

DISPERSAL OF SUBADULT MOOSE FROM A
LOW DENSITY POPULATION IN INTERIOR ALASKA

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Abstract: Dispersal of 1- to 3-year-old moose from a low density, but rapidly growing, moose population was investigated. Radio-collars were placed on 17 offspring of previously radio-collared adult cows. Comparison of home ranges of independent offspring and their respective dams indicates a close spacial relationship between home ranges. No long distance dispersal resulting in the formation of a home range separate from that of the dam's was observed. Winter home ranges of offspring tended to deviate more from that of their dams than did summer home ranges. Thus, this moose population demonstrated a very slow rate of dispersal. For managers this conclusion has important consequences: 1) newly created habitat will not be rapidly located and occupied by dispersing moose; 2) locally overhunted areas will be repopulated primarily by offspring of the area's surviving moose; and 3) since declining moose populations adjacent to low density populations derive few new members by immigration, each population must be managed with respect to its individual potential growth rates.

The extent of dispersal from a moose (*Alces alces*) population can alter the management strategy for that population and adjacent populations which may receive dispersing moose. Therefore, it is useful to predict when dispersal may occur, which sex and age classes are prone to disperse, and the approximate magnitude of dispersal.

Expansion of moose range through dispersal has been documented in North America (Houston 1968; Mercer and Kitchen 1968; Peek 1974a, 1974b; Coady 1980), the Soviet Union (Likhachev 1965; Yurlov 1965; Filonov and Zykov 1974), and Europe (Pullainen 1974). In those studies for which age specific dispersal was determined, yearling and 2-year-old moose dispersed more frequently than adults (Likhachav 1965; Houston 1968; Peek 1974a; Rousset et al. 1975; Lynch 1976). Adult bull and cow moose were relatively faithful to previously established seasonal home ranges (Houston 1968; Goddard 1970; Berg 1971; Saunders and Williamson 1972; Phillips et al. 1973; LeResche 1974; Coady 1976; VanBallenberghe 1977, 1978). Therefore, the fidelity that adults demonstrate toward their home ranges minimizes the role of adult moose in the colonization of new ranges through dispersal.

Dispersal of moose appears to be associated with relatively high population density (Likhachev 1965; Yurlov 1965; Houston 1968; Filonov and Zykov 1974; LeResche 1974; Peek 1974a, 1974b; Irwin 1975; Rousset et al. 1975; Coady 1980). Although not specifically stated by most of the above authors, the densities of moose populations from which dispersal was recorded may have approached or exceeded the carrying capacity of the range based on our interpretations of information presented in these studies. Dispersal from a moose population that was clearly at low density relative to carrying capacity was found only in Mercer and Kitchen (1968).

Many moose populations in Alaska are presently at low densities relative to the carrying capacities of their ranges. Management plans should consider the dispersal patterns of moose in these low density

populations as well as dispersal patterns exhibited by moose in adjacent populations closer to carrying capacity.

This study was designed to investigate the frequency, direction, and distance of dispersal, and the age and sex of dispersing moose in a low density moose population. The population selected for study had an estimated peak density of approximately 0.8-0.9 moose/km² during the late 1960's (Bishop and Rausch 1974); however, reappraisal of past data suggests the density may have been nearly twice the earlier estimates. During the mid-1960's heavily browsed vegetation and winter die-offs suggested that these moose exceeded the carrying capacity of the range. Density had declined to approximately 0.23 moose/km² by 1975 as a result of severe winter weather, malnutrition, high harvest by hunters, and high rates of predation by wolves (*Canis lupus*) (Bishop and Rausch 1974; Gasaway et al. 1978). Following harvest reductions since 1975 and wolf control since 1976, this population has steadily increased through 1979. The mean density of moose in the study area had increased to an estimated 0.27 moose/km² by fall 1978 (Gasaway et al. 1979), and it is still considered to be below the range's carrying capacity. This is a preliminary report on a continuing study.

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STUDY AREA

The study area in interior Alaska (Fig. 1) includes the lowlands of the Tanana Flats, the rolling hills of the Tanana Hills, and the alpine zones and mountainous terrain of the north side of the Alaska Range. The Tanana Flats is a mosaic of habitat types ranging from herbaceous bogs to deciduous and white spruce (*Picea glauca*) forest and includes shrub-dominated seres following wildfires. Habitat of the Tanana Flats is described in detail by LeResche et al. (1974). Vegetation on hillsides and river bottoms of the Tanana Hills is influenced by aspect of the slope. Warm, well-drained soils support white spruce, quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) which grade into extensive stands of black spruce (*Picea mariana*) on saturated and cold soils. Shrub communities are located along creek and river bottoms and in recent burns. Vegetation in the Alaska Range is characterized as an upland climax community (LeResche et al. 1974). Willows (*Salix* spp.) are found along streams and intergrade into a shrub zone and eventually into alpine tundra on ridgetops and higher elevations. Spruce, aspen, and birch are characteristic of lower elevations.

METHODS

Forty-four adult moose were immobilized with a mixture of M99 (Etorphine hydrochloride, D-M Pharmaceuticals, Inc., Rockfield, MD) and Rompun (Xylazine hydrochloride, Chemagro Division of Bay Chemical Corp., Kansas City, MO), and radio-collared (AVM Instrument Co., Champaign, IL) during August and October 1976 (Gasaway et al. 1978). A representative cross-section of the adult moose population was radio-collared including

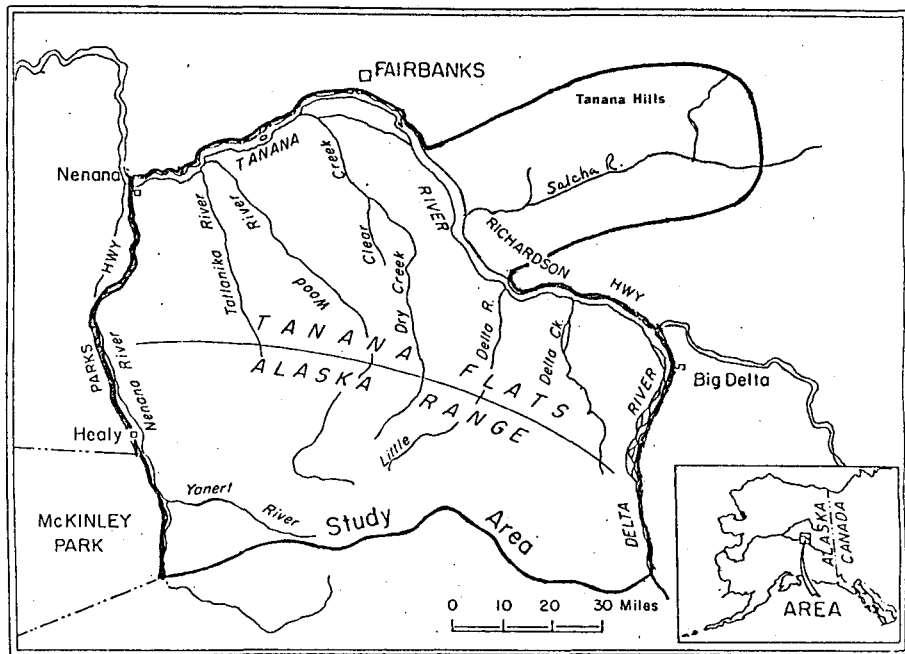


Figure 1. The study area in interior Alaska.

bulls, cows with calves, and cows without calves. The moose were radio-collared in conjunction with a project designed to determine the sightability of moose during aerial surveys. Although the sightability project was not designed as a moose movement study, radio-collared moose were routinely relocated from fixed-wing aircraft during sightability work. Periods of most frequent relocations included October-March 1976-1978 and May-June 1977-1978. Moose were generally relocated 1 to 3 times per month during these periods, and an attempt was made to relocate moose at least once per month during all other times of the year. However, longer gaps between relocations were common.

At the onset of the dispersal study in May 1978, 6 yearlings and 1, 2-year-old offspring of radio-collared dams were immobilized with a mixture of 5 mg M99 and 200 mg Rompun and fitted with radio-collars prior to separation of the dam/offspring bond. An accumulation of 19-21 months of movement data was available on the cows at that time and 12-24 months of movement data were available on the offspring during the time they accompanied their dams. We also radio-collared an adult cow that had previously been radio-tracked from October 1974 to July 1975 (Coady 1976); in addition, her yearling offspring was radio-collared. All radio-collared dams and their radio-collared offspring were relocated approximately once per month. More frequent relocations occurred during winter. All relocation points were plotted on 1:63,360 topographic maps.

From 9-16 May 1979 we replaced the radio-collars (Telonics, Mesa, AZ) on 11 adult cows that had been radio-collared in 1976 in order to maintain continuity of data on these individuals. Ten yearlings of

previously radio-collared cows were also radio-collared, along with 4 previously uncollared adult cows.

For purposes of this preliminary study we defined dispersal as the spatial separation of the home range of the independent offspring from the home range occupied by the offspring while accompanying its dam. Hence, the extent offspring disperse can range from no dispersal if the offspring remains within the home range experienced while associated with its dam to lengthy distances if the offspring moves to a new home range. Minimum year-round home ranges were drawn for radio-collared moose by connecting outside relocation points to generate a concave polygon of home range area (A, Fig. 2). Concave polygons were used because relocating moose on a monthly basis prohibited us from precisely defining the home range of individual moose. Also, during periods of more frequent relocation, occasionally moose were noted to make sporadic forays of short duration, in which individuals left and then returned to a central region of activity. If these forays were enclosed within a

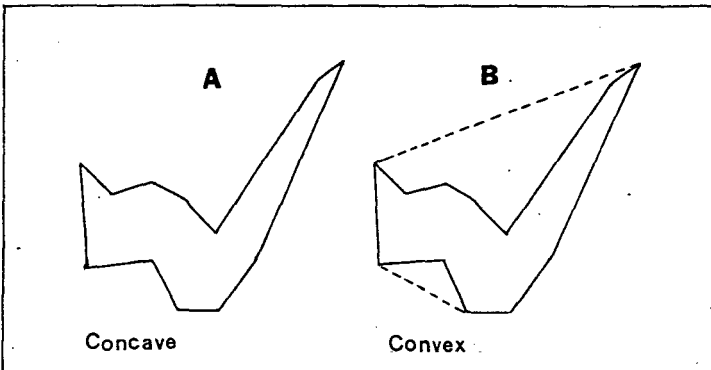


Figure 2. Concave polygons (A) were used to make estimates of minimum home range size of moose. Convex polygons (B) enclose large areas where the moose were not observed.

convex polygon, a substantial increase in the home range would result (B, Fig. 2). A concave polygon, however, better describes the area where moose were actually recorded. Seasonal polygons were calculated for both summer (May-August) and winter (September-April) home ranges of dams and their offspring.

Relocations of moose were not frequent enough to define migration routes for migratory moose. Therefore, arbitrary migration routes were created by drawing a straight line between the last relocation point prior to migration and the first relocation point after migration.

To quantify dispersal of radio-collared offspring, we measured several parameters based on the relationship of relocation sites of the independent offspring to the home range occupied by the offspring while accompanying its dam. This latter home range will be referred to as the dam's home range hereafter. These measurements included: 1-the length of year-round home range. This was the greatest linear distance between the 2 most widely separated relocation points (A, Fig. 3); 2-spatial separation between the year-round home range of dams and their offspring. This was determined by measuring the linear distance from each relocation point of the offspring to the closest portion of the home range of the dam (B, Fig. 3) including migratory routes (C, Fig. 3); relocation points of the offspring that were enclosed by the dam's home range were given a distance of 0 km (D, Fig. 3); and 3-spatial separation of seasonal home ranges. This was determined by measuring the linear distance from each relocation point of the offspring (including points during migration) to the closest point on the appropriate seasonal polygon of the cow (E, Fig. 3).

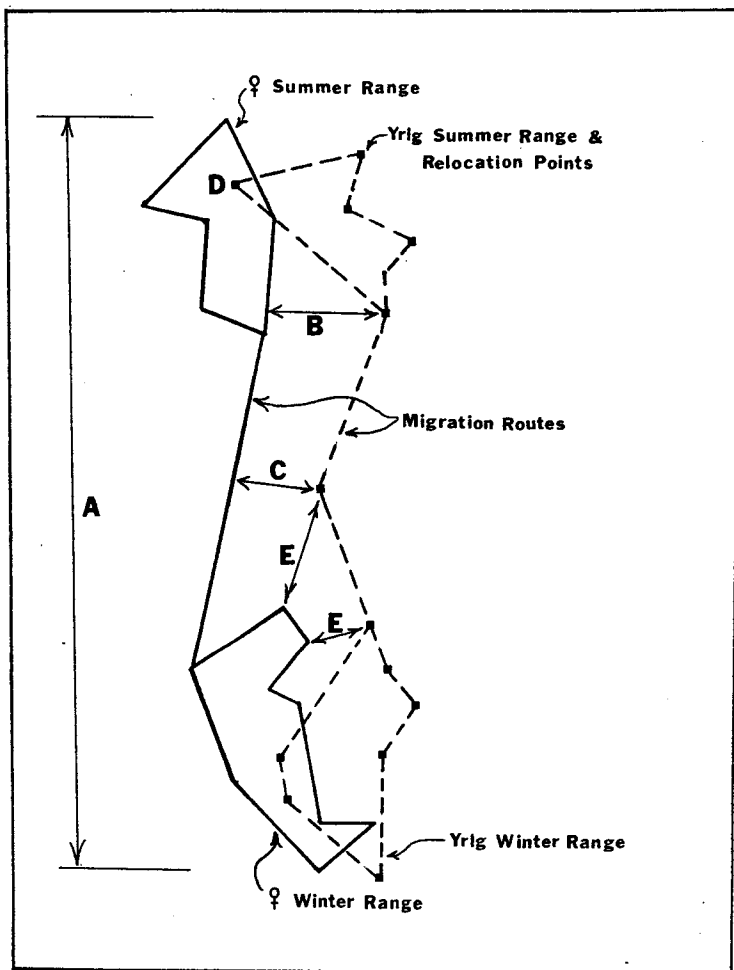


Figure 3. Examples of measurements used to quantify the spatial relationship between the dam's home range and relocation points of the offspring. "A" is greatest length of year-round home range. "B" is the minimum linear distance from a relocation point to any year-round home range polygon of the dam, or migration route "C." Relocation points within the dam's home range "D" received 0 km distance separation. "E" is the minimum linear distance of a seasonal relocation point of the offspring to the dam's appropriate seasonal polygon.

Student's t-test was used to detect significant differences between mean values ($P < 0.05$). In testing for significant differences of paired observations, i.e. dam versus the offspring or the same individuals between years, a paired Student's t-test was used (Simpson et al. 1960).

RESULTS

Two-year-old offspring did not differ significantly from yearling offspring in distances from their respective dam's home range (Table 1). In addition, of 5, 2- and 3-year-old moose that were followed since their birth, there was no significant difference between their first and second year of independence in spacial separation from their respective

Table 1. Mean Straight Line Distances Separating Relocations of Offspring From Year-round Home Range of Their Dams. Distances Are Reported in km. Standard Deviation and Range Are in Parentheses.

Age of Offspring n	Mean of Mean Separation	Mean of Minimum Separation	Mean of Maximum Separation
Yearling n=15	3.4a (4.7,0.0-18.7)	0.0a (0.0,0.0-0.0)	9.7a (9.3,0.0-38.9)
2 year old n=5	2.7a (2.4,0.2-5.6)	0.2a (0.2,0.0-0.5)	8.8a (4.2,1.6-12.1)
3 year old n=1	0.8	0.0	9.3
All Combined n=21	3.1 (4.0,0.0-38.9)	0.0 (0.2,0.0-0.5)	9.5 (8.0,0.0-38.9)

Means followed by similar letters in columns indicate no significant difference ($P > 0.05$) between yearlings and 2 year olds.

dam's home range (Table 2, Fig. 4). Therefore, we pooled all offspring into a single subadult category for investigating dispersal.

Table 2. Comparison of Straight Line Distances Separating Locations of Offspring From Their Dam's Year-round Home Range During Their First and Second Year of Independence From Their Dam. Distances Are Reported in km. Standard Deviation and Range Are in Parentheses.

No. of Offspring	Mean of All Observations		Mean Maximum Deviation	
	1st year	2nd year	1st year	2nd year
5	2.1a (1.6,1.0-4.7)	2.7a (2.3,0.2-5.6)	9.2b (4.0,3.7-13.2)	8.7b (4.2,1.6-12.1)

Similar letters following paired means for first and second years indicate no significant difference ($P > 0.05$) between means.

Based on relocations, subadult moose were separated by an average of 3.1 km from their dams' year-round home range; the mean greatest distance which offspring were separated from the dam's range was 9.5 km (Table 1). In all but 1 case, a portion of the subadult's home range overlapped that of its dam. A mean dispersal of approximately 3 km is a relatively short distance when compared with the lengths and areas of home ranges which were observed. The total length of home ranges for all subadults and adults averaged about 40 km with a maximum of 90 km (Table 3). The mean home range area of 5 dams and their offspring collared in May 1978 was 60 km² with a range of approximately 25-110 km². It should be pointed out that the distances calculated for dispersal are maximum values since the concave polygons used to describe a home

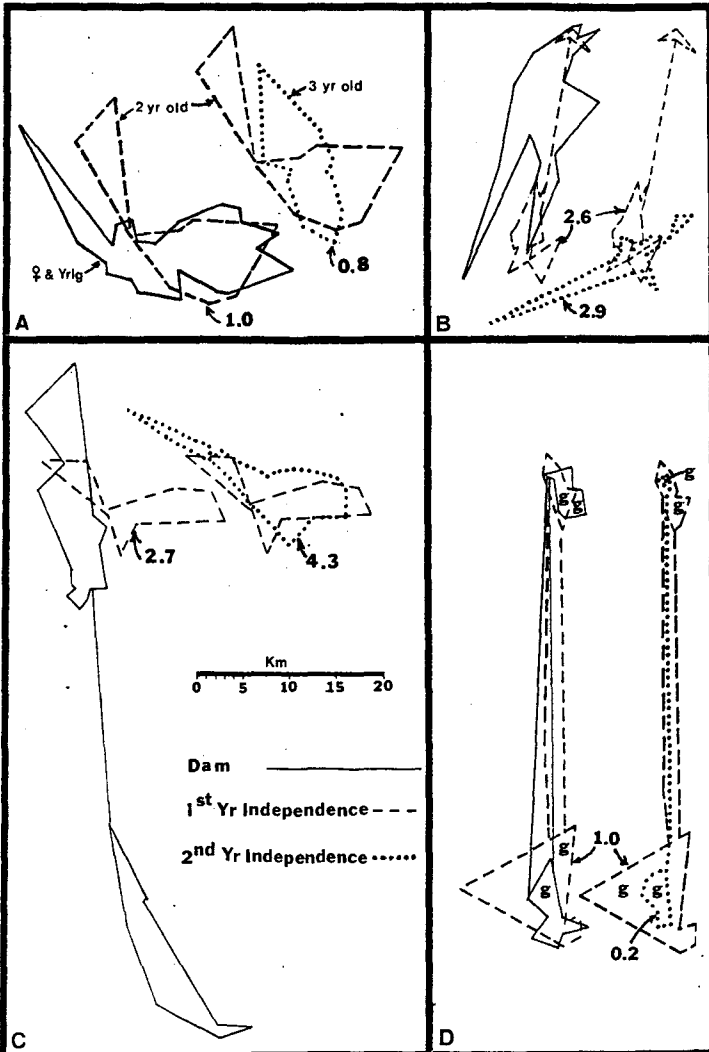


Figure 4. Examples of minimum home ranges of independent offspring in relation to its dam's home range. Numerical values indicate mean distance of all observed locations of the offspring from its dam's year-round home range. Home range polygons which are difficult to separate from migration routes are indicated by "g." To avoid congestion on the figure, home ranges for the second year of independence are offset and referenced to home ranges of the first year of independence.

Table 3. Comparison of Maximum Year-round Home Range Length Between Dams and Their Offspring. Distances Are Maximum Straight Line Measurements in km Between the Two Most Distant Points. Standard Deviation and Range Are in Parentheses.

Age of Offspring n	Dam	Offspring
	1	2
Yearlings n=15	43.8a (20.0,14.8-72.7)	38.3a (20.8,13.7-90.1)
2 year old n=5	51.0a (19.1,30.2-72.7)	34.4a (12.2,24.8-47.9)
3 year old n=1	33.8	20.4
All Combined n=21	45.0a (19.1,14.8-72.7)	36.5a (18.7,13.7-90.1)

1 Similar letters following paired means in rows for dam and offspring indicate no significant difference ($P > 0.05$) between means.

2 No significant difference ($P > 0.05$) was found between yearlings and 2 year olds (columns).

range tend to maximize separation between offspring and dam. During their first year of independence male and female offspring did not differ significantly in mean relocation distances from their dams' year-round home ranges. Figures 4 and 5 illustrate the juxtaposition of home ranges of dams and their offspring and show the mean distance of the offspring from the dam's year-round home range. These figures assist in visualizing the spatial relationships used to quantify subadult dispersal.

The mean maximum year-round length of yearling home ranges did not differ significantly from that of 2-year-old moose (Table 3). The mean maximum length of year-round home ranges for dams was not significantly

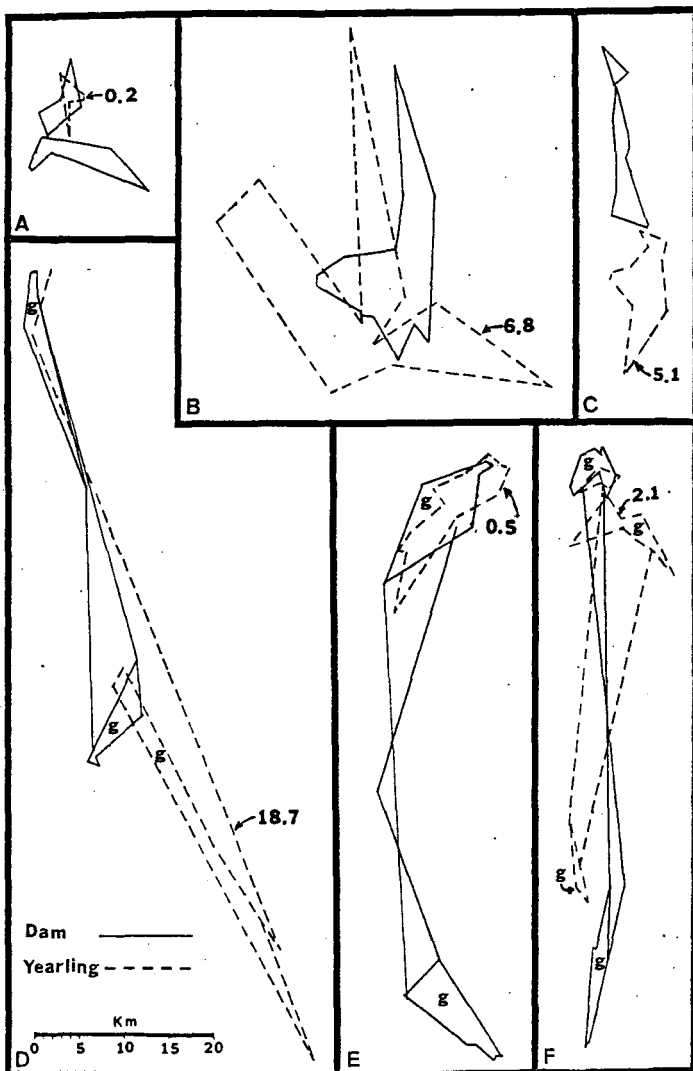


Figure 5. Examples of minimum home range estimates of independent yearling moose relative to its dam's home range. Numerical values indicate mean distance of all observed locations of the offspring from its dam's year-round home range. Home range polygons which are difficult to separate from migration routes are indicated by "g."

different from that of their yearling or 2-year-old offspring (Table 3). Therefore, yearling and 2-year-old moose did not exhibit greater home range lengths than their dams.

Although dam and offspring year-round home ranges were separated by a relatively short mean distance (3.4km), seasonal home ranges were often separated by considerable distances (Table 4). During winter the distance subadults were separated from the winter range of their dams averaged 9.3 km, with a mean maximum distance of 18.2 km (Table 4). The distances separating dam and subadult home ranges during summer were significantly shorter than during winter (Table 4).

Differences between seasonal and year-round spatial separation measurements (Tables 1 and 4) resulted from a combination of differences in chronology of migration for the dam and offspring and the dispersal of offspring from the dam's home range. When the timing of long migrations differs, a large seasonal separation can develop even though little separation in year-round home ranges exists. For example, Fig. 4C illustrates an extreme case in which the offspring of a migratory female became a resident on the dam's summer range. Year-round home ranges were in close proximity, while winter ranges differed substantially. Dispersal of offspring from the home range of the dam also contributed to the seasonal separation shown in Table 4, particularly during winter when the greatest dispersal occurred. Therefore, seasonal home range differences, as calculated in the present study, represent a general time specific spatial relationship of 2 moose and should not be thought of strictly as a measure of dispersal.

Table 4. Straight Line Distances Separating Locations of Offspring From the Seasonal Home Range of Their Dams. Distances Are Reported in km. Standard Deviation and Range Are in Parentheses.

Age of Offspring n	Summer (May-Aug)			Winter (Sept-Apr)		
	Mean of Mean Separation	Mean of Minimum Separation	Mean of Maximum Separation	Mean of Mean Separation	Mean of Minimum Separation	Mean of Maximum Separation
Yearling n=15	3.2a ¹ (4.7,0.0-19.0)	0.0a (1.1,0.0-0.3)	10.6a* (15.3,0.0-33.6)	9.7a (12.2,0.0-48.3)	3.4a (10.0,0.0-38.9)	20.1a* (17.1,0.0-54.4)
2 year old n=5	2.9a (3.4,1.1-8.8)	0.2a (0.3,0.0-0.6)	11.7a (13.0,2.3-34.4)	10.6a (14.0,0.5-34.3)	2.7a (3.5,0.0-7.4)	15.3a (16.3,1.3-40.9)
3 year old n=1	3.7	0.5	9.3	0.5	0.0	2.9
All Combined n=21	3.2* (4.2,0.0-19.0)	0.2 (0.2,0.0-0.6)	10.8 (14.0,0.0-21.4)	9.3* (12.2,0.0-48.3)	3.1 (8.5,0.0-38.8)	18.2 (16.6,0.0-33.8)

¹ Means followed by similar letters in columns indicate no significant difference ($P > 0.05$) between yearlings and 2 year olds.

* indicates a significant difference ($P < 0.05$) between comparable means in rows for summer and winter periods.

Several individual case histories will be used to describe the variation in movement of subadults in relation to the home range of their dams' during the period the offspring accompanied the cow.

1. The longest mean dispersal recorded on a year-round basis was 18.7 km between male yearling 7751 and his dam 7712 (Fig. 5D). Although 7751 overlapped the home range of his dam at times, he ranged up to 55.2 km away from his dam's range during the summer and 38.9 km away during the winter.

2. An offspring of cow 6915 was radio-collared in each of 2 successive years. Male yearling 7730 was radio-collared in May 1978 and male yearling 7753 (Fig. 5E) was radio-collared in May 1979. The greatest mean seasonal separation we recorded was between 6915 and 7753. During the summer 7753 dispersed an average of only 0.5 km from the dam's home range. However, 7753 did not migrate to the traditional winter range of 6915 and had a mean separation of 48.3 km during the winter. At the time of writing (March 1980), 7753 had remained on the dam's summer range for about 5 months after the dam traditionally migrated and may well reside there the remainder of the winter. A year earlier yearling 7730 also exhibited movement patterns similar to those of 7753 and lagged behind the dam's migration by 3-4 months. However, 7730 eventually migrated to the vicinity of the dam's winter home range in January-February of that year.

3. Male yearling 7758 was the most mobile yearling monitored (Fig. 5B). Although 7758 has not shown significant linear dispersal in any one direction of travel, he moved an average of 17.4 linear km between monthly relocation points and was rarely relocated within its

dam's home range. However, year-round 7758 had only dispersed a mean of 6.8 km from his dam's home range because he often travels back and forth through the home range of dam 7742.

4. The most sedentary offspring monitored was male yearling 7759 (Fig. 5A). Yearling 7759 was one of twin yearlings produced by dam 7713. We succeeded in radio-collaring both 7759 and its male twin 7756. Yearling 7759 dispersed a mean of only 0.2 km from the dam's year-round home range. The maximum distance 7759 was separated from the dam's home range was 0.5 km. Unfortunately, the transmitter on 7756 failed after 1 relocation within the dam's home range. We visually relocated 7756, 5.5 months later, approximately 250 m from 7759, and both yearlings were within 7713's home range at that time. Thus, both offspring appeared to remain very close to their dam's home range.

5. Adult cow 7704 and female yearling 7760 are the only pair not exhibiting overlapping of home ranges (Fig. 5C). However, yearling 7760 dispersed a mean of only 5.1 km on a year-round basis and was separated from the dam's home range a maximum of 15.0 km.

DISCUSSION

Dispersal by subadult moose in the study area was characterized by relatively short movement away from their dams' home range. Home ranges of subadults were generally established in close proximity to the dam with some overlap between dam and offspring ranges. Long distance emigration resulting in the formation of a home range entirely separate from that of their dams was not observed.

Some dispersal of subadult moose from the home range of their dams seems inevitable because offspring rarely retain persistent social bonds with their dams after 1 year of age. Only when family groups are maintained, as in mountain sheep (*Ovis dalli*) (Geist 1971) or elephants (*Loxodonta africana*) (Douglas-Hamilton and Douglas-Hamilton 1975), and only if fidelity to the annual home range is strong, would home ranges of the dam and offspring coincide completely. Even in those species which maintain family units, one sex usually leaves the family unit upon reaching puberty and establishes a separate home range (Geist 1971, Douglas-Hamilton and Douglas-Hamilton 1975). Considering the definition we used for dispersal and the absence of persistent maternal/filial bonds in moose, we expected to observe dispersal. The question to be addressed was what was the relative magnitude of dispersal in this particular moose population and its demographic significance to this and adjacent moose populations.

We were unable to compare much of our data with those of other investigators because no other studies were found that evaluated dispersal of subadult moose relative to the home range of their dams. However, data presented by Houston (1968), Roussel et al. (1975), and Lynch (1976) suggested that greater dispersal of subadults occurred than was observed in the present study. In each of the above studies moose were marked in what we interpreted to be high density moose populations relative to the carrying capacity of the range. However, we admit this interpretation may be incorrect.

The low density moose population in the present study would probably be slow to locate and exploit newly created, high quality seral habitat.

This is in contrast to the rapid reoccupation of a burn by moose in Minnesota where moose densities increased approximately 5-fold in 2 growing seasons following a wildfire (Peek 1974a). At that time moose had generally reached peak densities for recorded history in northeast Minnesota (Peek et al. 1976) and were probably near carrying capacity in the area adjacent to the burn (surmised from Peek 1974a).

Wildfire is the primary ecological factor creating extensive areas of seral moose habitat in interior Alaska. The first moose to reoccupy burns in our study area will probably be offspring of moose with home ranges adjacent to the burn, or adults partially, or totally, displaced by the effects of the wildfire and adopting new home ranges adjacent to the burn. The strong fidelity of adult moose to home ranges which we and others (Coady 1976; VanBallenberghe 1978) observed indicated that few adults, not living next to a burn or migrating through it, would ever encounter new burns and be faced with the choice of maintaining traditional home ranges or utilizing new habitat.

There probably is minimal environmental and social pressure to disperse into newly created, vacant habitat from low density populations as compared to high density moose populations such as those studied by Houston (1968) or Peek (1974a). Howard (1960) suggested that environmentally induced dispersal should move offspring only far enough to locate more favorable habitat or reduce social stress. Houston (1968) observed agonistic behavior by adult moose towards yearlings and suggested that it was the incentive which resulted in yearlings dispersing from high to low density areas. Therefore, when moose density is high more moose

should disperse farther and those which disperse in the direction of a burn, for example, may readily occupy it. Those dispersing moose not encountering the high quality habitat will presumably occupy marginal habitat where moose density is low and agonistic behavior is reduced (Houston 1968).

Wildlife and habitat managers should not expect rapid, short-term increases in moose density as a result of habitat improvement programs in interior Alaska where moose densities are low relative to carrying capacity. However, this does not discount the present value of habitat improvement programs through controlled wildfires. Wildfires are necessary for the long-term maintenance of high moose densities, and in some areas of interior Alaska where habitat quality is low wildfire must precede other management actions which could lead to increased potential growth of moose populations.

Moose populations which have been locally reduced by hunting or predation and which are adjacent to other low density moose populations should receive relatively few dispersing moose for reasons similar to those discussed for the reoccupation of burned sites. If immigration does not contribute substantially to restocking depleted range, then the offspring of surviving adults must be the primary stock for repopulating these areas (Goddard 1970). Even in relatively high density moose populations where dispersal of subadults was documented (Lynch 1976), no dispersal into heavily hunted and locally depleted areas was observed. Moose managers should, therefore, think of each low density moose population as a separate entity and manage it with respect to its unique demographic parameters.

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