5. Factors Influencing Dispersal in the Black Bear

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Black bear dispersal was studied from 1969 to 1982 as part of a study of social behavior, habitat use, and population dynamics in northeastern Minnesota (Rogers 1987). Objectives were to determine (1) age and sex of dispersers, (2) factors that promote dispersal, and (3) factors that induce dispersing bears to settle. For this study, dispersal is defined as movement from the mother's territory to a nonadjacent, more or less permanent breeding area. This definition differs from that of Shields (chap. 1, this vol.) in that bears that did not disperse to a nonadjacent territory were not considered to have dispersed; these nondispersing bears commonly continued to use part of their natal range, including their birthplace, while their mothers shifted slightly away.

STUDY AREA AND METHODS

Bears were captured in a 300 km^2 portion of the Superior National Forest in northeastern Minnesota. The capture area and surrounding region had gently rolling terrain with small rock outcrops. There were few towns, farms, large highways, large waterways, or other physiographic barriers except Lake Superior to hinder dispersal. Forest habitat was nearly continuous for more than 500 km to the north and for more than 150 km to the west. Lake Superior was 30 km to 60 km to the east and south. The human population was low over most of the forested habitat, so human selection against dispersal was probably minimal.

Bears studied for dispersal were born to radio-collared mothers in dens in January and ear tagged as 2-month-old cubs in March, shortly before the families emerged. The cubs remained with their mothers through the next winter and were radio collared in dens as yearlings. Young females were then radio tracked for the next several years as they matured, established territories, and produced cubs of their own. Radio collars were re-

placed each winter during hibernation. However, radio collars were removed from some males at 2 years of age after it became apparent that the majority dispersed at that age and were likely to move beyond signal range. Dispersal data from males without radio collars were obtained through ear-tag returns from Wisconsin, Ontario, and various parts of Minnesota. Radio-collared individuals were monitored up to 200 km outside the capture area.

MATING SYSTEM, SOCIAL ORGANIZATION, AND DEMOGRAPHY OF THE STUDY POPULATION

Characteristics of the capture area population are summarized here and detailed elsewhere (Rogers 1976, 1977, 1983, 1987). Social organization depended upon the distribution and abundance of food. In the few places where food was clumped, the bears formed hierarchies. In most places, food was dispersed, and females held territories averaging 3.5 km in diameter, while males used mating ranges averaging 12.25 km in diameter (average length plus average width of mating ranges divided by 2). Each mating range contained 7 to 15 female territories. However, the mating ranges were indefensibly large and overlapped to the extent that no male had exclusive access to any female. Both sexes were observed to be promiscuous. Mating occurred in June or early July. After that, some members of each sex foraged outside their usual ranges but returned for denning. They used approximately the same areas for mating each year. Minor shifts in territory locations are discussed later. Social organization of the bears differed in several respects from that of the more social carnivores discussed in this volume (Rood, chap. 6, and Mech, chap. 4). The differences may stem in part from the fact that bear foods are usually too small and scattered to support group feeding except by mothers and cubs (Rogers 1987).

Males began mating as early as 4.4 years of age (Rogers 1987). Females produced their first litters at 4 to 8 years of age (mode 7 years, average 6.3 years), depending on food supply (Rogers 1987). Sex ratios among cubs, yearlings, and 2-year-olds were even or slightly male biased (Rogers 1977). The proportion of males decreased with age; for bears over 4 years there was 1 male to 3 to 4 females (Rogers 1977). Population density was approximately 1 bear per 4.5 km^2, including cubs, or 1 adult (2:4 years old) per 12.37 km^2 during the years of most intensive study (Rogers 1987). This density is lower than has been reported for most other regions (Lindzey and Meslow 1977b).

FEMALE DISPERSAL

Ages and Movements

Of 31 females whose birthplaces and adult ranges were known, only 3 (10%) dispersed. The 3 included 1 of 22 that were radio tracked from the time they left their mothers and 2 of 9 that were repeatedly captured or

observed. Dispersal distances were only 3 km for the radio-collared bear and 8 km and 11 km for the other 2. These distances may not have removed the females from the mating ranges of their fathers. Three females dispersed unknown distances and settled in the study area. Four dispersed or immigrated at 3 or 4 years of age. All 4 probably dispersed at maturity because 3 of the 4 produced their first litters the subsequent winter and the fourth was in estrus when captured as an immigrant. No older female dispersed.

Relationships between Mothers and Independent Daughters

The low dispersal rate among females probably stemmed from benefits of remaining near their mothers' territories. Yearlings of both sexes changed their movement patterns after family breakup and began using small portions of their mothers' territories (Rogers 1987). These yearling ranges then were avoided by the mothers, giving the yearlings more or less exclusive feeding areas (Rogers 1987), as has been reported for various primates (Tilson 1981; Waser and Jones 1983). Two young bears that had exclusive feeding areas gained weight more rapidly than their same-sex siblings that used larger areas but fed in competition with their mothers (Rogers 1987). As the young bears grew, males dispersed and females increased their range size. Nine mothers shifted their territories away from 12 maturing daughters, thereby aiding daughters in obtaining territories. No mother shifted her territory toward a daughter. Of 22 subadult females that were radio tracked, 15 expanded yearling ranges, 6 left their yearling ranges and opportunistically established territories in adjacent areas, and 1 dispersed 3 km and usurped part of the territory of an older female whose weight of 45 kg was only 41% of her peak weight. The tolerance mothers showed daughters and the aggression mothers displayed toward nonkin (Rogers 1987) suggest that the shifting or spacing behavior probably resulted from differential aggression against nonkin when young females began expanding their ranges.

Without parental aid, young females may have had difficulty obtaining space. Two of the 3 immigrants had problems not found among the 31 philopatric females. One of them incurred lacerations on her head and neck as if from fighting. The other did not obtain an exclusive area as a pregnant young adult; she denned and gave birth in the territory of another bear. The next spring she obtained for herself and her cub the smallest exclusive area used by an adult that year. In late July, she permanently abandoned the exclusive area and the study area (Rogers 1977, 1987). The cub's fate after 18 July is unknown.

For territorial mothers, competition with philopatric daughters and the effort required to shift territories could conceivably decrease subsequent reproductive success. However, if mothers' efforts on behalf of their daugh-

ters enhance the reproductive success of the daughters by at least twice the amount that the mothers' reproductive success is decreased, those efforts will be favored by natural selection (Hamilton 1964; Wilson 1975). The 2:1 ratio holds because daughters possess half their mothers' genes; therefore, two grandprogeny carry the same amount of an individual's genetic material, on the average, as does one progeny

MALE DISPERSAL

Ages and Movements

In contrast with the largely nondispersing females, all 20 males that were studied dispersed: 13 as 2-year-olds, 5 as 3-year-olds, and 2 as 4-year-olds. Strongly male-biased dispersal is common in species with polygynous mating systems and female defense of resources (Greenwood 1980; Dobson 1982; Waser and Jones 1983).

Two males were radio tracked extensively before they dispersed. Both showed marked increases in travel outside their mothers' territories in the
I to 5 weeks before leaving permanently. Three that were followed during dispersal included the males that made the longest (219 km) and shortest (13 km) movements. The first moved 145 km in 12 months and then 74 km farther in only 15 days. The fact that he moved more than half as far in 15 days as he did in the previous 12 months suggests that the bears could have dispersed farther than they did. Another bear moved in an essentially straight line for 42 km in the first 5 days of dispersal, moved 47 km farther the next 55 days, then reversed direction and moved 133 km back past his birthplace to settle approximately 48 km from it. The bear that dispersed the shortest distance moved only 13 km to the area he would use for mating as an adult but then roamed more than 40 km away from it while foraging. The main areas he used as a 2-year-old, after dispersing, were reused for at least the next 2 years at approximately the same times each year. The average distance that 18 dispersing males were recovered from their birthplaces was 61 km (median 49 km, range 13 km to 219 km). This distance represented less than 5 mating range diameters (range 1-18 diameters), which probably was not far enough to disrupt genetic adaptations to regional conditions (Shields 1982, 1983; Rogers 1987).

Food Shortage and Aggression

Dispersal was not prompted proximally by local food shortages at the observed population densities. Males showed no more likelihood to disperse at the minimum age of 2 years in years of fruit and nut crop failures (7 of
11 2-year-olds dispersed) than in years of abundant food (6 of 9 2-year-olds dispersed). Five males that ate supplemental garbage all dispersed at 2 years of age. For comparison, bears in another part of Minnesota, where natural food was more abundant and growth was more rapid, dispersed

as yearlings in 4 of 7 instances (D. Garshelis and K. Noyce, pers. comm.). Similarly, black bears in Pennsylvania showed unusually rapid growth (Alt 1980) and dispersed mainly as yearlings (Alt 1978). On Long Island, Washington, where black bear density was more than 5 times that of northeastern Minnesota, 3 of 4 males delayed dispersal until 4 years of age (Lindzey and Meslow 1977a, 1977b). The fact that dispersal was delayed rather than hastened at high density suggests, further, that any aggression associated with high density did not initiate dispersal. If there is differential aggression against male nonkin in the natal range, as was observed among females (Rogers 1987), the observed pattern of delayed dispersal at high population densities would be expected because risks of dispersal by bears with small body size probably would be greater under those conditions. Under the same logic, dispersal by males would be expected to occur at an earlier age where abundant food accelerates growth and sexual development. Aggression is known to deter dispersing bears from settling in new areas.

Aggression did not appear to initiate male dispersal in northeastern Minnesota. For example, after a mother died in winter, her radio-collared son nevertheless left in spring at the usual age of 2 years. His abandoned range and that of another 2-year-old that dispersed that spring were not immediately used by territorial neighbors or siblings, all or nearly all of which were radio collared. Both dispersed in a year (1972) when the potential for aggression by adult males was unusually low: 2 of 3 adult males that had overlapped the ranges of those subadults the year before were dead, and there was evidence that the third was incapacitated for several weeks by injuries from a fight in mid-June (Rogers 1987). The loss of influence of those 3 adults opened the capture area to immigration by 7 subadult males, which was nearly as many as immigrated in all of the remaining 8 years in which immigration was assessed (8 bears). Thus, although space was available locally in 1972, both males that reached 2 years of age that year dispersed. Further, movements of 32 km, 74 km, and 80 km were recorded for dispersing subadult males in September and October when aggression was unlikely. Aggression and testosterone levels are particularly low at that time of year (McMillin et al. 1976), and many bears of both sexes are either lethargic or in dens. In three other movements not readily explained by aggression, 3 subadult males moved 75 km, 80 km, and 100 km outside the bear range in southern Minnesota. These data and the fact that all males dispersed led to a conclusion that the initial dispersal movements and some subsequent movements by males were voluntary. This conclusion suggests that dispersal confers advantages on the dispersing individual.

Inbreeding Avoidance

All males dispersed before mating, and all males dispersed farther than any female. These facts are consistent with the hypothesis that dispersal

evolved as a mechanism for avoiding inbreeding. However, this explanation is weakened by three observations. First, dispersal was mainly by males even though in a polygynous system this sex would stand to lose less with inbreeding than would females, due to males' smaller parental investment and their larger reproductive potential (Smith 1979; Dawkins 1979). Second, the few females that did disperse probably did not move outside their fathers' mating ranges. Third, males did not disperse a second time when daughters began to mature in their mating ranges (Rogers 1987). Twenty-five percent of the adult males were over the minimum age of 8 years, at which father-daughter matings would become possible if males and females began mating at the minimum ages of 4 years and 3 years, respectively (Rogers 1987). Fifteen percent of the adult males were over the age of 10 years, at which father-daughter matings would become possible if males began mating at 4 years and females began mating at 5 years. Males did not avoid pairing with females young enough to be their daughters (Rogers 1987), but paternity was not certain for any female.

For females, the benefits of remaining in or adjacent to their mothers' territories apparently outweighed any potential disadvantages of remaining in their fathers' ranges. No deleterious effects of inbreeding were noted when a sibling pair was mated in captivity. They produced 34 cubs in 11 litters of normal number (2 to 4 cubs) with no mortality or obvious birth defects (D. Eggleston, pers. comm.). This could imply that bears may be at least mildly inbred in nature (Shields 1982; Templeton, chap. 17, this vol.). Avoidance of close inbreeding is logically a factor promoting dispersal, but it may be of limited importance relative to other factors influencing reproductive success and dispersal in black bears.

Food, Females, and Dominant Males

With few exceptions, the foods of black bears are small items that cannot efficiently be carried to offspring (Rogers 1987). Therefore, males cannot efficiently provision their offspring, and they do not directly aid in raising them (Rogers 1987). Instead, they attempt to maximize reproductive success by inseminating as many females as possible. At population densities observed in northeastern Minnesota, reproductive success of males appeared to depend upon ability to find receptive females before other males do and upon ability to defeat other males that find the same females. Females became attractive before they became receptive, thereby heightening competition among males (Rogers 1977). Mating privileges appeared to be obtained primarily through male-male competition rather than as an obvious result of female choice. The outcome of mating battles depended heavily upon body size. Where contestants differed significantly in size, the larger simply chased the smaller away (Rogers 1987).

Consequently, dispersing males might be expected to establish mating ranges where there are few dominant males, many mature females, and

sufficient food for rapid attainment of large body size. Costs of dispersing to look for such an area might be small for three reasons. Black bears have few predators (Rogers and Mech 1981). Mating ranges are so much larger than natal ranges that most of the mating range would initially be unfamiliar whether males dispersed or not. And the large size of mating ranges precludes males from obtaining meaningful amounts of space from their mothers (as do daughters).

Evidence that dispersing males tended to establish mating ranges in areas with reduced numbers of dominant males was obtained in this study and in a study in Alberta. In this study, the loss of influence of 3 adult males in the study area resulted in a great increase in immigration in 1972. In that year, 12 new males remained in the study area long enough to be caught, and 7 of them established permanent ranges there. By comparison, in the 8 other years of intensive trapping, an average of only 5 new males per year remained in the study area long enough to be caught, and only 1 new male established a range there per year (Rogers 1987). In Alberta, 26 adult males were experimentally removed from a population, with the result that 95 new bears, mostly subadult males, immigrated (Kemp 1976; Ruff, Young, and Pelchat 1976).

However, areas with few or no dominant males may not be attractive to dispersing males if the areas lack females. In the wooded vicinities of towns there were few bears of either sex due to people shooting them (Rogers 1976). Dispersing males commonly stopped to feed in those areas (Rogers 1976), but none was known to settle permanently. Two that were radio tracked fed around towns for 23 and 39 days, respectively, before moving farther (Rogers 1987). Food supply influenced movements to the extent that dispersing males stopped to feed at garbage dumps for up to 72 days, despite the presence of numerous dominant males (Rogers 1987). Conversely, food, females, and reduced numbers of dominant males did not induce young males to remain in their natal ranges (Rogers 1987). Possible explanations for this behavior, in addition to avoidance of inbreeding, are presented later in this chapter.

Inclusive Fitness

The majority of males dispersed 2 years before reaching sexual maturity. They typically dispersed at 2 years of age, while the youngest male to pair with a female was 4 years of age (Rogers 1987). Testicle size and body size of Minnesota bears, when compared with those of Michigan bears (Erickson, Nellor, and Petrides 1964), indicate that Minnesota males less than 4 years of age were probably sexually immature in most cases (Rogers, unpub. data). By dispersing prior to maturity, males might increase the time available for finding areas favorable to reproductive success. However, the fact that the males were immature suggests that the dispersals involved factors not directly related to obtaining mates. Early dispersal may increase inclu-

sive fitness by reducing competition among the kin left behind (Rogers 1977; Shields 1983, and chap. 1, this vol.). Males in Minnesota dispersed when they weighed 29 kg to 59 kg *(N* = 17). At that size, due to sexual dimorphism, they usually outweighed their sisters and were approaching the weights of their mothers. If they remained, they probably could have displaced female kin from preferred feeding sites, which might have interfered with the females' growth and reproductive success (Rogers 1976, 1987). If they remained and showed deference to female kin, they might have reduced their own growth, which could have reduced their potential for winning future mating fights. In a new area, males could compete vigorously without reducing their inclusive fitness. Any resulting gains in reproduction by female kin would cumulatively increase the male's inclusive fitness. Although the proximal mechanism for the pattern is unclear, 9 of 10 males that had living sisters dispersed at 2 years of age, whereas only 4 of 9 without living sisters dispersed that early (difference significant; $p < 0.05$; $X^2 = 4.55$).

Early dispersal can reduce competition for the nondispersers only if the latter prevent immigration by other potential competitors. The effectiveness of resident adult males in deterring immigration was discussed earlier. The effectiveness of territorial females in deterring immigration by young males is not as well documented, but during 1,480 hours of radio tracking a territorial female, 3 transient subadults (males by circumstantial evidence) were observed fleeing from her (Rogers 1987).

If resident adults can prevent or reduce immigration, and if dispersing males establish mating ranges where chances of mating are no worse, on the average, than in their fathers' ranges, dispersal may further improve the inclusive fitness of young males by reducing mate competition with fathers and brothers. Males benefit more by taking matings away from nonkin than from kin. Where a male's competitors share half his genes, he can achieve, by dispersing, up to a 50% increase in gene copies passed to the next generation. For example, if by dispersing, a young male enables his father to mate with a female that the young male otherwise would have mated with, while the young male mates elsewhere, 50% more of the young male's gene copies are passed to the next generation than if he had taken the mating away from his father. All males dispersed at least 1 mating range diameter from their birthplaces. By dispersing long distances, males may reduce the degree of genetic relatedness of their competitors.

CONCLUSIONS

Despite their solitary habits, bears behaved in accordance with kinship theory. Movements of mothers in relation to daughters and of brothers in relation to sisters were consistent with a hypothesis that individuals recognize their independent offspring and littermates and behave in manners

beneficial to them within limits dictated by the degree of genetic relatedness (Hamilton 1964; Wilson 1975). Differential aggression by mothers toward nonkin may partly explain delayed dispersal by males where growth rates were slow or population densities were high. This differential aggression by mothers also aided daughters in establishing adjacent territories, which may explain the low dispersal rate among females. If the parent most involved in resource defense shows differential aggression against nonkin in other mammal and bird species, thereby aiding same-sex offspring in establishing adjacent territories, such behavior may partly explain the fact that the philopatric sex in polygynous species tends to be the sex most involved in resource defense (Greenwood 1980; Waser and Jones 1983).

Evidence indicated that initial dispersal movements by males were voluntary and not forced by aggression or food shortage. Costs of male dispersal probably were low because of low predation risk and small natal: adult range-size ratios. Dispersal may enable males to find more favorable locations for establishing mating ranges. Dispersal also may increase males' inclusive fitness by reducing mate competition with male kin and feeding competition with female kin left behind. The increase in inclusive fitness depends upon the ability of the dispersers' kin to prevent immigration by other competitors. Given that demonstrated ability of kin, dispersing males can achieve up to a 50% increase in gene copies passed to the next generation if they mate where they will take mates away from nonkin rather than kin. Inbreeding avoidance may not have been the primary factor promoting dispersal.

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