

DISPERSAL OF JUVENILE FISHERS IN MAINE

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Abstract: We studied natal dispersal of fishers (*Martes pennanti*) in a harvested population in southcentral Maine during 1984–90 because of concern over the high level of harvest and a lack of information about fisher dispersal. Probability that an individual would disperse by the end of its first year was 73 and 100% for males and females, respectively ($n = 21$ M, 12 F). However, 32% of males and no females dispersed before the age of 9 months. Mean distance between natal and adult home ranges did not differ ($t = 0.16$, $P = 0.88$) between males ($n = 8$, $\bar{x} = 10.8$ km, range = 4.1–19.5) and females ($n = 5$, $\bar{x} = 11.2$ km, range = 5.0–18.9). Dispersal, in combination with intrasexual territoriality of adults, may limit fisher density and competition for food. Dispersal of nearly all juveniles allowed them to quickly replace adults removed by fur trapping. However, the short distances moved by dispersing fishers may limit their ability to recolonize areas from which fishers have been extirpated, and may reduce interchange among isolated populations.

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Dispersal was defined by Howard (1960) as movement by an individual away from the area of its birth to another area where it might reproduce. Greenwood (1980) further defined natal dispersal as movement by a juvenile before its first mating season; and breeding dispersal, as movement by an adult to a new area for mating. Patterns of natal dispersal vary greatly among mammals, both in the distance traveled by dispersers and in tendencies for 1 or both sexes to disperse from the natal home range (Greenwood 1980, Dobson 1982). Little information is available concerning dispersal of solitary carnivores, especially mustelids. Natal dispersal is male-biased in black bears (*Ursus americanus*) and red foxes (*Vulpes vulpes*); juvenile females of both species disperse either less frequently or for shorter distances than males (Phillips et al. 1972, Harris and Trehwella 1988, Elowe and Dodge 1989, Allen and Sargeant 1993). Dispersal occurs among juvenile wolverines (*Gulo gulo*) of both sexes, however, some juvenile females may remain in or near their mother's home range (Magoun 1985). In mink (*Mustela vison*), both sexes disperse, but males may disperse sooner than females (Gerell 1970). Adult fishers and many other mustelids maintain intrasexually exclusive territories (Powell 1979, Arthur et al. 1989a). Such spacing implies that juveniles of both sexes must leave their natal ranges. Many juvenile (<1 yr old) fishers travel extensively (Leonard 1980, Arthur et al. 1989a), and 4 juveniles (2 M, 2 F) in Manitoba dispersed distances of 9.5–60.0 km (Leonard 1980, Raine

1982), but no additional information about dispersal of juvenile fishers is available.

Knowledge of dispersal characteristics may provide insight on underlying behavioral and ecological mechanisms (Bekoff 1977). Dispersal may also influence a species' ability to compensate for harvest mortality or to colonize new areas. Because of concerns about the high level of harvest of fishers in some areas of Maine and the species' susceptibility to overharvest (Coulter 1960, Strickland and Douglas 1981), we studied several aspects of fisher ecology in southcentral Maine from January 1984 through June 1990 (Arthur et al. 1989a,b; Paragi 1990; Krohn et al. 1994). Specifically, our objectives were to determine the frequency and timing of dispersal from the natal range, distances traveled by juvenile fishers, and whether these characteristics differed between sexes.

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STUDY AREA AND METHODS

Our 500-km² study area extended approximately 50 km inland from Penobscot Bay near Belfast, Maine. Temperatures ranged from a mean low of -9 C in January to a mean high of 20 C in July (U.S. Weather Bur. 1982). The area was 83% forested, mostly with mixed second-growth coniferous and deciduous species, and the remainder consisted of small towns, farms, pastures, lakes, and ponds (Vonk 1975, Arthur et al. 1989b). Human population density was 15/km² (U.S. Bur. of Census 1982). Trapping fishers for fur was permitted from late October through early December each year, and harvests were not limited except by the season length. Harvest density of fishers in the area was the highest in New England, averaging 1 fisher/11 km² during 1980-83 (Me. Dep. of Inland Fish. and Wildl., unpubl. data).

Fishers (≥ 6 months old) were captured in cage traps or padded foot-hold traps and radio-collared as described by Arthur (1988) and Paragi (1990). Trapping was conducted during January-May and September-December of 1984; in subsequent years we trapped only during late January-March and September-October, when our trapping success was greatest. Age of each captured fisher was estimated by palpating for a sagittal crest and counting cementum annuli of a premolar tooth (Strickland et al. 1982, Arthur et al. 1992). After release, fishers were located by triangulating on the direction of the radio signal from ≥ 2 points (usually ≥ 3 points) on the ground, by following the radio signal and visually observing the animal, or by using standard aerial techniques from a Cessna 172 aircraft equipped with 2 directional antennas (Mech 1983). Tests indicated that $\geq 75\%$ of locations determined from the air and by ground triangulation were ≤ 10 and ≤ 175 m, respectively, from actual positions of stationary transmitters (Arthur et al. 1989b, Paragi 1990).

During 1988-89 we also marked fisher kits in natal dens. We monitored adult females daily

during spring to locate these dens (Paragi 1990, Arthur and Krohn 1991). We examined dens 6-8 weeks after the estimated birth date of the offspring, while the adult females were absent (Paragi 1990). We removed juveniles from dens and marked each with 2 numbered ear tags, then replaced the juveniles and left the sites before the mothers returned. If livetrapped at a later date, marked fishers were identified based on the presence of ear tags or scars from tags that had been lost. One additional kit was captured with a tranquilizer dart and marked with ear tags when found in a tree during July 1986. Although other litter-mates were observed nearby, the den was not found.

During autumn livetrapping and radiotracking, we assumed that marked juveniles captured within the home ranges of their mothers and unmarked juveniles that remained in the area surrounding the capture site for ≥ 1 week had not yet dispersed from the area of birth. We assumed dispersal began when a juvenile first moved ≥ 9 km from the initial capture site, and did not return. We chose this distance based on the lengths of home ranges of adult fishers in the area (Arthur et al. 1989a). Adult ranges determined by minimum convex polygons averaged 7.7 km in length (F: $n = 6$, $\bar{x} = 6.6$ km; M: $n = 7$, $\bar{x} = 8.7$ km; $t = 1.15$, $P = 0.27$), and 75% were < 9 km long (S. M. Arthur, U.S. Fish and Wildl. Serv., unpubl. data). Previously unmarked juveniles that moved ≥ 9 km from the capture sites during the first week after capture and did not return were assumed to have begun dispersing before capture.

We calculated the probability that an individual would disperse for each sex using the survival analysis of Pollock et al. (1989), substituting dispersal for death of an animal. In our analysis, the survival rate calculated by the model is the pre-dispersal residency rate, or cumulative probability that an individual has not dispersed as of a specified date. Thus, probability of dispersal by that date is $1 - \text{residency}$. With this analysis, days may be grouped into periods, which may be of any length. During autumn, when animals were located most frequently, we considered 7 periods. The first extended from birth to 7 October; the other six were each 2 weeks long, ending 21 October, 4 November, 18 November, 2 December, 16 December, and 30 December. Animals were located less frequently during winter and spring. To include animals for which dates of dispersal were not

known precisely, we used 2 longer periods extending from 31 December to 8 February and from 9 February to 8 April.

This analysis requires that dispersal of each animal be assigned to a specific period. We attempted to locate each animal at least once per week during autumn and at least twice per month during the remainder of the year. However, some juveniles were located infrequently during winter and spring 1989 and 1990 because of logistical constraints. A minimum of 2 locations within a period (1 before and 1 after dispersal) were required to determine when a fisher dispersed; for each period, we included only fishers for which ≥ 2 locations were obtained. Fishers that were already dispersing when captured were included in the model only if captured before 7 October. This period included, by definition, all possible prior dispersals. Otherwise, fishers were included in this analysis only if they were initially classified as residents. Animals that died or were lost from radio contact before dispersing were dropped from the model for the period in which monitoring stopped and all subsequent periods, because they might have dispersed if monitoring had continued. However, we included these fishers in previous periods during which they were monitored. Thus, we assumed that dispersal probability was independent of future death or collar failure.

We tested for differences in dispersal rates between sexes within sampling periods using the Z-statistic recommended by Pollock et al. (1989: 11) at the 0.05 level of significance. The log-rank test presented by Pollock et al. (1989) was not appropriate because it assumes that 2 curves being compared are of the same shape; we believe this was not true of the dispersal curves. Furthermore, by using periods of unequal length, we weighted different seasons unequally.

Adult (≥ 1 yr old) fishers maintained stable home ranges during May–December (Arthur et al. 1989a). Therefore, we assumed dispersal of a juvenile ended when all subsequent locations were contained within the minimum convex polygon used by the fisher during May–December of its second year, or until the animal's death or loss of collar. We measured distance dispersed in 2 ways. Minimum separation between natal and adult home ranges was measured from the initial capture site of an animal to the nearest location within its subsequent home range (min. distance). We also measured the distance from the capture site to the furthest location of the

dispersing animal to indicate the maximum separation that might have been achieved (max. distance). For these measurements, we excluded animals that did not disperse or that died or were lost from contact before ending dispersal. However, we included fishers that already were dispersing when first captured and others that died or lost collars after establishing stable ranges, but before December of their second year. Thus, our measurements are minimum estimates of the distances moved by dispersing fishers.

RESULTS

We captured and radiocollared 45 juvenile fishers. Of these, we excluded 3 females and 7 males for which dispersal status could not be determined because they were monitored for <1 week or because insufficient data were obtained. Two males that seemed to be dispersing when caught in November and January, respectively, also were excluded from the analysis of dispersal probability, but were used to estimate dispersal distance. If these animals actually began dispersing during the first week after capture, then by excluding them we slightly underestimated dispersal probability of males. However, we believe that both animals began dispersing during earlier periods, because the fisher caught in November was caught on the first day of the period. The other fisher was caught within the range of a radio-collared adult female that had not produced young the previous spring, in an area where we had trapped intensively during the previous autumn.

We eartagged 10 juveniles (7 M, 3 F) from 5 litters found at natal dens and 1 male captured in a tree whose natal den was not located. Six marked juveniles (4 M, 2 F) were later recaptured and radiocollared. One of these had lost both ear tags, and was identified by the scars left by the tags. In addition, 26 previously unmarked fishers (16 M, 10 F) were live-trapped before dispersal, and 1 dispersing male was live-trapped before 7 October, so we determined dispersal probability using 33 fishers (21 M, 12 F). Of these, 1 male was first radiocollared during August, 20 males and 11 females were first radiocollared during September or October, and 1 female was first radiocollared during November. Assuming births occurred during March (Paragi 1990, Arthur and Krohn 1991), most juveniles were first radiocollared at 6–7 months of age. Radiotracking of 20 fishers was inter-

Table 1. Cumulative probability of dispersal of juvenile fishers in southcentral Maine, 1984–90.

| Period | Pre-dispersal ^a | | Dispersals ^b | | P(D) ^c | | Var(D) ^d | |
|---------------|----------------------------|----|-------------------------|---|-------------------|------|---------------------|------|
| | M | F | M | F | M | F | M | F |
| Birth–7 Oct | 12 | 6 | 2 | 0 | 0.17 | 0 | 0.01 | 0 |
| 8 Oct–21 Oct | 15 | 8 | 2 | 0 | 0.28 | 0 | 0.01 | 0 |
| 22 Oct–6 Nov | 16 | 10 | 1 | 0 | 0.32 | 0 | 0.01 | 0 |
| 5 Nov–18 Nov | 10 | 5 | 0 | 0 | 0.32 | 0 | 0.01 | 0 |
| 19 Nov–2 Dec | 7 | 6 | 0 | 0 | 0.32 | 0 | 0.02 | 0 |
| 3 Dec–16 Dec | 7 | 6 | 0 | 0 | 0.32 | 0 | 0.02 | 0 |
| 17 Dec–30 Dec | 7 | 6 | 0 | 0 | 0.32 | 0 | 0.02 | 0 |
| 31 Dec–8 Feb | 5 | 5 | 1 | 3 | 0.46 | 0.60 | 0.03 | 0.02 |
| 9 Feb–8 Apr | 4 | 2 | 2 | 2 | 0.73 | 1.00 | 0.01 | 0 |

^a Number of radio-collared fishers that had not dispersed at the beginning of the period.^b Number of fishers that dispersed during the period.^c Cumulative probability of dispersal as of the last day of the period.^d Variance of the estimated probability of dispersal (Pollock et al. 1989).

rupted; 19 of these died (18 killed by humans; 1 cause of death unknown) before dispersing. The other animal's transmitter failed, but this fisher was later recaptured within its natal range. Thus, these animals had not dispersed by the time monitoring stopped.

Juveniles stopped using natal dens at the age of 6–8 weeks (Paragi 1990), the age when captive fishers are weaned (Coulter 1966, Powell 1982), but remained with their mothers until approximately 150 days of age. We observed adult females accompanied by their offspring during July–August, 120–150 days after birth, and we captured and radiocollared a juvenile male with its mother on 10 August. However, this juvenile was never located with its mother after that date (although telemetry errors might have mistakenly placed the fishers apart), and we found little evidence of association between adults and juveniles after mid-August (Paragi 1990).

Dispersal probability differed between sexes during autumn (Table 1). No females dispersed by 30 December, whereas 2 males had begun dispersing by 7 October, and dispersal probability was 0.32 by 30 December (different from 0; $Z = 2.22$, $P = 0.03$). By 8 February, dispersal probability did not differ between sexes (0.60 and 0.46 for females and males, respectively; $Z = 0.69$, $P = 0.49$). Although by 8 April, probability of dispersal was higher for females than males (1.00 vs. 0.73; $Z = 2.34$, $P = 0.02$), during the final period we monitored only 2 females and 4 males that had not dispersed previously (the difference may have been due to the small sample size).

Of the 2 males that did not disperse, one slipped its collar at age 13 months and the other

had not dispersed when it slipped its collar as a 2 year old. Both non-dispersing males made brief forays out of their home ranges, but then returned. No juvenile dispersed to, or remained in, an area used by a radio-collared adult of the same sex. However, 1 male remained in, and 2 males and 1 female dispersed to, areas where radio-collared adults of the same sex had died within the previous 15 months. No radio-collared adults were present in the home ranges occupied by the 2 non-dispersing males.

We measured dispersal distances for 5 females and 8 males (Table 2). One female dispersed <9 km, but we classified this animal as a disperser because it used 2 distinctly different home ranges separated by 4.1 km. Another female died in late March, approximately 1 month

Table 2. Timing and distances of dispersal of juvenile fishers in southcentral Maine, 1984–90.

| Sex | Beginning month | Ending month | Distance (km) | |
|-----|----------------------|----------------------|-------------------|-------------------|
| | | | Min. ^a | Max. ^b |
| M | Nov ^c | May | 4.1 | 10.9 |
| M | Oct | Apr | 10.9 | 20.8 |
| M | Feb/Mar ^d | Apr | 19.5 | 23.0 |
| M | Sep ^c | May | 9.2 | 17.4 |
| M | Jan ^c | Apr | 13.1 | 18.0 |
| M | Mar | Apr | 8.4 | 14.3 |
| M | Jan | Feb | 11.1 | 15.0 |
| M | Oct | Jun | 10.4 | 19.0 |
| F | Feb | Mar | 18.9 | 22.6 |
| F | Feb | Feb | 14.0 | 15.1 |
| F | Feb | Mar | 8.4 | 13.3 |
| F | Jan/Feb ^d | Feb/Mar ^d | 5.0 | 7.5 |
| F | Jan | Feb | 10.0 | 16.1 |

^a Distance from capture site to closest point of subsequent home range.^b Distance from capture site to furthest location of dispersing fisher.^c Fisher already was dispersing when first captured; beginning month may have been earlier.^d Dates were uncertain because of infrequent locations.

after ending dispersal. Based on behavior of other females, we assumed that this fisher would have remained in its newly established home range if it had survived. Minimum distance of dispersal averaged 11.3 and 10.8 km for females and males, respectively (range = 5.0–18.9 and 4.1–19.5 km; SD = 5.3 and 4.3; $t = 0.16$, $P = 0.88$). Maximum distance averaged 14.9 and 17.3 km for females and males, respectively (range = 7.5–22.6 and 10.9–23.0 km; SD = 5.4 and 3.8; $t = 0.92$, $P = 0.38$). Overall means for minimum and maximum distances were 11.0 and 16.4 km, respectively (SD = 4.6 and 4.5 km). The longest movement we recorded was 30.6 km by a male that was caught by a fur trapper while dispersing and not included in the calculations of dispersal distance.

Patterns of movement during dispersal differed between sexes and among individuals. All 5 females that established new home ranges did so by March, ≤ 2 months after beginning dispersal (Table 2). Only one of the 8 males finished dispersing by March. Three males established new home ranges during April, two during May, and one continued wandering until late June (we modelled this animal's adult home range from Jul–Dec). Duration of dispersal was ≤ 2 months for 3 males, ≥ 3 months for 1 male, 6–7 months for 3 males, and ≥ 9 months for 1 male (Table 2). Four of 5 males that began dispersing during October or November confined their movements to small areas (used < 3 weeks) during mid-winter, before resuming widespread movements during February and March. The remaining male moved extensively from November through April.

DISCUSSION

In mammals, dispersal rates or distances are greater for males than females of many species in which males compete for mates (Greenwood 1980). Dobson (1982) predicted that in polygynous and promiscuous species, mate competition would be greater among males than females, leading to increased dispersal of subordinate and juvenile males. Leonard (1980) suggested that such competition may occur in fishers, but juvenile fishers of both sexes dispersed with similar frequencies and over similar distances. Thus, the major function of natal dispersal of fishers may be to maintain the intrasexually exclusive territories of adults. Previously (Arthur et al. 1989a), we suggested that territoriality among adult fishers serves to reduce

competition for a fluctuating and unpredictable food supply.

Adult fishers are solitary, and mating pairs associate only for brief periods during spring (Coulter 1966, Powell 1977). Most ($\geq 95\%$) adult females in Maine become pregnant every year (Shea et al. 1985), but it is unknown whether females commonly mate with > 1 male. During the mating season, adult males travel extensively outside of their usual home ranges (Buck 1982, Johnson 1984, Arthur et al. 1989a), and probably attempt to mate with several females. Thus, male fishers undergo both natal and breeding dispersal. In contrast, adult females maintained consistent home ranges for as long as we monitored them (nearly 5 yr for 1 fisher; Arthur et al. 1989a, Paragi 1990). Male-biased breeding dispersal supports the hypothesis that adult males compete for mates. Sandell (1986) suggested that breeding dispersal of adult male stoats (*Mustela erminea*) allowed them to mate with more females, while preventing mating by subordinate and juvenile males. Dispersal by some juvenile male stoats may have helped them locate areas with no adult males and improved their chances for mating. This also may be true of fishers in areas where adult males are abundant, provided that juveniles can disperse to areas with fewer adult males. However, it is unknown whether 1-year-old male fishers are effective at mating, even if given the opportunity (Wright and Coulter 1967, Leonard 1986).

Juvenile fishers dispersed only 1–3 times the mean length of adult home ranges. These distances were no greater than those moved by adult males during breeding dispersal, and would therefore have little effect on the level of inbreeding within the population. Distances may have been affected by the high trapping mortality (estimated at 62, 42, and 21% annually for juveniles, adult males, and adult females, respectively [Krohn et al. 1994]), which probably increased the availability of vacant home ranges. If dispersal is stimulated by the presence of conspecific competitors, then fishers might disperse farther in populations with lower mortality rates and higher densities. However, increased density also might discourage dispersal, by reducing the chance of finding a vacant home range and thereby increasing the cost of leaving the natal area. Dispersal distances of red foxes (Trehwella et al. 1988) and field voles (*Microtus agrestis*; Sandell et al. 1990) increased as density increased. Allen and Sargeant (1993) re-

ported that male red foxes in North Dakota were less likely to disperse when density was greater, although dispersal distances of both sexes were not affected by density.

MANAGEMENT IMPLICATIONS

Within the well-established but intensively harvested population in southcentral Maine, natal dispersal by almost all fishers of both sexes allowed them to rapidly reoccupy vacant home ranges, and fisher density was estimated to be similar to untrapped populations in comparable habitat (Arthur et al. 1989a). However, the short dispersal distances we observed suggest that fishers will not readily recolonize large areas from which they have been extirpated, and that expansion of isolated populations will be slow. According to Coulter (1960), fishers were slow to recolonize central and coastal Maine during the 1950's. Although areas of low-quality habitat may have inhibited fisher movements (Coulter 1960) in most of southcentral Maine, populations increased rapidly after fishers arrived, suggesting that habitat was not limiting. Thus, intensive reintroduction efforts, as were conducted in the eastern United States and Great Lakes regions (Pack and Cromer 1981, Berg 1982) may be necessary to reestablish populations elsewhere.

Short dispersal distances also suggest that maintaining viable fisher populations may be difficult in areas where suitable habitat patches are small and widely separated because fishers may be reluctant to travel farther than 10–20 km to find appropriate habitat. This may partly explain why fishers in the western United States have not shown the range expansion typical of populations in the Northeast. In the western states, forested habitat preferred by fishers (Buck 1982, Rosenburg and Raphael 1986, Jones 1991) generally occurs in mountainous areas, which are often separated by open grasslands or shrublands. Although timber harvests on small, irregularly-shaped blocks may increase forest diversity favored by fishers in the Northeast (Kelly 1977, Arthur et al. 1989b), large-scale clearcutting of western forests may create additional barriers to fisher movements and hinder efforts to maintain or enhance fisher populations.

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