

BREEDING BEHAVIOR OF BLACK BEARS

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Abstract: Movements of radio-collared black bears (*Ursus americanus*) were documented during the 1980 and 1981 breeding seasons on Long Island, Wash. Males and females were first found in association 21 May 1980 and 10 May 1981 with no associations documented after 5 July 1981 and 2 July 1980. The peak in breeding associations occurred between 12 and 30 June both years. Individual females were visited periodically by males for 4–7 week periods during the breeding season. Most associations were brief, lasting only 0.25–2 hours, presumably as males assessed the estrous stage of a female. These brief associations preceded and followed extended associations that lasted 2–5.25 days. These longer associations, believed to be the actual breeding period, were characterized by the pairing of the female with 1 of the 2 dominant males (identified through observations of male/male observations) and frequently the presence of 1 or 2 of the other males. In these situations the dominant male generally remained closest to the female during the entire period. The 3 most dominant males were associated with each of the 7 females without cubs in 1981. The 4th male was associated with 3 of the 7 females.

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Induced ovulation, and the accompanying constant nature of the estrous period, enhance the probability of successful matings in wide-ranging, solitary animals such as the black bear (Nalbondov 1976). Further, delayed implantation provides a mechanism by which growth of the fetus and accompanying energetic demands, as well as the subsequent care of dependent young, is postponed until the female is more nutritionally fit to withstand these demands. Breeding and parturition periods are presumably timed to maximize reproductive success.

Breeding takes place in June and July, and parturition occurs in late January or February throughout black bear range (Bunnell and Tait 1981). Black bears are promiscuous in breeding habits, although this trait apparently varies with local differences in bear density during the breeding season (Jonkel and Cowan 1971, Rogers 1977). Length of the receptive period for individual females should vary with how quickly a female is bred after she comes into estrous. Ammons (1974) found the receptive period of 8 captive female black bears to range from 6 to 16 days and to average 9.75 days. Observations of associations between free-ranging male and female black bears ranged from 2 days (Lindzey and Meslow 1977b) to 5 days (Rogers 1977). Copulations may occur frequently during this period (Ludlow 1976). Hornocker (1962) observed a female grizzly bear (*U. arctos*) that copulated 10 times with 4 different males in a single 2-hour period.

The following paper describes the associations between male and female black bears during the 1980 and 1981 breeding seasons on Long Island, Wash. Bear populations over 1 year of age on the island in the spring of 1980 and 1981 were 33 and 24 bears, respectively (Lindzey et al., this volume). Home ranges of adult females averaged 362 ha, whereas adult males often used the entire island. Considerable overlap of home ranges was evident between and among sexes, and in most cases bears used their entire home range during each season (Barber 1983).

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STUDY AREA

Long Island is a 21.1-km² island located in Willapa Bay of southwestern Washington. Approximately 30% of the island is less than 500 m from the mainland. Maximum elevation is 80 m, and climate is typically cool marine. Temperatures range from 1.6°C in winter to 20°C in summer. Average precipitation is 280 cm.

The island is situated in the *Picea sitchensis* zone (Franklin and Dyrness 1969), a belt of vegetation

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along the coast of Oregon and Washington; the island is similar ecologically to most of coastal Oregon and Washington (Barber 1983). Past logging on the island between 1900 and 1935 and again between 1952 and 1968 resulted in clear-cut areas and second growth stands in various stages of secondary succession during the study period. Numerous sloughs bordered by high tidelands enter the interior of the island. For a more complete description of the vegetation see Lindzey et al. (this volume).

Recreational use of the island included shoreline camping and archery hunting each fall. About one-third of the island is privately owned, but it is managed by agreement with other landowners by the Willapa Natl. Wildl. Refuge.

METHODS

We captured bears between April 1980 and August 1981 using methods described by Lindzey and Mellow (1977a). We ear-tagged each bear with color-coded, individually identifiable tags and fitted 24 of 28 bears with real-time, motion-sensitive, color-coded radiotransmitters (Telonics, Inc., Mesa, Ariz.). We noted the color and degree of vulval swelling of adult females and examined all bears for scars.

After releasing the bears, we located them on the ground by triangulation from known points on the island, using hand-held receivers and antennas. The abundance of logging roads (23 km) on the island made it possible to minimize the distance to the bear, which seldom exceeded 300 m. In addition, the time between successive fixes was generally less than 5 minutes. We also attempted to make at least 2 of the multiple readings intercept at 90 degrees. This procedure allowed us to accurately locate the bears. Before a specific bear was located all frequencies of the bears on the island were checked and all associated bears were located simultaneously. Analysis did not include locations of rapidly moving bears. All bears were readily accessible while on the island and in only a few instances were we unable to locate a specific bear.

We attempted to locate bears at least once daily in 1980 and varied the time of day individual bears were located. Throughout the 1981 breeding season, we located bears during their active period (about 0600–2200 hours) in 1 of 2 ways. First, we emphasized the location of adult males, because all the adult males on the island had transmitters. We located each male at least once a day before 11 June and more often when they were associated with radio-collared

females. Relocations averaged 4 times a day after 11 June. Although this approach resulted in fewer relocations of bears when associations were uncommon (during May), it provided the best procedure for documenting associations, particularly short ones. Secondly, 6 selected bears of both sexes were relocated hourly while they were active for at least 1 48-hour period in 1981. We also attempted to locate each collared female without cubs at least once daily regardless of her proximity to adult males.

We monitored diel activity of bears bimonthly, in both 1980 and 1981, from a fixed tower on the high point of the island. Monitoring occurred for 3 min every 2 hours for 24 hours. Change in pulse rate or signal status indicated whether bears were active or inactive.

Relocations were assigned to 1 of 4 4-hour periods from 0600 to 2200. Because placing relocations into 1 of the 4 time periods might indicate that bears were in association when they actually were not, we reviewed the data and excluded relocations that were temporally separated during the time period. Although visibility was limited, we attempted to verify associations by sight when bears were in areas where they could be observed without disturbing them.

Male-female associations were determined by distance between bears over time and relative movements of each. Using these criteria, males and females in association were occasionally separated by as much as 250 m. We interpreted the frequent location of 2 or more males in an area not occupied by a radio-collared female as indicating the presence of an uncollared female. Such interpretations were generally later supported by the capture or sighting of an uncollared female in the area. Examinations of the dens of adult females in late February 1981 and 1982 determined the reproductive success of the females.

Because sampling intensity was lower and some bears were not captured until the breeding season or later in 1980, this paper emphasizes results of the 1981 monitoring period.

RESULTS

In 1980 we monitored 3 adult males and 4 adult females throughout the breeding season. We captured and radio-collared an additional 5 females between 16 June and 11 July. None of the females monitored in 1980 were accompanied by cubs. A 4th adult male was captured on 5 June and a 5th on 1 July. Two additional males were present on the island in 1980,

1 of which was captured on 30 May but not instrumented and another that was observed intermittently during the breeding season.

During the 1981 breeding season we monitored 13 bears: 4 adult males and 9 adult females. Six of the females were not accompanied by cubs, 1 lost her cubs early in the breeding season, and 2 females were accompanied by cubs throughout the breeding period (Table 1). We captured all but 1 of the adult females monitored in 1981 in 1980 and monitored females 5 and 9 throughout the entire breeding season in both 1980 and 1981. Of the 3 additional females captured after the breeding season in 1981, only 1 had cubs. The 4 adult males monitored in 1981 (Table 2) were captured in 1980, and 3 had been monitored through the entire 1980 breeding season. Male 1 was first captured in 1974, and males 1 and 2 were known to be residents of the island since 1978. The other 2 males captured in 1980 were killed before the 1981 breeding season. No other males were observed on the island during the 1981 breeding period. The 13 bears monitored during the 1981 breeding season were relocated a total of 1,444 times.

Breeding Season

We first observed males and females in association on 10 May 1981 and 21 May 1980. Because of less frequent monitoring in 1980 and the smaller number of bears being monitored, we may have missed earlier associations, however. We last noted associations on 2 July 1980 and 4 July 1981. Figures 1 and 2 display the monitoring intensity and periods of association of individual bears during the 4-hour intervals in the

57-day period in 1981. Because we generally knew the locations of each male it was unnecessary to monitor all females for associations.

The general pattern of male-female associations consisted of short-term (0.25–2 hour) associations, before and after a more lengthy association that ranged 2–5.25 days. In short-term associations, generally only 1 male was with the female. We believe these associations occurred when males checked a female and found her not to be in estrous or receptive. In contrast, more than 1 male (occasionally 3) was associated with a specific female during long-term associations. We assume that the female was most receptive to males and probably bred during such long-term associations.

Based on long-term associations indicating breeding, the 1st female could have bred as early as 21 May each year with all available collared females breeding by 28 June in 1981 and 2 July in 1980. The peak of breeding associations during both years occurred between 11 and 30 June. Vulval swelling and color of 18 adult females captured between 10 May and 16 August indicated that females were in estrous as early as 22 May and as late as 11 July.

Most visual observations of males and females together and associations determined through radio-monitoring indicated that females played an active part in maintaining the pair bond. The only times that females were located distant from their home ranges, other than when individuals left the island, occurred during the breeding season ($N = 4$). In each case it appeared that the female had actually followed the male (male 1 or 2) with which they had been associating out of their range. In addition, on

Table 1. Age, weight, and reproductive success of females monitored during the 1981 breeding season on Long Island, Washington.

Bear	Date of capture	Age ^a	Weight (kg)	Cubs in 1981 ^b	Cubs in 1982 ^b
5	8 May 1980	11	56.8	2 ^d	2
6	20 Jun 1980	9	50.8	0	0
7	19 Jun 1980	9	58.1	3 ^d	2
8	30 May 1981	9	49.4	0 ^c	0
9	21 May 1980	6	46.3	2 ^e	2
10	16 Jun 1980	5	41.3	0	2
11	11 Jul 1980	5	47.2	0	0
12	10 Jul 1980	9	58.5	2	2 yrlns
13	16 Aug 1980	13	74.6	2	2 yrlns

^a Ages adjusted to 1981.

^b Cubs in den in late February.

^c No cubs when captured in 1981.

^d No cubs present during 1981 breeding season.

^e Cubs lost after 31 May 1981.

Table 2. Age, weight, and characteristics of female associations of adult male black bears during 1981 breeding season on Long Island, Washington.

Bear	Age	Weight (kg)	% of quarter-day periods with a female ^a		Avg. no. days with females per visit ^b		% of subsequent quarter-day periods male with same female ^c	
			Total	11–30 Jun	Total	11–30 Jun	Total	11–30 Jun
1	11	181	58 (84)	68 (53)	0.44 (29)	0.51 (19)	50 (40)	
2	6	142	42 (98)	58 (50)	0.39 (30)	0.34 (26)	26 (35)	
3	8	102	51 (84)	62 (42)	0.33 (34)	0.36 (21)	38 (24)	
4 ^d	5	107	36 (22)	100 (4)				

^a Numbers in parentheses are quarter-day periods monitored.

^b Numbers in parentheses are total number of visits to a female. If the male was located with more than 1 female in a single quarter-day period and had not been with a female in previous or subsequent quarter-day periods, we counted this as 1 visit. If the male was located with more than 1 female in a single quarter-day period and was with 1 of these females in the previous or subsequent quarter-day period, we did not count the single location with the other female and counted the 2 quarter-day periods he was with the 1st female as 1 visit.

^c Numbers in parentheses are the instances in which the male was monitored in consecutive quarter-day periods.

^d Only intermittently on island during breeding season.

2 occasions, we saw females following males from which they had recently been separated. On 3 occasions, Lindzey (pers. commun.) also saw females following the scent trail of males they had become separated from.

Behavior of Males

Adult males generally were on the island only during the breeding season. The 5 adult males captured and radio-collared in 1980 left the island between 27 June and 23 July of that year. Only 1 male (male 2) returned later to den on the island. The single adult male captured in 1980 but not radio-collared was killed on the mainland on 20 September 1980. Three of the 4 remaining males (males 1, 3, 4) returned to the island between 5 April and 17 April 1981. The 5th collared male was captured on 17 May 1981 and died, apparently as a result of being trapped. The 4 remaining males monitored in 1981 once again left the island after the breeding season (27 June–5 July 1981). These males were subsequently located 10–20 km from the island in about the same area they had been located the year before. Males 1–3 had returned to the island by 29 April 1982 (male 4 was killed on the mainland) and left by 7 July.

We determined the relative dominance of these 4 males through visual observation and by monitoring their movements during 1980 and 1981. We ranked them 1 through 4 and subsequently numbered them accordingly for purposes of this paper. Male 1 displaced males 2 ($N = 1$) and 3 ($N = 2$) from females. Similarly, male 2 displaced male 3 ($N = 2$). When associations included more than 1 male with a female, male 1 was closest to the female 73.9% ($N = 23$) of the times. Male 2 was closest to the female (66.7%, $N = 6$) when only male 3 or 4 was present. Male 4 was never closest to a female when other males were present. We observed males chasing other males for short distances on 3 occasions but never observed physical contact. Additionally, no scars that could be related to fighting, 1 indication of physical interactions, were found on the males when they were captured ($N = 9$). Male 1 was the largest and oldest (Table 2).

Males 1, 2, and 3 were located with all 7 of the radio-collared females without young during the 1981 breeding season. Male 4, on the other hand, was located with only 3 of the 7 and was only intermittently on the island during this period (Fig. 1). Each of these 4 males associated with at least 3 of the 4 radio-collared females monitored through the 1980

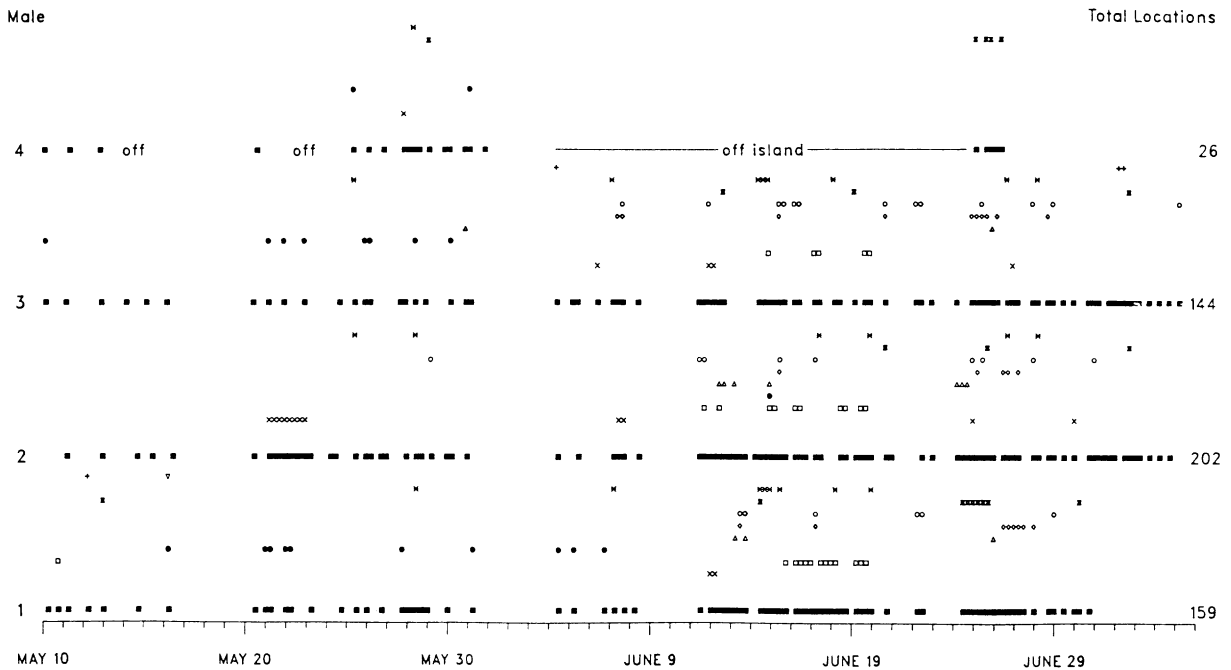


Fig. 1. Breeding associations of adult males during 4-hour time intervals (0600-2200) on Long Island, 1981. ■ Locations; × female 5; □ female 6; ● female 7; △ female 8; ◇ female 9; ○ female 10; ⋈ female 11; + female 12; ▽ female 13; * males with uncollared females (see text).

breeding season as well. Additionally, both males 1 and 3 were located briefly with 1 or 2 of the females with cubs in 1981 (Fig. 2). Although the range of male 4 included the ranges of these females, we did not locate him with them. The range of male 2 apparently did not include females 12 and 13. Cubs in both litters survived. Because there were 4 uncollared females on the island during the 1981 breeding season, estimates of time males spent with females (Table 2) may be conservative. We excluded the locations of males while they were rapidly moving between females. Thus, these analyses do not include the time males spent in transit.

Short-term associations of males and females occurred as early as 36 days before a long-term association (breeding period) (female 6, Fig. 2) and as much as 38 days afterward (female 5, Fig. 2). Males periodically visited females that apparently bred early in the year (females 5 and 7) throughout the remainder of the breeding season. Males checked females that bred later in the season (females 11 and 9) frequently before breeding but seldom afterward. Males, however, left the island soon after these females were bred. Males occasionally visited as many as 5 females in a single 16-hour period. Because visits to females were often brief (15 min) and males could

move quickly among females, the frequency of short-term visits depicted in Figures 1 and 2 is probably a conservative estimate.

Most long-term associations included male 1 or male 2. More than 1 male was found with a female on 28 occasions. One male was generally located with the female (<25 m) and the others were 75-250 m distant. When males grouped around a female during these long-term associations, the most dominant male was generally closest to her (18 of 23 cases). A more dominant male replaced the subordinate male in the subsequent monitoring period in 3 of the 5 associations where the less dominant male was closest (i.e., Fig. 2, female 6, 16 June), suggesting that the dominant male was just arriving at the time of the earlier location. When more than 1 male was associated with a female before and after the long-term association, often neither male was very close to her or the subordinate male was actually closest ($N = 5$, Fig. 2). In each of 4 observations in 1980 of more than 1 male being associated with a female, the most dominant male was closest. Male 2 appeared to actively avoid male 1, but male 3 followed male 2 on 3 occasions and male 1 in 2 instances as the more dominant male moved from a female to another between 11 June and 30 June 1981.

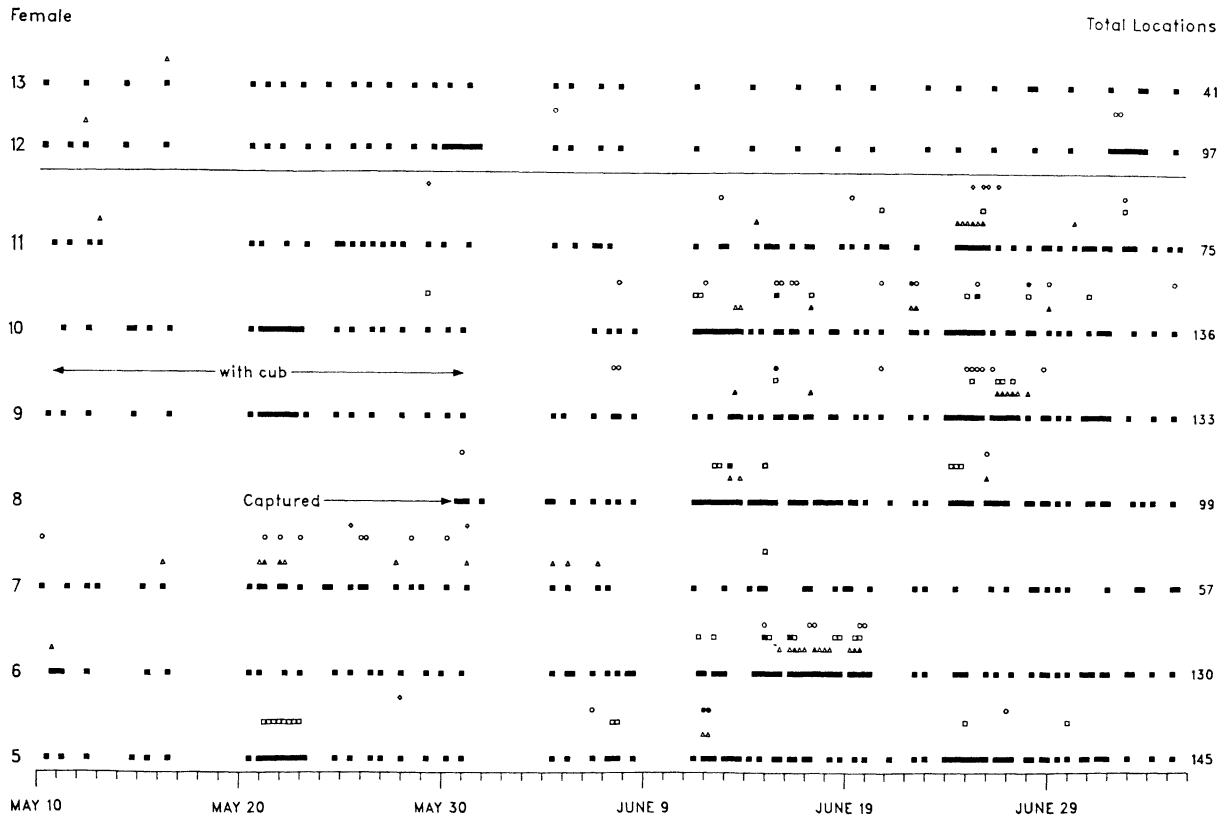


Fig. 2. Breeding associations of adult females during 4-hour time intervals (0600–2200) on Long Island, 1981. ■ Locations; Δ male 1; □ male 2; ○ male 3; ◇ male 4. (Darkened symbol indicates male closest to female.)

We noted only 1 occasion in 1981 in which a male had sole possession of a female during a long-term association. Male 2 was alone with female 5 from 21 to 23 May in 1981 (Fig. 2). Males 1 and 3 were with female 7 at this time, and male 4 was not on the island. Interestingly, in 1980 male 2 was again the only male associated with female 5 when she apparently bred. Male 1 was located more frequently with a female than the other males and stayed longer with each female (Table 2).

Based on the exclusive presence of a male during the long-term association or the male closest to a female during this period, male 1 presumably bred all females except female 5. Male 2 could have bred females 5, 6, 8, 9, and 10 and male 3 females 6, 7, 9, 10. Male 4 may have copulated with females 7 and 11 (Fig. 2).

Behavior of Females

The average age of adult females on the island was 8.4 years (Table 1) with none younger than 5 years of age. All should have been capable of breeding

except for 2 females with cubs (females 12 and 13). Lindzey and Meslow (1977a) determined earlier that the minimum breeding age of females on the island was 3.5 years.

The 7 females without cubs for all or part of the 1981 breeding period were each located with males 1, 2, and 3 between 10 May and 5 July. Females 5, 7, and 11 were also associated with male 4. The 4 females monitored through the entire 1980 breeding period (females 2, 5, 9, and 26) were associated with at least 2, 1, 3, and 4 males, respectively. Most females monitored in 1981 seemed to have a fairly well-defined period in which they were most attractive to males (long-term associations). These periods, which we interpreted as the period in which the females bred, lasted 2.0–5.25 days. Female 10, on the other hand, was with males intermittently between 11 June and 28 June, and female 8 was apparently attractive to males during 2 distinct periods (Fig. 2).

The average length of time between the 1st and last visit by a male was 38 days and the range 25–50 days, excluding female 9. The 1st female bred between 21 and 23 May and the last between 25 and

28 June (Fig. 2). We estimated the breeding period for female 5 in 1981 to be 21–23 May; female 6, 15–20 June; female 7, 21–23 May; female 8, 12–5 June and/or 24–26 June; female 9, 25–28 June; female 10, 11–28 June; and female 11, 24–26 June. Also, 3 of the 4 male-male associations in the absence of radio-collared females we observed in 1981 were after 11 June, suggesting that most of the uncollared females bred after 11 June as well.

The 2 females monitored throughout the 1980 and 1981 breeding seasons (females 5 and 9) appeared to breed at similar times each year. Female 5 bred between 21 May and 23 May in 1981 and between 21 May and 24 May in 1980 with the same male (male 2). Female 9, who bred between 25 and 28 June 1981, apparently bred between 14 and 18 June in 1980. Males 1, 2, and 3 were located with female 9 in both years during these periods. Female 11, who was captured after the breeding season in 1980, and had been with males between 28 June and 2 July of that year, bred between 24 and 26 June in 1981. The other 2 females monitored in 1980 (females 14 and 25) bred between 1–3 June and 7–5 June, respectively.

The percent time females without cubs spent with males during the 1981 breeding season ranged from 15% ($N = 67$) of each quarter-day interval monitored for female 8 to 35% ($N = 52$) for female 7. The average for the 7 females was 25% ($N = 574$). Females 12 and 13, who were accompanied by cubs, were with males 9% ($N = 46$) and 3% ($N = 35$) of the quarter-day intervals in which they were monitored. Female 7 was in estrous at a time when few other females were, perhaps accounting for the increased amount of time males spent with her. Because we did not capture female 8 until 30 May, we may have missed some of her associations with males during the breeding season. The remaining 5 females breeding after 11 June were with males between 21% ($N = 82$, female 5) and 28% ($N = 75$, female 6) of the time. During the peak of breeding activity (11–30 June) we located females not already bred with males from 32% ($N = 41$, female 11) to 41% ($N = 49$, female 14) of the quarter-day intervals in which they were monitored ($\bar{x} = 36\%$, $N = 186$). Females that had apparently bred and conceived, on the other hand, were with males an average of only 7% ($N = 34$) of the time during this period. Female 12 was visited once and female 13 was never visited between 11 and 30 June.

We last saw female 9 with her cub on 30 May 1981 and first observed her without it on 12 June. During the period (7 and 8 June) she was located with male

3. She apparently came into estrous by 25 June and successfully bred.

Both of the females monitored during the 1980 season that survived until winter, and 4 of the 7 females monitored in 1981 had cubs when examined in their dens the subsequent winter (Table 1). Female 5 apparently bred only with male 2 each year and produced cubs both years. Although females 6 and 9 were both associated with numerous males for similar time intervals in 1981, female 9 had cubs and female 6 did not. Further, the intermittent nature of female 10's associations with males (Fig. 2) resulted in her giving birth to cubs, whereas the extended association of female 11 with males apparently did not result in the birth of cubs.

DISCUSSION

The breeding season was characterized by short-term associations of males and females, which were interpreted as the male assessing the estrous condition of the female. These short-term associations became increasingly more common until females actually bred, which we inferred from longer-lasting associations. Longer associations generally included the presence of more than 1 male with a specific female. Each female had ample opportunity to breed with more than 1 male, thus guarding against a single sterile mating. The length of breeding associations may have been influenced by the timing of estrous of other females in the population. Presumably, females receptive at the same time would compete for services of the males. We were unable to determine the degree to which a female's behavior (rejection of additional copulations) contributed to the length of breeding associations. Females, however, appeared to play a role in maintaining the male-female bond by actively maintaining contact with the male with which she was associated. Such behavior, which was generally directed at the dominant male, would increase the chances of a female's breeding with the male of her choice. It appeared, however, that mate selection for the female was generally decided through earlier contests among the males and expressed proximally through their dominance hierarchy.

All males had opportunities to breed, but the scheduling of efforts of subordinate males was dictated by the location of more dominant males. The dominant male, because of the close spacial arrangement of females, was able easily to monitor the estrous condition of a number of females. To some extent,

this undoubtedly allowed him to reduce the time subordinates spent with all females. When more than 1 female became receptive at the same time, breeding opportunities increased for the subordinate males. Presumably, different strategies exist in other populations as suggested by Bunnell and Tait (1981). If adult females are more distant from one another, a dominant male would have greater difficulty preventing them from associating with other males; the dominant male might thus be expected to remain longer with a specific female. In a population where females are widely separated and become receptive at the same time, subordinate males would have the greatest opportunity to breed. The strategy employed by the dominant male on Long Island was to copulate frequently with a female over a relatively short period, during which he maintained exclusive control over her and then moved quickly to another female.

Although it is tempting to infer that the strategy employed by a dominant male in a given situation affords him the greatest reproductive fitness, such inferences would be difficult to establish. Many characteristics of induced ovulation are unknown for bears. Among these are the amount of stimulation (copulation) necessary to induce a female to ovulate and the time lag between coitus and ovulation. Ovulations may occur as long as 10 hours after coitus in the rabbit (Nalbandov 1976) and 33–72 hours in the mink (*Mustela vison*) (Venge 1959). As pointed out by Bunnell and Tait (1981), cubs in the same litter possibly could have different fathers. There was no obvious indication from our data that would suggest any 1 pattern of male-female associations resulted in a greater probability of cubs being born. Nutritional condition of females on the island apparently influenced their reproductive success (Lindzey et al., this volume), however, potentially masking any trend.

Strife among adult males appears reduced in relatively stable black bear populations. This was apparent on Long Island, where breeding protocol was determined by a well-defined dominance hierarchy. Ruff and Kemp (unpubl. data) provide corroborating evidence from an Alberta population from which adult males were removed.

Generally, the same males returned to the island in 1981 and 1982 and fathered the cubs born on the island. The exceptions were those males killed on the mainland between breeding seasons. Because each of the males may have bred most or all of the females present, the potential existed for nearly each cub to be related to any 1 of the males. Given the potential for relatedness, it would appear maladaptive for any

of these males, particularly the dominant males, to kill cubs on the island. Schaller (1972) discussed the relationship between infanticide and lineage for the African lion (*Panthera leo*), and Rogers (1977) speculated about this relationship in the black bear. This thesis would predict a negative correlation between infanticide and degree of stability in the adult male cohort. Further, as suggested by Rogers (1977) this stable group of adult males may protect their offspring by repulsing other males that might be expected to kill the cubs.

Because hunting is a major cause of death in many black bear populations, it will influence the degree of turnover in the adult male cohort and thus, presumably, the level of infanticide in that population. A hypothesis that results from this line of reasoning is that level of infanticide is positively correlated with intensity of harvest.

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