REPRODUCTIVE LIFE HISTORY AND FERTILITY OF MOOSE IN NORTH ASIA

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ABSTRACT: We studied reproduction and fertility of moose (*Alces alces*) in North Asia from 1976 to 1990. Aerial moose surveys were conducted to determine moose population demographics, breeding seasons, breeding group composition, habitat use, calf survival, and frequency of twinning. Moose were also observed from the ground and we investigated fertility using harvested animals. Breeding seasons occurred from mid-September through early October throughout the study area. Habitat types used by moose included poplar (*Populus* spp.) - *Chosenia* forest, sparse larch (*Tamarisk*) forest, and willow (*Salix* spp.) /alder (*Alnus* spp.) forest. Aggressive interactions between bulls were more frequent at higher population densities and when females were associated with > 1 bull. The most frequently observed breeding groups were male:female pairs, and 1 male: 2 females. Frequency of twinning was 23.8%. Our data were consistent with previous research that documented increased fertility with decreasing latitude. North Asian moose are a species with limited polygamy that can be displayed at varying degrees depending on population status, sex ratios, and other factors.

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Breeding behavior, fertility, and breeding group demographics for moose (*Alces alces*) inhabiting the extremes of their range in North Asia are not documented, and these parameters are of interest to biologists. In Yakutia where natural conditions are similar to those of the far north, these aspects of moose populations and the behavior of individuals during the breeding season are relatively undocumented (Egorov 1965, 1971). We investigated breeding group size, composition, habitat use, fertility, and behavior for breeding moose in the Enmyvaam, Shuchia, and Yurumkuveem River basins. We also collected general population data to characterize the spatial distribution and demographics of moose inhabiting the study area.

STUDY AREA

Reproduction and fertility of moose were studied in 4 regions of North Asia. These were Chukotka, Anadyrsky River basin (1976 through 1990); the Magadansky Oblast, North Evensky region, Omolon River basin and upper Kulu River basin; South Yakutia, upper Indigirka River basin; and northern Khabarovsky Krai, in the Okhota, Ulbeja, and Inia River basins.

METHODS

We observed adult moose and counted yearling moose during the fall breeding season, September through October, via aerial surveys and ground based surveillance in 4 regions of North Asia. We conducted aerial surveys and ground-based observations to count newborn calves during spring (May-

June). Moose harvested during regular seasons from October through February were tallied annually and harvested females were examined to determine number of embryos present in reproductive systems.

We used aerial survey data, ground observations, and hunter harvest report information to investigate size and age/sex structure of breeding moose groups and overall population structure. Aerial surveys for moose were conducted by flying moose habitat along large river valleys within the study areas. The aircraft used was a model AN-2 that was able to accommodate 2 observers. During all surveys, an observer was seated on either side of the plane. While overflying groups, observers recorded number and sex of animals in the group, male:female ratio, and presence of calves and yearlings. A total of 193 hours were spent surveying moose habitat and transects were $\leq$ 34.5 km. We determined calf survival by using newborn:yearling ratios. This ratio reflected calf mortality within the first 4-5 months of life. All data were recorded with the use of a dictaphone (audio recorder) and were transcribed following field work.

RESULTS AND DISCUSSION

Breeding Season/Habitat

Although the regions studied were widely separated in latitude, moose were observed to breed during the same months, from the second half of September through early October. The peak of rut occurred during late September and first half of October. This allowed calves to be born at the most favorable time, from late May through mid-June. These times coincide with those recorded in Alaska and Canada (Edwards and Ritsew 1960). During this time moose form pairs and most females are accompanied by, and breed with, a bull at some time. Bulls of 1.5 years old are often observed to travel in pairs or individually and to remain close to other breeding pairs.

Many breeding groups (58.1% of the total observed) were seen during aerial surveys in the Ernik tundra at the forest border or near it. In the Shuchia River valley, a breeding moose pair was observed late in September 1976, and they stayed beyond the valley forest, in the shrub tundra. During the breeding season, we surveyed (by aircraft) repeatedly with 2-5 day intervals and we observed most of the animals staying in the same lots, although certain groups changed members and mating participants. This switching was especially apparent in breeding groups with young males or older females. During the breeding season moose were often seen in open mountain valleys near forest or shrub boundaries; however, moose are most visible in these habitats and moose sightability may have biased these observations about moose habitat use. Three habitat types were identified for moose in the upper river valleys of the study area: poplar (*Populus* spp.) - *Chosenia* forest, sparse larch (*Tamarisk*) forest, and willow (*Salix* spp.)/alder (*Alnus* spp.) forest. These habitat types were in the forest tundra zone, and in the boreal taiga subzone. Most moose were observed to move towards the upper-reaches of the Belaya, Yurumkuveem, and Enmyvaam Rivers during the breeding season. Moose used sparse larch (*Tamarisk*) forest in the Maly Anui basin. While occupying boreal taiga subzone, moose used only willow (*Salix* spp.) alder (*Alnus* spp.) forest. While in forest tundra zone, moose usually bred on terraces with thin alder or young *Chosenia* shrubs, as well as in sparse larch areas near streams in the river valleys. There was one observed occurrence of mating in an open, gravel area. In the typical breeding areas, on dry glades, especially in the willow (*Salix* spp.)/alder (*Alnus* spp.) forest, there were numerous "tochok" (i.e., pawed holes into which the bull has

urinated). On the old pebble terraces, "tochok" can be up to 10-12 cm deep, as large as 1-1.5 m^2 in area, and as numerous as 5 holes per 100 m^2. At the beginning of the rut, male moose were seen butting shrubs of young *Chosenia*, willow, and alder to scrape velvet from their antlers (one bull harvested on September 17, 1977, had shed all its' velvet). Our long-term data indicate breeding season timing may be extended up to 1.5 months or more in North Asia. Natural conditions within moose habitats become significant factors influencing such a situation. Breeding seasons in Chukotka (Anadyrsky River basin) and in the Okhotsky Region do not begin simultaneously. In more southerly latitudes, breeding begins 2-2.5 weeks earlier, habitats and weather conditions being similar. The first breeding pairs of moose in the upper-reaches of the Ulbeja River were observed late in August. Also, the area used by breeding moose increased from an average of 20-40 m^2 to as much as 50-100 m^2.

Male Behavior and Aggression

Prior to breeding, bull moose traveled in the river valleys along mountain slopes through large and sparse shrub thickets where they searched for females and prepared to breed. In habitats where water was abundant, wet meadows or open tundra, moose used thinly forested, shrub, or floodplain terraces. Bulls that were preparing to breed and traveling in close proximity to estrus females had large antlers, up to 1.5 m in spread. Male moose are known to experience physiological changes associated with the rutting season much earlier than females, and this stimulates the females to enter an estrus state (Likhachev 1955). In the far northeast, breeding pairs were observed at all times of day, (i.e., morning, afternoon, and evening), but they copulated most actively from 1500 to 2200 hr. Bulls, however, were most active in the morning hours, with numerous individuals gathering in similar habitat types. During the rut, male feeding regimes are often changed; they eat little and their behavior patterns are altered. Males in the Belaja River basin lost up to 27% of their total mass during the rut (Yazan 1961) and it has been documented that bulls may spend as little as 2% of daylight hours feeding (Geist 1963). During the rut, bulls become more active and less careful while searching for females. They often travel quickly across *Chosenia* islands on floodplains. They often appear on hearing human steps and will rapidly disappear on perceiving the cause of the noise as human (the first author encountered a large bull on 4 October 1982 in the Chuvan Stream region along the Belaya River, at about 1000 hr; the bull appeared when the author passed by on the dry pebble stream, and fled into the alder thickets when it realized a human was 4-5 m from him), or alternately, will charge the human (the first author encountered another bull 9 October 1974, in the morning near the Enmyvaam River, above Mukhomorny Stream; the bull moose was strong and large, and for a long time he was pawing the ground on a dry near-terrace glade among the poplars; watching the animal, the author decided to get closer to take a picture and evidently made a sharp noise; the bull turned sharply towards him, and rushed directly at him; his loud blow (noise) stopped the animal and he hid in a moment). During this time, bulls change both physically and from a behavioral standpoint. Physically, their eyes often become bloodshot and hair on the withers is more likely to stand on end (Kaplanov 1935). Behaviorally, male moose have been observed to moan audibly in the morning and evening (the first author heard typical male moans twice, once by the Enmyvaam River [from 0400 to 0500 hr] and by the Yurukveem River [2200 hr]). Altercations between male moose are

less frequent when females are associated with single, as opposed to multiple, bulls. This situation was observed during 1974, 1976, and 1977 in the Anadyrsky Basin. In addition, 3 different bulls were observed to be paired with at least 2 females. These types of interactions have been documented in other regions of the country, for example, the Upper Pechora (Yazan 1972). During the 1970s, moose densities were low in Chukotka (<500 animals in the Anadyrsky Basin). This situation limited selection of breeding partners by moose. By 1986 the number had increased to 2,200 animals due to management restrictions. Consequently, the rutting behavior as well as the sex and age structures of the population changed dramatically. At high moose densities, males more actively searched for females prior to copulating. During aerial surveys, some young bulls were observed to travel 30 km along river floodplains in a single day. The number of aggressive contacts between male moose increased during this time. Observations of aggressive behavior during this time period included: bulls facing one another in silence for long time periods; butting and circling trees (young bulls); pawing the ground; circling other moose; and locking antlers by setting their racks against one another's (without running blows). These altercations usually occurred in forest areas or shrub thickets that were at least as tall as the moose. The aggressive encounters ended when bulls became exhausted or left the area. No mortalities due to aggressive bull:bull encounters were observed.

Breeding Group Composition

Variations in the numbers and composition of breeding pairs (groups) were documented during this study. There were a total of 19 types of breeding groups documented (Table 1). Breeding moose groups with 2 and even 3 males per female occurred. There were breeding groups that included calves-of-the-year and yearlings. There were 6 types of breeding groups where a female had 1 or 2 calves. A considerable percentage of breeding animals belonged to breeding pairs and groups where 1 female was observed to have ≤ 3 males. Far fewer animals (3.2%) participated in breeding groups where 1 male had 4 females. There were a wide variety of other types of breeding moose groups; ranging from single males paired with ≤ 6 females, single females paired with ≤ 3 males, and groups of ≤ 9 males and ≤ 12 females. The types of breeding groups most often observed were the male:female pair (38.7 %) and 1 male paired with 2 females (21.0%). A total of 216 moose took part in the breeding season and 69 moose were observed to be single and not participating in the rut.

Sex Ratios/Polygamy

Of the total moose population, 36.5% participated in breeding activity. Of the total number of moose observed during the breeding season (592 individuals) there were 203 males (34.3%) and 279 females (47.1%) (Table 2). When taking into consideration the non-breeding females, the percent of females drops to 22.2%. Other animals observed were calves-of-the-year and yearlings (10.0 and 8.4%, respectively). The male:female ratio was 1:1.44 (i.e., 1.44 females per male). Females were more numerous than males by 8.8%. A 10-year period without the effects of industrial development on the moose population considerably changed the sex ratio of males and females during the breeding season; it became 1:1.4. However, there were only 1.5 females per male in breeding groups due to a great share of non-reproductive older females. Young male moose are a mobile part of the moose population. This observation is typical for moose subspecies in dif-

Table 1. Observations of individual moose and breeding group composition in the Anadyrsky Basin, October 11-13, 1986.

Breeding Group Composition				Observations			
males	females	yearlings	calves	Number of observations	% of total	Number of moose	% of total
1	1	0	0	24	38.7	48	19.1
1	2	0	0	13	21.0	39	15.5
1	3	0	0	6	9.8	24	9.6
1	4	0	0	2	3.2	10	4.0
1	5	2	2	1	1.6	10	4.0
1	6	0	0	1	1.6	7	11.3
1	1	0	1	1	1.6	3	4.8
1	1	0	2	1	1.6	4	1.6
1	1	2	0	1	1.6	4	1.6
2	1	0	0	1	1.6	3	1.2
2	2	0	0	1	1.6	4	6.5
2	3	0	0	2	3.2	10	4
2	4	0	0	1	1.6	6	2.4
3	1	0	0	1	1.6	4	1.6
3	1	0	1	1	1.6	5	2.0
3	4	0	0	2	3.2	14	5.6
4	4	0	0	1	1.6	8	9.2
4	6	0	1	1	1.6	11	4.4
9	12	0	2	1	1.6	23	9.1
Totals				62	100	251	100

ferent regions and many authors (Kulagin 1932; Flerov 1952; Yazan 1959, 1964) have stated this. In areas where the age structure of the moose population is old, young males are not able to breed due to competition from older bulls. This is typical for the Anadyrsky moose population. Past data show that bull moose become pubescent much earlier than they begin to breed (Yazan 1961). Reliable data dealing with testicle maturation and rapid spermatogenesis were reported by Abramov (1949) and Yazan (1959). These findings are consistent with Norwegian and American studies (Denniston 1956). Denniston (1956) documented high rates of spermatogenesis (92% of males at the age of 1.5) in Wyoming. Others have also documented considerable numbers of spermatozoans in the testicles of 1.5-year-old males prior to the rut (a young bull taken by the first author on October 4, 1976 near the Shuchia River, Anadyrsky Basin had a sufficient volume of spermatic liquid). Thus, numerous investi-

Table 2. Sex and age composition of the moose population in the Anadrysky River basin during breeding season based on aerial surveys 11-13 October 1986.

Age/Sex Class	Number of Moose Observed		Number of Breeding Moose Observed	
	n	%	*n*	%
males	203	34.3	216	36.5
females	279	47.1	43	19.9
yearlings	51	8.4	-	-
calves	59	10.0	62	28.7
Total	592	100	251	100

gations support the conclusion that within the Holarctic, bull moose have become pubescent by the beginning of the second year of life. However, they only take part in reproduction when there are available females (Knorre 1949, Flerov 1952, Peterson 1955). It is generally accepted that moose are polygamous (Kuklin 1946, Belyk 1948, Kalnynsh 1950, Knorre 1959, Yazan 1972), and the data collected during this study support that conclusion. Bulls travel a great deal and opportunistically mate with available females during the breeding season. Older bulls can often prevent younger bulls from breeding and therefore the individuals that comprise pairs and groups of moose can change many times throughout the breeding season. Groups that changed in member composition or were redistributed were as many as 20% of the total number. In all cases when a male or female left a breeding pair or joined another one, there were adjacent groups of ≥ 4 adults. According to our observations, males tend to remain for an indefinite period of time with the last female they breed. Based on these data and the findings of other authors (Peterson 1955, Denniston 1956, Nasimovich 1961, Yazan 1972), North Asian moose are a species with limited polygamy that can be displayed at varying degrees depending on population status, sex ratio's, and other age and sex related factors.

Female Moose/Fertility

Most female moose in Chukotka and Khabarovsky Krai become sexually mature during their second year of life and they are bred by males that same year. These data are valid for other regions, in particular, for Pechora and North America (Peterson 1955, Knorre 1959, Yazan 1964), and according to these studies, some moose females can potentially be pubescent at the age of 3.5. In addition, Pimlott (1959) and Dorn (1970) found that moose females can calve by the end of the third year of life, and they can begin to participate in breeding at the age of 1.5. Pimlott (1961) pointed out that females can ovulate at 1.5 years, but only 46% of them participated in breeding. In the Pechorsko-Ilychsky Reserve, Knorre (1959) found some domesticated female moose to be pubescent at the age of 1.5 (15%), and others at the age of 20 months (35%). Few females became mature at ≥ 3 years (25%), and only 5% of females became pubescent at > 4 years of age. During the hunting season, 25 cow moose (2 years old) were taken and only 7 of them (28%)

were pregnant. In Ontario, Canada, Simkin (1965) found that 38% of 1.5-year-old females participated in breeding, and 45% of them became pregnant. In the Anadyrsky Basin only 7% of 1.5-year-old female moose participated in the rut. Because our ability to determine fertility of female moose using placenta scars and embryo numbers was limited, we used observations of females with calves in May-June, 1974-1976, to estimate fertility. We did not take yearlings into consideration because at that time they were easy to differentiate from adult animals. Total numbers of observations (n=21) showed that the percent of moose females bearing twins was 23.8%. On average, there were 1.24 calves per female (Table 3). The total potential productivity is 50-55% of the total moose population, due to sex ratios of 1:1.3 females: males. In the Omolon River basin moose females with twin calves only made up 16.4% of the sample (Cherniavsky et al. 1980). Data collected in 1986 in the Anadyrsky Basin (October 11-13) show 33 females with 1 calf each (84.6%), and 6 females with twins (15.4%) (Table 3). In comparison, the Anuisky River basin female moose population showed 15 females with 1 calf (75%) and 5 females with twins (25%). Ten years later, in October, we observed 1.2 calves per female from the total number of sightings in the Anadyrsky basin, and 1.3 calves per female in the Bilibinsky. For both regions these indices remained at relatively the same level. Yearlings, or moose aged 1.5 years, made up 8.4% (Table 2) in the Anadyrsky population, which was 1.6% lower than the indices of the calves born that year. Many explanations exist for differential fertility rates (twinning rates) in moose. Some believe this to be connected with the age of cow moose (Buturlin 1934, Flerov 1952, Yazan 1972). Others (Teplov 1960) suppose fertility is affected by snow cover regime. Pimlott (1961) believed fertility to be dependent on moose numbers and food availability. Compared with other regions of the Northeast, North America, and Alaska, moose fertility in Chukotka is low,

Table 3. Compilation of moose fertility data for 7 regions throughout their range in the Northern Hemisphere.

Region / Data Source[1]	Calf:Cow Ratio	% Cows Bearing Twins
Chukotka, Anadyr River basin, Zheleznov (1974-1976)	1.24	23.8
Chukotka, Anadyr River basin, Zheleznov (1986)	1.20	15.4
Chukotka, Anui River basin, Zheleznov (1986)	1.30	25.0
Yakutia, Tokko River basin, O.V. Egorov (1965)	1.28	28.6
Verkhoyansky Range, western slopes, O.V. Egorov (1965)	1.35	35.7
Aldan River basin, O.V. Egorov (1965)	1.42	42.1
Adycha River basin, O.V. Egorov (1965)	1.47	47.2
Kamchatskaya Oblast, Penzhina River basin, V.I. Fil (1975)	1.35	35.7
B.C. Canada, Wells Gray Park, Edwards and Ritsew (1960)	1.25	24.5
North America, Alaska, Peterson (1955)	1.30	30.0

[1] See References for full citations.

but it is close to the fertility indices in Canada (Table 3). All of the moose females examined in the Anadyrsky basin in 1974-1976 had 1 embryo. April embryo mass was 3.522 kg. In the Belaya River basin (1987-1988), 14 females were sampled, and 10 embryos were observed (1.4 embryos per female). Pubescent moose females' dryness was 17.6%. During 1986-1987, in the Anadyr River basin (including the Yablon, Peledon, Balaganchik, and Eropol Rivers), 38 females were sampled and 6 of them (15.8%) had 2 embryos, while 16 (42.1%) had 1 embryo. Thus, 10 years later there were 1.27 embryos per female, and the total dryness was 42.1%. The Anadyrsky moose population increased in reproductive potential in spite of the numbers, then the fertility of female moose began to decline. For the Maly Anui River basin these indices are similar. Of 13 females, 2 of them (15.4 %) had 2 embryos, 6 of them (46.1%) had 1 embryo, and 5 animals (38.5%) were dry. These figures are similar to those for the Anadyrsky basin (differences are not significant). In the Anuisky River basin the number of females with 1 embryo was lower (1.25) (Zheleznov 1976, 1990, 1999). If we compare female fertility of the moose *A. a. Buturlini* with other subspecies, it is not very different. In Yakutia the average percentage of females with 2 calves was 3.84, and the highest was recorded in the upper Adycha River at 47.2%. These indices were exceeded by the moose females of the *A. a. cameloides* subspecies. In Primorie and Priamurie, sightings of cow moose with twins made up 36.8% of all observations (n=68). The number of calves per cow was 1.16, and there were 1.46 calves per nursing female (Bromlei and Kucherenko 1983). The number of embryos ranged from 1 to 1.72 in females with calves, and was less, 0.83 - 1.46, in pubescent moose females. These indices are close to those in Estonia (Ling 1973). The number of calves per female with offspring ranged from 1.23 to 1.52 (pubescent females 0.35 - 0.82). Rates of dryness were high, 61 and 48%, respectively. Comparisons of fertility data across the northern part of the range are as follows: Leningradsky region: 36 cows with 2 embryos (23.8%), 58 cows with 1 embryo (38.5%), and 60 (37.7%) cows were dry (n=151), for a ratio of 1.43 embryos per cow (Vereshchagin and Rusakov 1979); North Pechora region: 29 cows with 2 embryos (39.7%), and 44 cows with 1 embryo (60.3%), for a ratio of 1.4 embryos per cow (n=73) (Knorre 1959); and Yakutia region: 41 cows had twins (39.4%), and 63 cows had 1 calf (60.6%) (n=104). These data indicate much variability in female moose fertility. Most authors (Yazan 1972; Vereshchagin and Rusakov 1979; Kozlo 1980, 1983) believe the variability to be a result of changes in the female reproductive systems over time; that is a decrease in fertility as the cow ages. Therefore, the documentation that female moose are most fertile at the age of 3.5-8 years (Yazan 1976) is reasonable, and fertility sharply decreases thereafter. Some researchers believe fertility of moose to be influenced by latitude; i.e., fertility increases with decreasing latitude. This was illustrated by Chervonny (1975a,b) and Perovsky (1976, 1978). Our data, collected in the Far Northeast, Khabarovsky region, south far east, and in the central northeast of our country support this paradigm. This trend has remained constant over a quarter of the twentieth century and does not seem to depend on the size of the moose population or on its dynamics. Our data from the forest tundra zone also affirm this paradigm. In the taiga zone (1962-1980) the number of embryos per cow was 0.73-0.76, and cows with 2 embryos made up 24.6-31.1% of the population (Danilov 1986). Toward the south, in the mixed and large leaf forest zone, these

indices were higher, 0.94-1.05 and 32-45%, respectively. We have not observed any females with 3 embryos or calves. Such a phenomenon is very rare and it has only been documented in the southern regions of our country (Knorre 1959; Zaripov and Znamensky 1964; Pavlov and Yazan 1967; Ling 1974; Perovsky 1974, 1976; Kozlo 1980, 1983). Nevertheless, moose females with 3 calves were observed in Alaska, although this may have occurred due to a calf joining a twin pair. Lower fertility of moose females in the northern zones of the Holarctic could be explained by more severe climatic conditions and restricted forage availability.

Additional factors that could affect fertility are condition of overwintering areas, forage availability, predation, and pressure from human presence and harvest. The factors that seem to influence female fertility the least are population structure and density. Filonov (1983), who studied fertility of moose females in many reserves of the country, reports fertility to be changeable depending on time and space. Severe winters with deep snow in combination with late onset of spring were found to reduce potential fertility of moose cows (Teplov 1948, 1960; Knorre 1959; Zykova 1965; Ling 1973, 1974; Kozlo 1980; Kudriashova 1980). While analyzing the status of the Pechorsko-Ilychsky Reserve's moose population Filonov (1977) discovered a correlation (r = -0.79, t = 3.84) between the proportion of newborn calves and depth of snow cover the previous winter. Such a relationship was noted to be typical for the regions with abundant snow. In the Darwinsky Reserve, where snow cover was lighter, the relationship between snow depth and proportion of calves the following spring was less noticeable. It was quite the opposite in the Oksky Reserve (Filonov 1977) where there was a close connection between snow cover depth and occurrences of females with calves (r = -0.45, t = 2.5).

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