302 km). Les déplacements des mâles semblaient suivre un trajet mieux défini que ceux des femelles, mais les mâles ne se déplaçaient qu'entre territoires de même taille.

[Traduit par la Rédaction]

Received February 28, 2001. Accepted September 19, 2001. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on December 21, 2001.

S.C. Amstrup,¹ G.M. Durner, D.M. Mulcahy, and G.W. Garner.² U.S. Geological Survey, Alaska Science Center, 1011 East Tudor Road, Anchorage, AK 99503, U.S.A.

T.L. McDonald. Western Ecosystems Technology, Inc., 2003 Central Avenue, Cheyenne, WY 82001, U.S.A.

¹Corresponding author (e-mail: Steven_Amstrup@USGS.GOV).

²Deceased.

Introduction

Effective satellite telemetry systems have allowed gains in understanding the movements of mobile animals that live in remote habitats. Polar bear (*Ursus maritimus*) researchers and managers are among the greatest beneficiaries of the success of this technology. Building platform transmitter terminals (PTTs) into neck collars and attaching them to polar bears has provided previously unobtainable insights into polar bear movements, behaviors, and denning ecology (Amstrup et al. 1986, 2000; Messier et al. 1992; Amstrup and Gardner 1994; Bethke et al. 1996; Amstrup 2000). Neck-collar radios, however, can only be attached to adult female polar bears. Young animals cannot be fitted with collars for fear of injury that could result as they grow and the collar does not. Further, because the diameter of the neck of adult male polar bears exceeds that of their head, even a tight-fitting collar slides off during the normal activities of the animal. Females, it could be argued, are the most important component of the population from a management perspective (Taylor et al. 1987). Nonetheless, males and subadults constitute a large portion of the population. Polar bear populations can sustain higher harvests of males and subadults than of adult females (Taylor et al. 1987) and both appear to be more vulnerable to human hunters than adult females. Males are necessary for population maintenance, and in terrestrial bear species at least, they may also play a role in limiting population size (McCullough 1981; Young and Ruff 1982; Stringham 1986). The dearth of knowledge on movements and activities of males is a significant management and research shortcoming.

Mark and recovery studies suggest that distances moved by polar bears of different sex and age classes are similar (Stirling et al. 1980, 1984; Schweinsburg et al. 1981; Lentfer 1983). Telemetry studies, however, are superior to tag and recovery studies in assessing movements (Seidensticker et al. 1973), and have shown that male brown (*Ursus arctos*) and black (*Ursus americanus*) bears are much more mobile than females of the same species (Amstrup and Beecham 1976; Ballard et al. 1982; Rogers 1987; Nagy and Haroldson 1990). It appears that movements of terrestrial female bears are designed to secure food sources, while movements of males, at least during the breeding season, maximize overlap with the home ranges or territories of females (Rogers 1987). Female polar bears do not defend territories and their home ranges are larger and less rigid than those of terrestrial female bears (Amstrup et al. 2000). The need to overlap ranges of many females could, nonetheless, lead male polar bears to occupy larger areas and move longer distances than females. Nagy and Haroldson (1990) suggested that male grizzly (brown) bears which had very large breeding-season ranges reduced their movements after the breeding season in order to maximize nutritional intake. Swenson et al. (1998) suggested that expansive movements of male brown bears create the lead wave in population expansions. Such exploratory movements may explain why male bears appear to be more vulnerable to hunting and other human-caused mortality factors than females.

If seasonal and annual movements of male polar bears differ from those of females as they do in terrestrial species, our understanding of movements of radio-collared females cannot be extrapolated to males. This is more than an eso-

teric issue. Current worldwide management of polar bears is based upon the results of existing radiotelemetry studies. If male polar bears move in patterns that are significantly different from those of females, adjustments to current management plans (Treseder and Carpenter 1989; Nageak et al. 1991) will be required. Here we summarize the movements of 7 adult male polar bears equipped with implanted subcutaneous PTTs and make the first attempt, using satellite radiotelemetry, to compare the movement patterns of male and female polar bears.

Materials and methods

Field procedures

Our study area was the coastal portions of the Chukchi and Beaufort seas adjacent to Alaska (Fig. 1). We captured polar bears, for the purpose of attaching radio transmitters, by injecting immobilizing drugs (phencyclidine hydrochloride (Sernylan®, Park, Davis and Company), etorphine hydrochloride (M-99®, Lemmon Company), and tiletamine hydrochloride plus zolazepam hydrochloride (Telazol®, Warner-Lambert Company)) by means of projectile syringes fired from helicopters (Larsen 1971; Schweinsburg et al. 1982; Stirling et al. 1989). Capture protocols were approved by independent animal care and welfare committees. We captured female polar bears in the Beaufort Sea and adjacent areas each spring (except for 1990) between 1985 and 1994 and in the autumn of 1985, 1986, 1988, 1989, and 1994. Autumn captures were made in October and November each year and spring captures between March and May. PTTs were attached to adult female polar bears with neck collars (Amstrup et al. 2000). Male polar bears were instrumented in March 1996 and 1997 by surgically implanting a transmitter on the midline of the neck rostral to the dorsal border of the scapulae (Mulcahy and Garner 1999).

PTT collars also carried VHF beacons that could be located with aircraft. VHF transmitters built into ear tags were used to allow aerial radio-tracking of implanted male polar bears (Mulcahy and Garner 1999). Geographic locations of PTT-equipped animals were determined by sensors on the satellite that interpreted frequency-shift patterns caused by changes in the relative positions of the satellites and animals (Fancy et al. 1988). Data retrieved from PTTs were processed by the Argos Data Collection and Location System (ADCLS; Fancy et al. 1988).

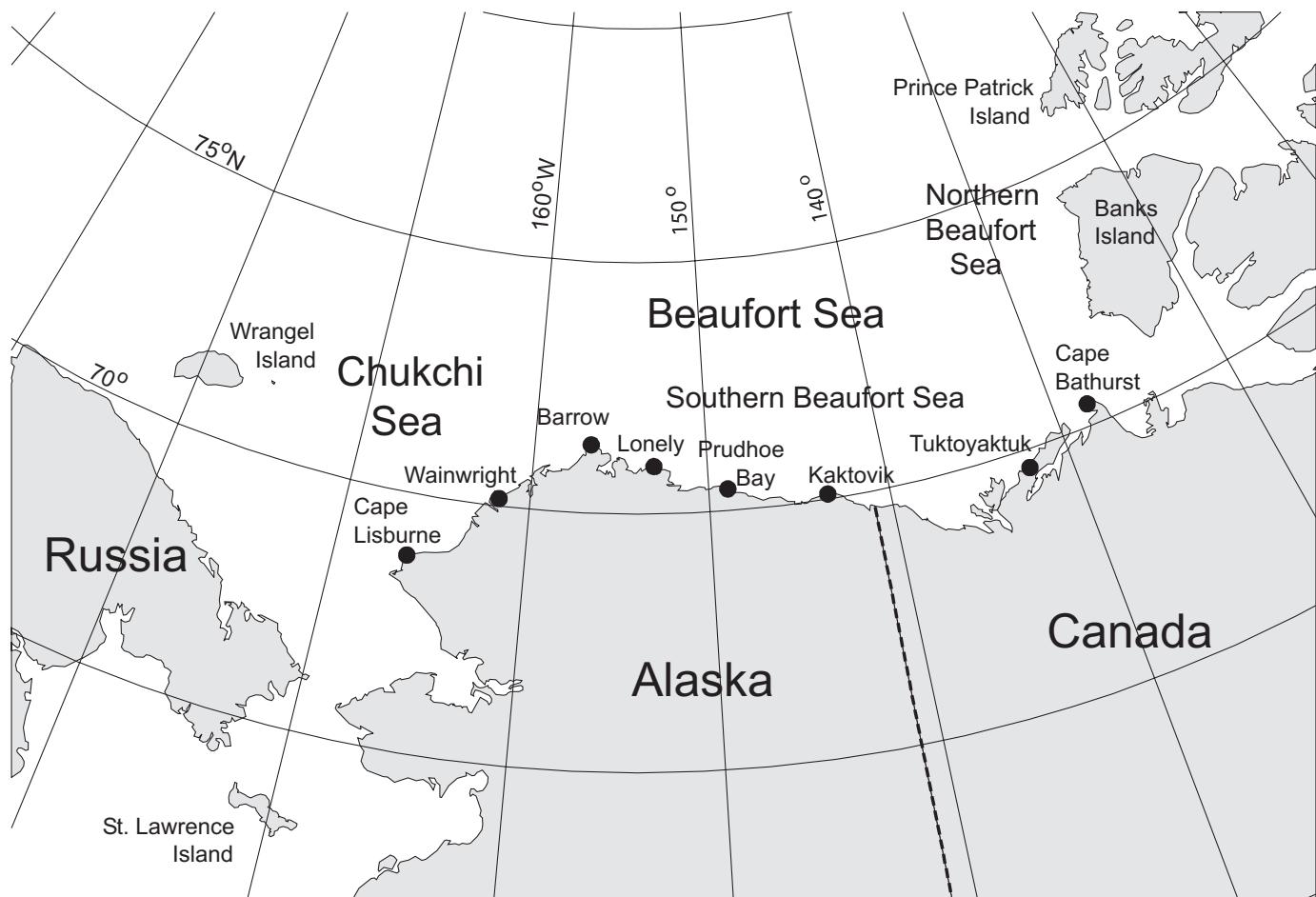
Analyses

Satellite radiolocations were ranked by Service Argos for their presumed location quality (LQ). Higher LQ scores reflect more accurate position fixes. LQ 1, LQ 2, and LQ 3 fixes are presumed to be within 1000, 350, and 150 m of the true location of the animal (Harris et al. 1990). A high proportion of fixes from polar bears historically have been rated LQ 0 and LQ -1 or below. No level of accuracy is presumed for those fixes. We compared the performance of PTTs implanted in males with that of radio collars worn by females by measuring the proportions of relocations in each of five LQ categories. For movement analyses we deleted all observations that were not in ARGOS class LQ 1, LQ 2, or LQ 3.

Transmitter performance

Because radios implanted in male polar bears had a different antenna configuration than radio collars attached to females, we speculated that the quality of position fixes from males and females might differ. For the first 6 months post deployment, we evaluated two response variables characterizing the quality of radio signals generated. The proportion of LQ 1 – LQ 3 fixes was calculated and labeled the proportion of "quality" radio signals. The proportion of

Fig. 1. Map of northern Alaska and adjacent areas where polar bears (*Ursus maritimus*) were captured and radio-tracked. Place names used in the text are also shown.



LQ 3 radiolocations was also calculated and labeled the proportion of "high-quality" radio signals.

We repeatedly measured LQ proportions for each bear for up to 6 months post deployment. We controlled for autocorrelation that could have resulted from repeated measures by calculating two parameters for each bear in the analysis and then comparing averages for those parameters between males and females. The two parameters computed through time for each bear were (1) the proportion of quality (and high-quality) radiolocations averaged over time and (2) the change in the proportion of quality (and high-quality) radiolocations each month post deployment. Change in the proportion of quality radiolocations was calculated as the coefficient of the month covariate in a logistic regression that related the proportion of quality locations to the month after deployment. We tested for differences in each of these parameters by computing *P* values with the normal approximations to Wilcoxon's two-sample rank-sum procedure (Sokal and Rohlf 1981).

Movements

We used Albers conic equal-area projection for plotting recorded locations of radio-collared polar bears. In areas like the Beaufort Sea, that extend more in an east–west than a north–south direction, Albers-projected shapes have minimal distortion and are proportional to the same areas on the earth (Environmental Systems Research Institute 1992). All locations of bears were recorded in latitude north and longitude west. For analyses, however, all geographic locations were converted to square Albers grid coordinates with a scale in metres. Hence, movements in all directions were measured on the same distance scale. We shifted the geographic

center point of the Albers grid to assure that all grid locations in our study area were positive.

Instrumented females were categorized according to whether they were solitary (not accompanied by young of any age), accompanied by cubs (aged <1 year), yearlings (aged 1–2 years), or 2-year-olds (aged 2–2.5 years). We used aircraft radiotelemetry to obtain visual observations of instrumented females at intervals throughout their transmission periods. This allowed us to confirm that females were accurately allocated to each of these reproductive-status categories. It also allowed us to confirm survival, changes in reproductive status, and denning and other behaviors. Because of the small sample size, all males were included in one class.

PTTs did not transmit continuously. Rather, they operated with a duty cycle that included short bouts (e.g., 4–8 h) of transmission every 3–7 days. The high proportion of dormant time was designed to maximize battery life. The duty cycles of our PTTs allowed us to evaluate rates of movement between relocations that were separated by 0–8, >8–20, >20–28, 68–100, and >100–168 h (there were no duty cycles that resulted in relocations at 50-h intervals, for example). We usually recorded multiple observations during the transmission bout of each duty cycle. If >1 location per duty cycle was ranked LQ 1 – LQ 3, we deleted, for analyses other than short-term movement rates, all but the one with the highest quality (for details on data standardization see Amstrup et al. 2000).

We determined rates of hourly movement (km/h) by measuring the linear distance between consecutive radiolocations and dividing by the number of hours separating these locations. Movement rates of females declined precipitously as the time separating relocations increased (Amstrup et al. 2000). Because of the rapid drop in

hourly movement for all periods greater than 8 h, we combined those longer periods for subsequent evaluation. Long-term movement rates (>8 to 168 h separation between locations) were derived from measurements between the highest quality locations recorded in adjacent duty cycles. Short-term movement rates (0–8 h temporal separation) were derived from multiple locations recorded within duty cycles. For those comparisons, all LQ 1, LQ 2, and LQ 3 locations separated by at least 1 h were retained for analyses.

Net movement, or shift in geographic position, of each animal in each month was defined as the linear distance between the first and last radiolocations recorded for each month. Total distance moved each month was calculated by summing the distances (km) between consecutive satellite re-observations of each bear each month. Total distance moved and net movement for each month were measured only if ≥20 days elapsed between the first and last locations recorded each month. Direction of movement from the first to the last location in each month (mean azimuth and angular deviation or “dispersion” from the mean) was determined by converting angles to the appropriate trigonometric functions. We tested for significant directional tendencies in movements by comparing azimuths of net movements for each month using Rayleigh’s test of uniformity of distribution (Zar 1984, p. 443).

We used the program CALHOME version 1.0 (Kie et al. 1996) to estimate home-range sizes of the different categories of polar bears by means of the convex-polygon method (Hayne 1949). We calculated the size of monthly activity areas for each month in which an individual bear generated ≥8 high-quality relocations over a period ≥20 days within that month.

We were interested in comparing hourly movement rates, total distances traveled, net movements, and sizes of activity areas among the main effects (*i*) month and (*ii*) reproductive-status category. Data pertaining to all movement measures were recorded for individual bears in multiple months and in the same month during different years. Also, some individual bears appeared in more than one reproductive-status category (e.g., a female with cubs in one year might be recorded as a female with yearlings the next year). Hence, the sampling unit was the individual bear. Previous analyses confirmed that the repeated measures from each individual resulted in significant temporal autocorrelation among relocations (Amstrup et al. 2000). We controlled for this autocorrelation when we compared main effects with univariate repeated measures ANOVAs. The main effect tests in these ANOVAs were valid, assuming that the statistical errors between measurements on the same bear adhered to either the compound-symmetry or Huynh–Feldt condition (Huynh and Feldt 1970; Milliken and Johnson 1984; Neter et al. 1990; Littell et al. 1994). These conditions are known to apply to broad categories of spatial and temporal autocorrelation. The compound-symmetry condition specifies that observations through time on a single bear are equally correlated. The Huynh–Feldt condition is more general than compound symmetry and specifies that all variances of the differences between pairs of statistical errors are equal. Our experimental design was equivalent to evaluation of split plots (Neter et al. 1990, pp. 1066–1072). Multiple comparisons among status categories and monthly means were made with the Tukey–Kramer HSD test (Neter et al. 1990:584).

We performed statistical analyses on a Unix workstation running SAS version 6.11 software (SAS Institute Inc., Inc., Cary, N.C.) and on a Pentium personal computer running Excel (Microsoft Corp., Redmond, Wash.) and S-Plus (v. 2000, ©Mathsoft, Inc.). We report actual probabilities of our statistical tests unless $P < 0.0001$. P values >0.10 were deemed not significant and also are not reported.

Results

We equipped 4 male polar bears with implanted PTTs in 1996 and 3 in 1997. These 7 bears provided 3217 relocations

during April through September. During an extensive study of female polar bears we deployed 152 PTTs on 104 adult females. Collars were deployed on females along the mainland coast of the southern Beaufort Sea between 1985 and 1995 and provided 39 554 location records. Details of these records have been reported elsewhere (Amstrup et al. 2000) and are not duplicated in this report. Here we compare movement patterns of implanted male polar bears with those of females during April through September. Because most females wean their 2-year-old young in March, movements of females with 2-year-olds could not be compared with those of males and those data were deleted. Filtering data to 1 relocation per duty cycle left 260 locations from males for movement analyses. The “matching” female dataset comprised 6476 relocations from 100 individual females.

Ages of the 4 bears implanted in 1996 were 14, 14, 7, and 4 years. Ages of the bears implanted in 1997 were 8, 12, and 15 years. Hence, 6 males we radio-tracked were adults and 1 was a subadult (DeMaster and Stirling 1981). Three of the male bears implanted in 1996 were recaptured about 3 weeks following surgeries to inspect the implantation site; the fourth was out of range of shore-based aircraft and could not be captured. Sutures in 2 of the 3 polar bears examined required repair, the sutures in the third were healing properly (Mulcahy and Garner 1999). In 1997, instrumented male bears evaded capture in the weeks post surgery. We used a fixed-wing aircraft equipped for VHF telemetry to search for instrumented males in October 1996 and September 1997. However, none were located.

Transmitter performance

Implanted transmitter life ranged from 30–161 days, with a mean of 97 days. This was far short of the projected lifespan of 20–24 months. The bear implanted as an 8-year-old in 1997 was recaptured in spring 2000 at age 11. He had shed his radio transmitter and examination revealed only a scar where the surgical implantation had been performed.

Although longevity was poor, the signal strength of implanted radios was generally good prior to transmitter failure (Fig. 2). During the months they were on the air, implanted radios of male bears provided a significantly higher proportion (11.2%) of high-quality (LQ 3) locations than did radios deployed on females (4.4%; $P = 0.0015$). In contrast, radios deployed on females produced a significantly higher proportion (82.9%) of quality (LQ 1 + LQ 2 + LQ 3) radio signals than radios deployed on males (64.3%; $P = 0.0121$). There was no significant temporal trend in the average rate at which the proportion of quality ($P = 0.7081$) or high-quality ($P = 0.1494$) radio signals changed between males and females. Implanted radios showed no unusual premature signal deterioration. In short, they broadcast strongly and quit suddenly ≤ 6 months post deployment.

Movements

Rates of movement

Mean hourly movement rates, measured over the short term (≤ 8 h) varied among reproductive-status categories ($F_{[110]} = 7.82$, $P < 0.0001$) and among months ($F_{[346]} = 12.31$, $P < 0.0001$), but interactions between month and status were not present ($F_{[346]} = 1.11$, $P = 0.35$). According to

Fig. 2. Proportion of satellite radiolocations of each quality class collected from male and female polar bears during the first 6 months post deployment. Location accuracy increased from class LQ -1, for which there was no gauge of accuracy, to LQ 3, which were advertised to be within ± 150 m of the true location.

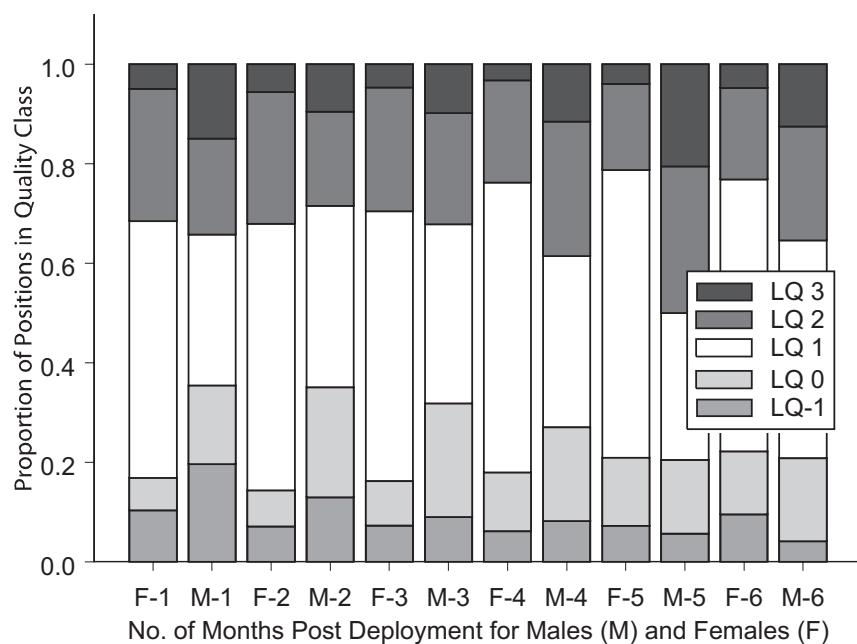


Table 1. Hourly movement rates (km/h) of polar bears (*Ursus maritimus*) in the southern Beaufort Sea.

	n	Summary statistics				Quantile value				
		Mean	Min.	Max.	SD	5%	25%	Median	75%	95%
Adult males	298	1.18	0.04	7.11	0.99	0.15	0.43	0.83	1.71	3.02
	248	0.67	0.01	3.01	0.47	0.12	0.31	0.53	0.97	1.45
Females with cubs	815	1.70	0.02	8.73	1.37	0.19	0.67	1.37	2.39	4.18
	571	0.45	0.00	4.32	0.41	0.07	0.20	0.35	0.60	1.16
Females with yearlings	972	1.84	0.01	8.43	1.32	0.28	0.81	1.57	2.61	4.25
	816	0.62	0.02	2.93	0.48	0.10	0.27	0.51	0.83	1.56
Solitary females	3293	1.95	0.02	9.51	1.50	0.25	0.79	1.59	2.75	6.92
	2529	0.63	0.00	4.79	0.51	0.09	0.28	0.50	0.83	1.57

Note: Male polar bears were subcutaneously implanted with satellite radio transmitters in 1996–1997. Females wore satellite radio collars from 1985 to 1995. Movement rates shown here were for travel between consecutive relocations. The first line in each reproductive-status category shows movement rates measured between relocations separated by ≤ 8 h. The second line shows rates measured over time periods >8 h; n indicates the number of measurements between consecutive relocations made for each class of animal.

the Tukey–Kramer HSD test, short-term movement rates of male polar bears were consistently lower than those of solitary females ($P < 0.0001$), those with cubs ($P = 0.0083$), and those with yearlings ($P = 0.0013$) (Table 1, Fig. 3).

Movement rates measured over the long term (>8 h) also varied by reproductive status ($F_{[112]} = 6.81$, $P = 0.0003$), but in a different pattern. In contrast to short-term movements, long-term movements of males were comparable to those of females (Table 1). Also, although overall differences among months were not significant, there was a significant interaction between status and month ($F_{[363]} = 2.55$, $P = 0.0012$). Long-term movement rates of males climbed to a peak in May, but dropped by July to levels comparable to those of females with cubs (Fig. 4). Overall, the Tukey–Kramer HSD test suggested that hourly movement rates of male bears were significantly higher than those of females with cubs ($P = 0.0645$). Long-term movement rates of males in May

significantly exceeded long-term rates in May of females with cubs ($P < 0.0001$), females with yearlings ($P = 0.027$), and solitary females ($P = 0.062$). Thereafter, long-term movement rates of males were comparable to those of females of all classes.

Net monthly movements

The net distances moved by male polar bears from the beginning to the end of each month did not differ significantly from those of any class of females present between April and September. Monthly net movement distances of male polar bears fell in the midst of those for all classes of females and there was no clear monthly trend (Table 2, Fig. 5). Differences among months were not significant, and there were no significant interactions of the main effects of month and reproductive status.

The azimuths of net monthly movements recorded for

Fig. 3. Mean short-term movement rates for 7 male and 104 female polar bears fitted with satellite radio transmitters. The movement rate is the quotient of the distance traveled between consecutive relocations divided by the number of hours separating those locations. Short-term movement rates were calculated only when temporal separation of relocations was ≤ 8 h.

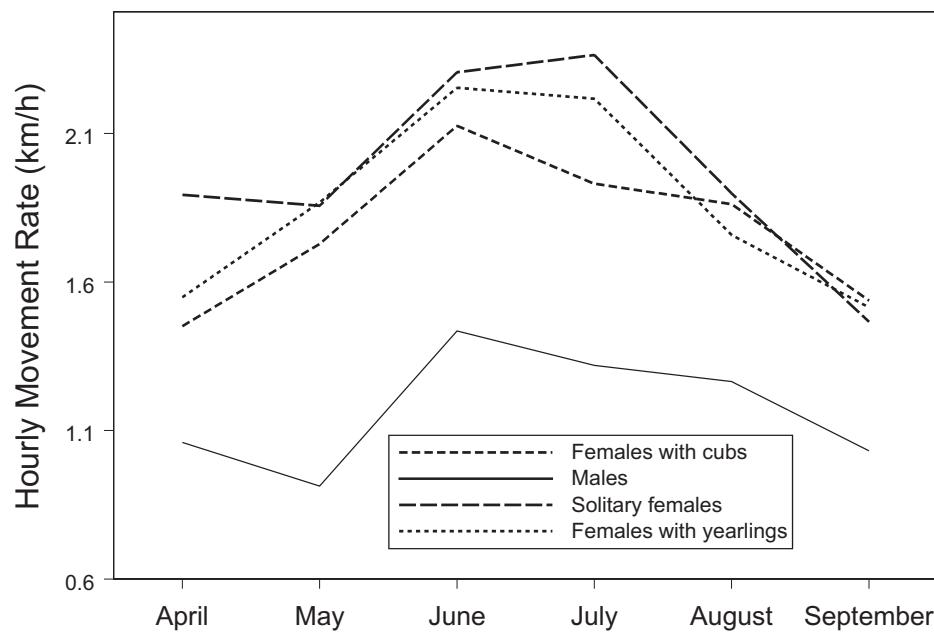
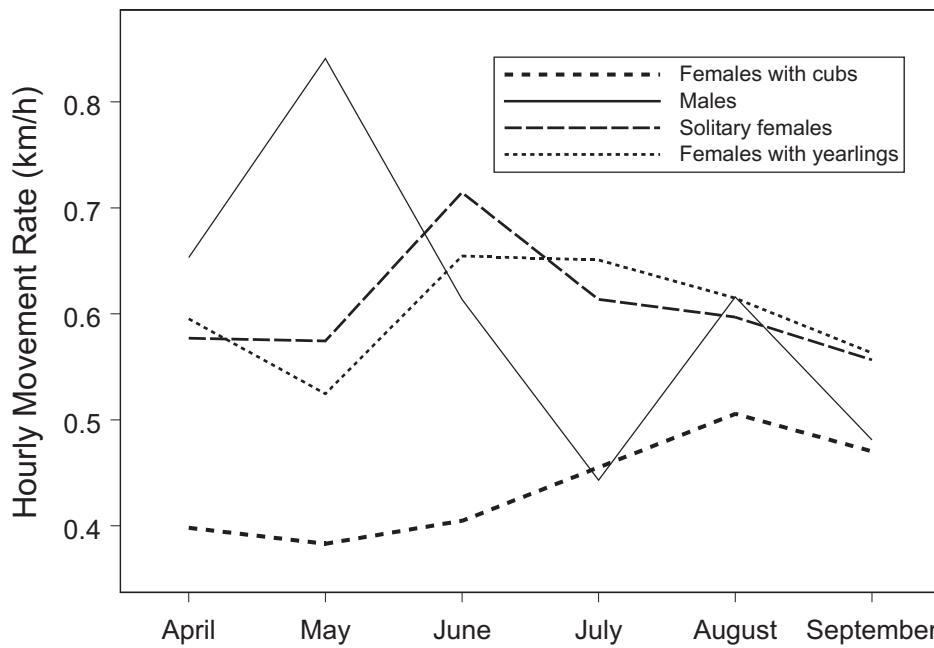


Fig. 4. Mean long-term movement rates for 7 male and 104 female polar bears fitted with satellite radio transmitters. The movement rate is the quotient of the distance traveled between consecutive relocations divided by the number of hours separating those locations. Long-term movement rates were calculated only when temporal separation of relocations was >8 h.



instrumented male polar bears were very similar to those recorded for female polar bears during the same months. In April, male polar bears moved significantly in a westerly direction (Table 3). Likewise, the mean movement of females was westerly in April, although the trend for females was not significant (Table 6 in Amstrup et al. 2000). In May, June, July, and August, net movements of female polar bears deviated from uniformity, all in northerly directions (Table 6 in Amstrup et al. 2000). Likewise the mean azi-

muths of net movements for male polar bears during June, July, and August were northerly, although none were significant. The average azimuth for males in May was easterly, but it also lacked significance (Table 3). The single net movement recorded for a male bear precluded comments about the direction of net movements in September.

Total distances

Although net movements and movement rates of male

Fig. 5. Mean net monthly movements of 7 male and 104 female polar bears fitted with satellite radio transmitters. Net movement is the distance separating the first and last relocations obtained for a bear each month.

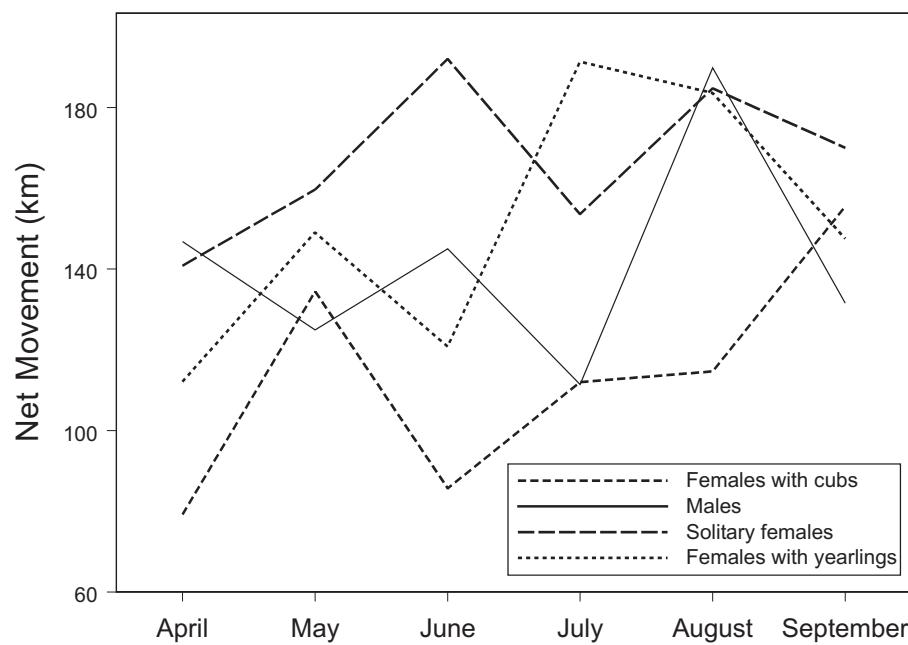


Table 2. Summary of net movements (km) from the first to the last location each month for polar bears in the southern Beaufort Sea.

	Summary statistics				Quantile value				
	Mean	Min.	Max.	SD	5%	25%	Median	75%	95%
Adult males (<i>n</i> = 18)	135	7.2	252	81	7.2	61	139	206	252
Females with cubs (<i>n</i> = 64)	114	13.3	356	77	24.2	49	101	158	250
Females with yearlings (<i>n</i> = 84)	152	10.8	526	115	27.5	72	121	200	376
Solitary females (<i>n</i> = 355)	168	5.3	920	111	32.9	88	150	224	365

Note: Male polar bears were subcutaneously implanted with satellite radio transmitters in 1996–1997. Females were fitted with satellite radio collars from 1985 to 1995; *n* indicates the numbers of bear-months from which data were derived. Net movement distance from the beginning to the end of the month was recorded only if ≥20 days elapsed between first and last observations within each month.

Table 3. Azimuths (degrees true) of net movement from the beginning to the end of each month for male polar bears in the southern Beaufort Sea with PTTs implanted subcutaneously in the top of the neck.

	Mean azimuth of displacement (0° = true north)	Angular dispersion ^a	Rayleigh's Z test value ^a	P	No. of animals
April	293	45	2.84	0.05	6
May	77	60	1.38	0.28	7
June	36	69	0.48	>0.50	6
July	13	72	0.17	>0.50	4
August	328	21	1.74	na ^b	2
September	324	0	na ^b	na ^b	1

^aAccording to Zar (1984).

^bTest was not performed because of sample-size limitation.

polar bears were either smaller than or comparable to those of most classes of female bears, male polar bears appeared to cover more ground each month than females ($F_{[105]} = 6.01$, $P = 0.0008$) (Table 4). Mean total monthly distances moved by males over all months were significantly greater than

those moved by females with cubs ($P = 0.0111$). They were qualitatively greater, but not significantly greater, according to HSD, than total monthly movements of other classes of females. Total distances moved by males did not differ significantly among months for which we have data, and there

Fig. 6. Mean total monthly movements of 7 male and 104 female polar bears fitted with satellite radio transmitters. Total movement is the sum of the distances separating all consecutive relocations obtained for each bear each month.

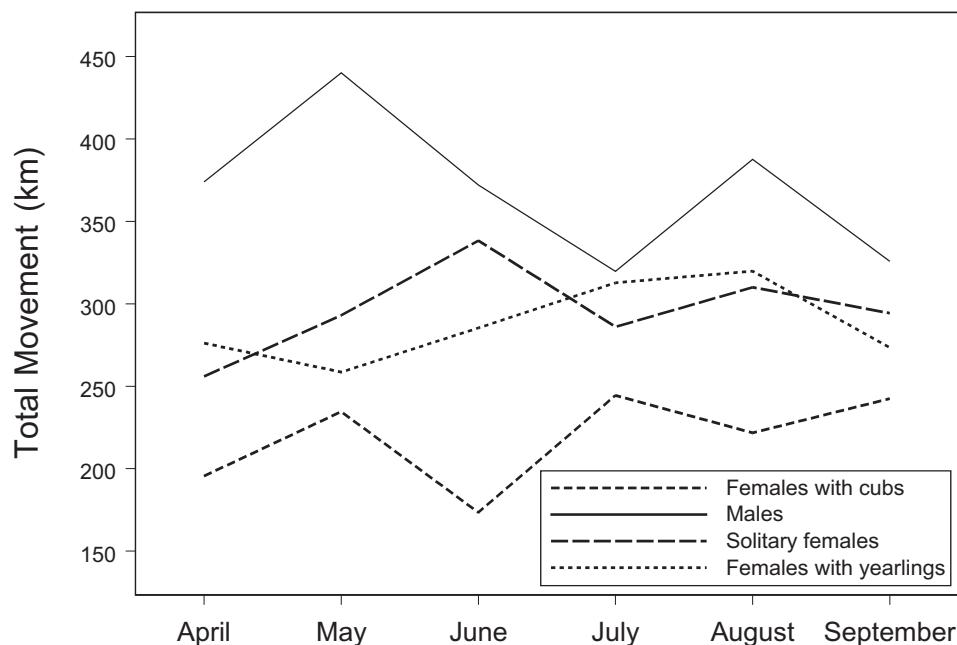


Table 4. Total distances (km) traveled per month for polar bears in the southern Beaufort Sea.

	Summary statistics				Quantile value				
	Mean	Min.	Max.	SD	5%	25%	Median	75%	95%
Adult males (<i>n</i> = 18)	387	304	546	81	304	318	359	415	546
Females with cubs (<i>n</i> = 64)	217	26	504	101	88	152	197	274	384
Females with yearlings (<i>n</i> = 84)	289	54	639	134	115	196	256	339	578
Solitary females (<i>n</i> = 355)	302	24	779	134	111	202	289	377	559

Note: Male polar bears were subcutaneously implanted with satellite radio transmitters in 1996–1997. Females were fitted with satellite radio collars from 1985 to 1995. Total distance traveled per month was recorded only if ≥20 days elapsed between the first and last observations within each month.

were no significant monthly interactions between month and class of bear (Fig. 6).

Activity areas

The sizes of monthly activity areas occupied by males were comparable to the range of activity-area sizes for females (Fig. 7). Summary statistics were quite similar (Table 5), and there were no significant differences between the sizes of areas occupied by males and those occupied by females. Figure 8 shows the monthly activity-area boundaries for 2 PTT-implanted male bears and two radio-collared female polar bears that occupied similar geographic areas in the months for which we had data on males. These activity-area boundaries corroborate the similarities between movement patterns of males and females suggested by other measurements that we recorded.

Discussion

Transmitter performance

Implanted PTTs provided greater numbers of high-quality (LQ 3) locations than did radio collars attached to females. When all classes (LQ 1 – LQ 3) of quality locations were compared, implanted radios did not perform better, however.

In fact, they provided significantly fewer quality fixes than did collars worn by females. The greater number of LQ 3 fixes may have resulted from the orientation of the antennae on implanted radios. Antennae tend to operate most efficiently if the radiating element is isolated from objects (in this case the body of the polar bear) that might reflect, absorb, or bend the outgoing signal (Carr 1989). The antennae of implants extended directly from the body of the male bear into free space. Antennae built into collars worn by females wrapped around the neck of the bear and were enclosed in conveyor-belt material to prevent damage. We cannot explain why implanted radios generated more high-quality fixes but fewer quality fixes. Nonetheless, based on signal quality for the time during which they transmitted, and recognizing that this was the first attempt to implant polar bears with PTTs, we conclude that implanted radios transmitted effectively.

Unfortunately, the high level of performance of implanted radios was compromised by a very short transmission life. The failure to capture implanted males at intervals after surgery prevented collection of data related to the cause of this premature failure. Electronic failure of the transmitter components, removal or expulsion of the transmitters from the bears, and antenna breakage seem to be the most plausible

Fig. 7. Mean sizes of monthly activity areas of 7 male and 104 female polar bears fitted with satellite radio transmitters. Activity-area sizes were calculated with the convex-polygon (CP) method (Hayne 1949).

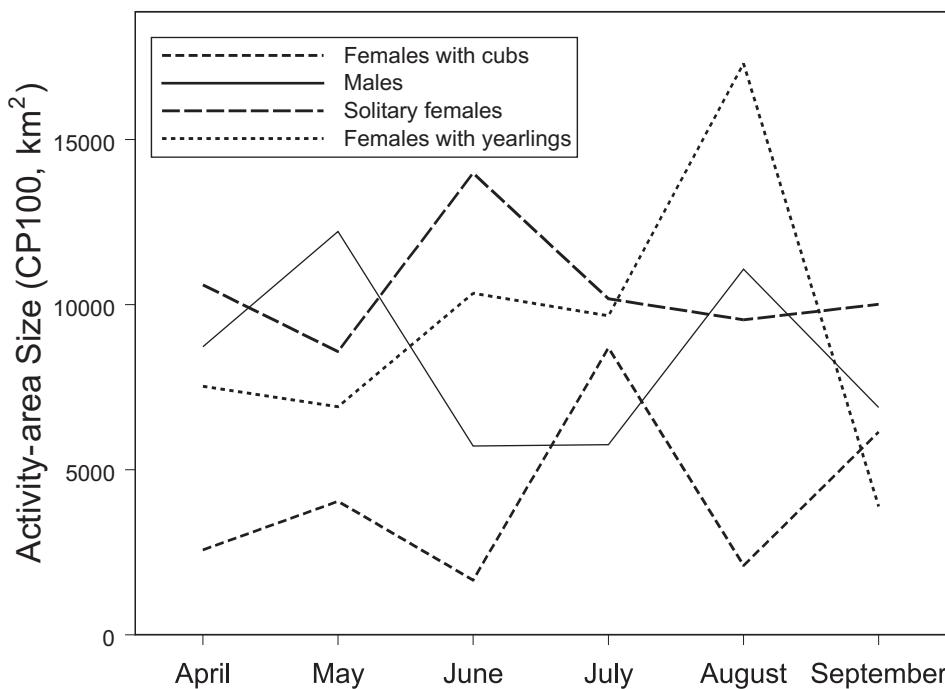


Table 5. Monthly activity-area sizes (km^2) for April–September (calculated by the convex polygon method) for polar bears in the southern Beaufort Sea.

	Summary statistics				Quantile value				
	Mean	Min.	Max.	SD	5%	25%	Median	75%	95%
Adult males ($n = 18$)	8 541	1385	26 500	6 920	1385	5013	6480	8 540	26 500
Females with cubs ($n = 32$)	3 698	58	16 320	4 298	195	794	1940	4 512	13 990
Females with yearlings ($n = 46$)	9 397	502	58 540	10 586	1499	3099	5804	12 330	29 620
Solitary females ($n = 139$)	10 585	29	51 110	9 039	1054	4627	7761	13 930	30 490

Note: Male polar bears were subcutaneously implanted with satellite radio transmitters in 1996–1997. Females were fitted with satellite radio collars from 1985 to 1995. Monthly activity-area sizes were calculated for individual bears only if ≥ 8 locations were recorded per month; n indicates the numbers of bear-months from which data were derived.

explanations of the premature failure of implanted PTTs. The temporal change in quality of transmissions from implanted radios did not differ from the change in transmissions generated by radio-collared females. The implanted radios operated well until they quit suddenly. In collar-mounted PTTs, premature signal losses due to battery exhaustion or failing circuitry (caused by leakage, etc.) were usually preceded by gradual declines in signal quality or increasingly variable performance. Radio collars that failed suddenly, on the other hand, usually showed evidence of mechanical damage to the antenna or transmitter housing. Therefore, the sudden failure of implanted transmitters suggests some sort of mechanical rather than electronic damage.

One implanted polar bear was recaptured 3 years after implantation. That bear had removed the implant, or the implant was passively shed, some time before its recapture, and the wound was totally healed. Despite surgical procedures to prevent it (Mulcahy and Garner 1999), expulsion was apparently a possible cause of premature signal loss. Antenna breakage may be another explanation of premature transmitter failure. Early testing of radio collars for female polar

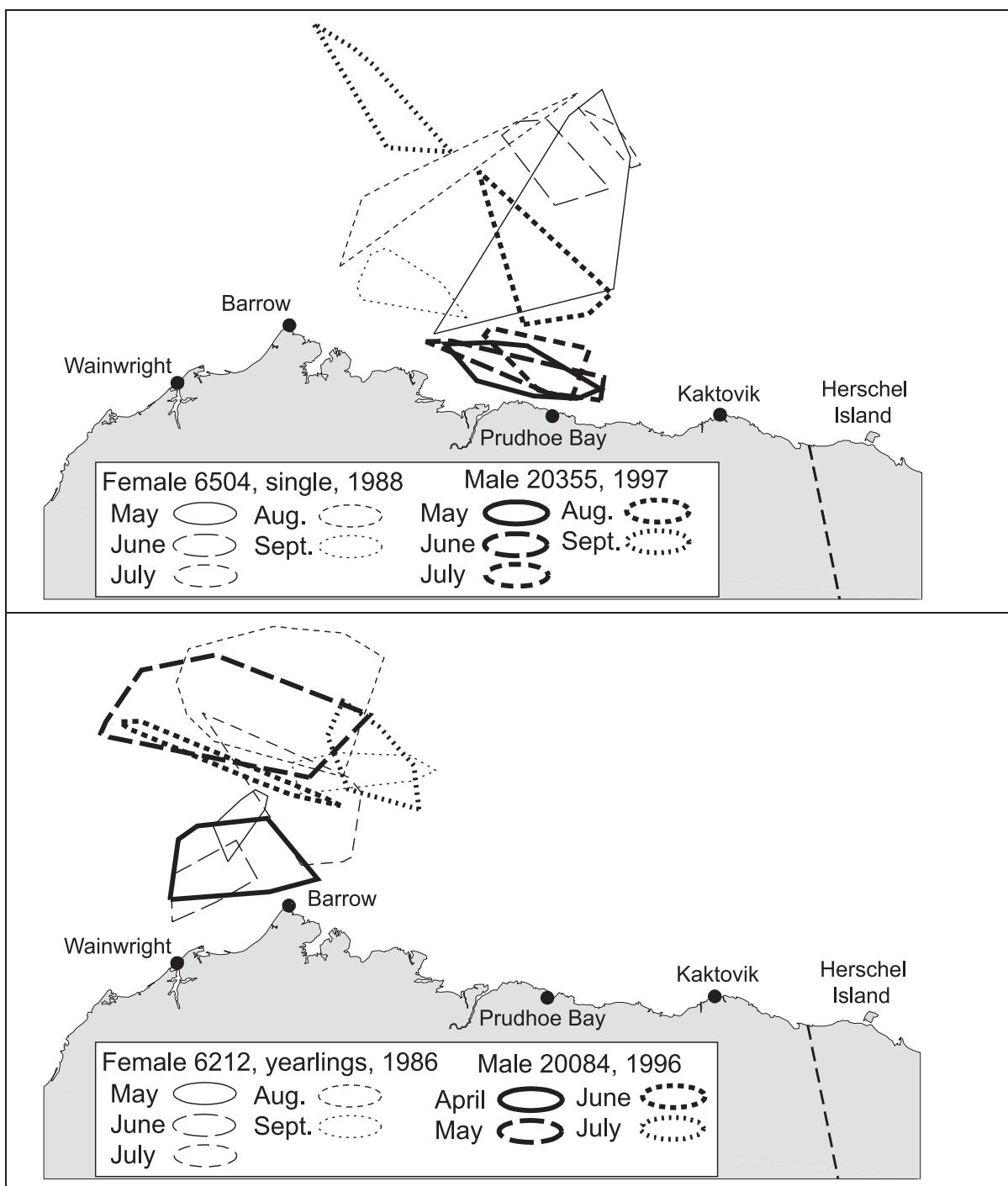
bears confirmed that exposed antennae, even those constructed of heavy cable, broke within 2–6 months of deployment (S.C. Amstrup, unpublished data). For protection from breakage, all antennae in modern transmitters for females are imbedded in the belting of the collar. Breakage of exposed antennae of implanted radios, therefore, could have contributed to the premature failures we observed.

Movements

Amstrup et al. (2000) concluded that “until we are able to instrument young growing polar bears and adult males, we will be unable to quantitatively compare the movements of adult females with bears of other age and sex classes”. This is the first report addressing that information gap. Overall, male and female polar bears did not differ greatly in their movements during April through September.

Rates of short-term movement reveal the pattern of movements over periods of several hours, usually within one duty cycle. Rates of long-term movement reveal movements between duty cycles and tend to smooth the zigzag pattern recorded over shorter time frames. Male bears moved at lower

Fig. 8. Monthly activity-area boundaries (calculated with the convex-polygon method; Hayne 1949) for 2 PTT-implanted male polar bears and 2 radio-collared female polar bears that occupied similar geographic areas in the months for which we had data on the males.



rates than females when measured over short durations and at higher or comparable rates when measured over longer time frames. This pattern indicates that female bears meander more within their daily activity areas, while movements of males within their activity areas were more directed. Males apparently moved more steadily than females over the long run because they tended to cover greater total distances each month. Our data suggest that all polar bears travel in a meandering or zigzag pattern. The zigzags of males, it appears, are coarser than those of females, however. When viewed

over a monthly time scale, males have comparable net movements and activity-area sizes and possibly greater total movement distances than females. Male bears, therefore, may move more constantly yet in a more deliberate and directed fashion than do females, but not over larger areas.

In many species of solitary carnivores, including terrestrial bears, movements of males are more extensive than those of females (Amstrup and Beecham 1976; Ballard et al. 1982; Rogers 1987; Sandell 1989; Nagy and Haroldson 1990; Swenson et al. 1998). Movements of terrestrial female bears

maximize their ability to secure food sources, while movements of males maximize contact with females (Rogers 1987; Sandell 1989). Movements of male bears may be more extensive during the breeding season (Nagy and Haroldson 1990) as they attempt to encounter as many females as possible, and less so at other times. When females occupy defended territories or home ranges to which they are strongly faithful (Rogers 1987; Nagy and Haroldson 1990; Sandell 1989), males can assure contact with numerous females by simply expanding their ranges to include multiple female home ranges. Female polar bears, however, do not defend territories. Further, their home ranges are larger and less rigid than those of terrestrial female bears (Amstrup et al. 2000). The volatility of the sea-ice substrate means less predictability in food for polar bears, and hence less predictability in the locations of females that are in breeding condition.

Polar bear breeding occurs from March through June (Amstrup 2003), and in the Beaufort Sea appears to peak in April and May. During the breeding season we recorded long-term movement rates and total monthly movement distances for males that were qualitatively (but not statistically) greater than those for females. This could suggest a pattern that matches those observed in terrestrial bears. Conversely, short-term movement rates, net movements, and monthly activity-area sizes were not even qualitatively different. During the period of transmitter function, which included the breeding season, the movements of 7 instrumented male polar bears were more similar to those of females than they were different. This suggests that male polar bears may use a different strategy for encountering mates than do terrestrial bears. With numerous females moving through large non-exclusive activity areas, there may be no adaptive advantage for males that greatly expand their breeding-season travels.

There appeared to be a substantial lack of concordance among the movement indices presented here. Amstrup et al. (2000, p. 963) concluded that the lack of concordance among different measures of movement mandated further studies to understand the information conveyed by each measure, the relationships between measures, and more generally, how polar bears utilize their environment. The lack of concordance in movement measurements for male polar bears further emphasizes the need for careful interpretation of telemetry data on movements. It also verifies that overall movement patterns are more likely to be discerned through cumulative interpretation of a variety of movement indices than through the use of just one or two indices.

Cumulatively, the radio-tracking observations reported here suggest that male polar bears move in a quite similar fashion to females. This corroborates early tag and recovery studies (Stirling et al. 1980, 1984; Schweinsburg et al. 1981; Lentfer 1983) which concluded that distances moved by polar bears of different sex and age classes were not greatly different. It is clear, however, that a complete understanding of the movements and activity patterns of male polar bears will not be reached until a more durable and more predictable method of attaching radio transmitters to male polar bears is developed.

Acknowledgments

Principal funding for this study was provided by the U.S. Geological Survey, Alaska Science Center (U.S. Department

of the Interior). Additional support was provided by the Minerals Management Service (U.S. Department of the Interior); the National Oceanic and Atmospheric Administration (U.S. Department of Commerce), the Canadian Wildlife Service, B.P. Exploration Alaska, Inc., and Phillips Alaska, Inc. We are especially grateful to D. Douglas for assistance with acquisition of satellite data.

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