BIOLOGICAL FEATURES OF MANCHURIAN MOOSE (*ALCES ALCES CAMELOIDES*) WITH SPECIAL REFERENCE TO COMPARATIVE RESEARCH

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ABSTRACT: Biological features of the Manchurian moose (*Alces alces cameloides*) are reviewed and compared with the six other recognized subspecies. The Manchurian moose is smaller bodied and differs in body build from *A. a. gigas* and *A. a. alces*. The antlers have fewer tines and a smaller palm surface area (25% to 69% that of other subspecies) and most closely resemble those of *A. a. pfizenmayeri*. The head is proportionately larger than in other subspecies and body hair is shorter. Limited data suggest that the Manchurian moose is similar in body build and antler features, but smaller in body size, when compared to *A. a. pfizenmayeri*. Reproductive biology of the Manchurian moose is similar to that of other subspecies, with the possible exception of an earlier rutting season. Further comparative studies of all moose subspecies are recommended.

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This paper summarizes knowledge, mainly from northeast China, on the Manchurian moose (*Alces alces cameloides*). A limited amount of published information (Zhitkov 1914, Kaplanov 1948, Abramov 1949, 1954, Heptner *et al.* 1961, Wang 1965, 1981, 1983, 1986, Heptner and Nasimovich 1967, Metelsky 1974, Zhao 1980, Yang *et al.* 1982, Bubenik 1986, Geist 1987, Wang and Liu 1989, Xu 1989, Yu and Xiao 1991, Yu *et al.* 1992, Li *et al.* 1992, Piao *et al.* 1993, Zheleznov 1993), is supplemented with previously unpublished data on *A. a. cameloides* (Piao pers. comm.). Comparisons with other moose subspecies are made using data from the published literature, and measurements of *A. a. alces* in Finland.

Seven geographic subspecies of *Alces alces* (*gigas, andersoni, americana, shirasi, alces, pfizenmayeri* and *cameloides*) are recognized in the circumpolar boreal forests of North America and Eurasia (Peterson 1952, 1955, 1974). An eighth subspecies, the Caucasus moose (*Alces alces caucasicus*), disappeared in the early 19th century (Heptner *et al.* 1961, Bubenik 1986). The Asian moose, *A. a. pfizenmayeri* (also known as the Yakutian moose or East Siberian moose) is found in the Yakutia and other areas of eastern Russia (Egorov 1965, Heptner and Nasimovich 1967), while *A. a. cameloides*, the Manchurian moose or Ussuri moose, is found in northeast China (Manchuria) (Jia 1992), far eastern Russia (Kaplanov 1948, Heptner *et al.* 1961, Heptner and Nasimovich 1967, Metelsky 1974, Ditsevich 1990, Myslenkov and Voloshina 1992) and perhaps the eastern-most corner of Mongolia (Heptner *et al.* 1961) (Fig. 1).

Cameloides has been exploited by humans throughout history (Kaplanov 1948, Metelsky 1974, Jia 1992). A moose rock painting was found in Inner Mongolia, China (40° N latitude, Fig. 1), dating back to the Bronze Age (Xu 1989). Fossils were found in the area of northeast China (Fig. 1) from Late Pleistocene deposits (Xu 1989).

Publications dealing with *cameloides* comprise less than 3% of the total world moose literature after 1940. *Cameloides* was initially studied by Russian scientists (Kaplanov 1948 and Abramov 1949, 1954), working in the taiga of Ussuri and Amur

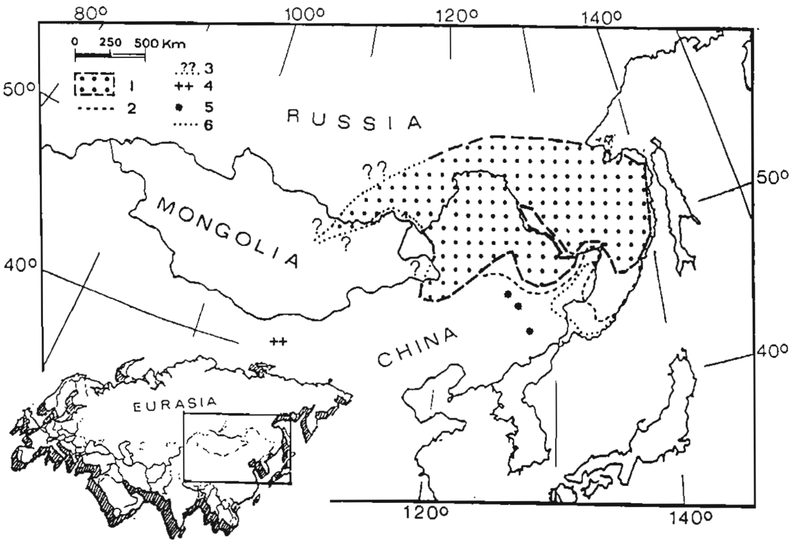

Fig. 1. The distribution of *cameloides*. 1. Present distribution; 2. Possible distribution in the 1940's; 3. Extent of distribution uncertain; 4. Rock painting site; 5. Fossil sites; 6. Possible distribution in the 1860's. Map is drawn according to Kaplanov (1948), Peterson (1955, 1974), Heptner *et al.* (1961), Metelsky (1974), Danilov (1987), Ditsevich (1990), Jia (1992), Myslenkov and Voloshina (1992) and Zheleznov (1993).

regions. Moose studies in China have been particularly weak, with only about 15 papers published in Chinese since 1960, accounting for about 1% of the literature reviewed (Fig. 2A).

Cameloides is regarded as a primitive moose (Heptner *et al.* 1961, Heptner and Nasimovich 1967, Bubenik 1973). Others have considered it the product of regressive gradualism or reverse recapitulation (Alberch *et al.* 1979, cited by Bubenik 1986), more advanced than the European moose but less advanced than the American moose (Geist 1987). *Cameloides* is well known for its small body, which may have resulted from poor nutrition in its glacial refugium (Geist 1987). Its cervicorn (deer-like) antlers are thought to represent genetic atavism due to stress (Bubenik, pers. comm.). In other respects, *cameloides* may be closer to the American moose because of similarities in skull and antler morphology, and body coloration (Geist 1987).

COMPARISONS OF MANCHURIAN MOOSE WITH OTHER SUBSPECIES

Body Size

Available data indicate that the body size of adult Manchurian moose is smaller than that of *gigas*, *andersoni*, *alces* and *pfizenmayeri* (Table 1). The smaller size is seen particularly in the length of the legs (hind foot being only 82-88% that of the other subspecies).

Data suggest that the Manchurian moose is smaller and morphologically different from samples of *gigas* and *alces* but similar in body build to the Yakutian moose (*pfizenmayeri*) and to *andersoni* (Table 1). Its body length and legs are relatively much shorter than those of *gigas* while shoulder height and legs are relatively shorter than those of *alces*. However, these comparisons are made on the basis of few available records and small sample sizes which may not be representative. For example, Kaplanov (1948) published some measurements for 5 male *cameloides* from the Sikhote-Alin of Russia that appear slightly

Table 1. Measurements (in millimeters) of adult Manchurian moose and comparisons with other subspecies.

Subspecies	Sample size[a]	Total length	Shoulder height	Chest girth	Hind foot length	Source	X^2-test[b]
cameloides	M2	2300	1655	1670	727	Wang & Liu	
	F4 + M1	2200	1568	1690	623	(1989)	-
gigas	M23-77	2883	1835	1748	801	Franzmann *et al.*	
	F96-254	2826	1760	1795	793	(1978)	
(*c./g.*)%[c]	87.6%[d]	79.6%	91.0%	97.5%	82.4%		P<0.001
andersoni[e]	M3-14	2561	1857	1963	808	Blood *et al.*	
	F3-14	2335	1818	1915	783	(1967)[f] & Peterson	
(*c./an.*)%[c]	88.4%[d]	92.8%	89%	89.1%	82.6%	(1955)[f]	n.s.
americana	M1-2	2693	1791	?	787	Peterson (1955)[f]	
	F1	2413	1753	?	797		
(*c./am.*)%[c]		87.4%	92%	-	83%		-
shirasi[e]	M4	2751	?	?	744	Doutt (1970) &	
	F4	2471	?	?	754	Peterson (1955)[f]	
(*c./s.*)%[c]		87%	-	-	87.7%		-
alces	M1460	2532	1946	1842	766	Nygrén (1986)	
	F649	2376	1880	1772	781		
(*c./al.*)%[c]	89.7%[d]	92.6%	85.5%	95.6%	84.9%		P<0.07
pfizenmayeri	M3	(3000)	1977	1953	807	Egorov (1965)	
	F2	1850	1850	720			
(c./p.)%[c]	86.8%[d]	(75.7%)	84.9%	90.3%	85.1%		n.s.

a. M: male, F: female.

b. Chi-square test for body build, df=3 or df=2; "n.s.": no significant difference.

c. Percentage ratios do not represent the situation in subspecies, only in the case of our comparison.

d. Average

e. Converted according to data from original papers.

f. Original paper in inches.

larger than the Manchurian moose we describe here.

The body weight of moose varies among subspecies (Table 2) and can be affected by seasonal changes, habitat, physique, age (Peterson 1974, Franzmann *et al.* 1978), and sexual dimorphism (Sæther and Haagenrud 1985). Body weight data for *cameloides* are scarce, with only a few records of whole weights reaching 400 kg (Kaplanov 1948). Most animals weigh less than 320 kg (Abramov 1954), with a mean weight slightly more than 200 kg (Heptner *et al.* 1961). One adult bull, shot in the Greater Khingan (Giant XingAn) Mountains of Manchuria, weighed 340 kg whole and 207.5 kg dressed (Wang and Liu 1989). In a 10-year study in the Amguny basin of Russia, the mean weight of

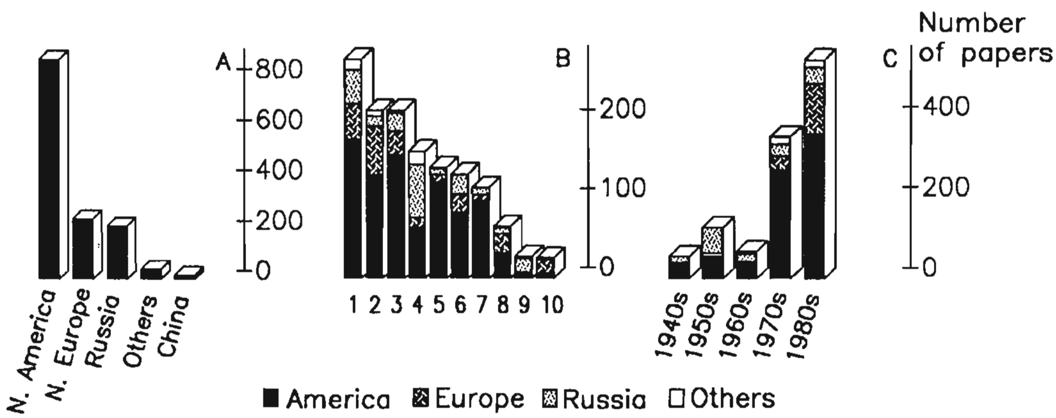

Fig. 2. Moose literature survey. (n=1352) A. Regional distribution of moose studies: North America includes USA and Canada; Northern Europe includes Finland, Sweden and Norway; Others includes Poland, Czechoslovakia, Estonia, Latvia, Lithuania and China. B. Subject distribution of moose publications: 1. Population, Behaviour, Reproduction, Movement; 2. Feeding habits, Food; 3. Management, Live-capture, Hunting, Socio-economics; 4. General, History, Status, Classification, Evolution; 5. Mortality, Disease, Prey death; 6. Morphology, Physiology; 7. Habitat, Natural effects, Interspecific relations; 8. Damage as pests, Negative effects by humans; 9. Feeding in captivity; 10. Genetics, Species introductions. C. World-wide moose publications since the 1940's (Information on the Russian literature after 1960 is not complete).

pure meat from an animal ranged from 185 to 205 kg (Metelsky 1974).

Skull

Previous authors report that *cameloides* has a relatively large head and short rostrum (Heptner *et al.* 1961, Heptner and Nasimovich 1967, Geist 1987). Based on 5 skull parameters (Table 3) and calculated ratios of body size (Table 1), our study supports this opinion. In the samples compared here, the body size of Manchurian moose is about 87.6% that of *gigas*, 90% that of *alces* and 87% that of *pfizenmayeri* (Table 1) yet there is no statistical difference in the size of the skulls to all three (Table 3). Accordingly, the skull size of the seven Manchurian moose measured is 114% of their theoretical skull size when compared to *gigas*, 117% when compared to *alces* and 109% when compared to *pfizenmayeri*. The relatively large head of *cameloides* was attributed to poor feeding conditions in Manchuria during the glacial period (Geist 1987).

Antler Morphology

Moose antlers are similar in proportion and shape, despite large differences in overall size among the 4 subspecies in North America. Typically, measurements are based on maximum spread, palm width and length, number of points and shaft circumference (Gasaway *et al.* 1987). Unfortunately, since Manchurian moose antler spread was not measured, we cannot compare this parameter. Moose trophies are seldom collected in China and antlers are classified according to the number of tines rather than the age of the moose (Wang and Liu 1989)(Table 4). However, when data on increase in antler length and number of tines are plotted (Fig. 3A), the curve is similar to that of Gasaway *et al.* (1987) and approximates the relationship between antler spread and age (Fig. 3B). As documented by Gasaway *et al.* (1987), moose begin growing prime antlers between the ages of 5 to 8 years, and have similar sized antlers thereafter until about 12 years of age. This suggests that *cameloides* antlers with more than 3 tines (Table 4) have approached a "prime size",

Table 2. Comparison of moose body weight (in kilogram).

Subspecies	Sample size[a]	Whole wt.	Dressed wt. (carcass)	Dr./Wht.%	Source
cameloides	?11	__ (260-320)	__	__	Abramov (1954)
	M1	340	207.5[b]	61%	Wang & Liu (1989)
	?	__	185(or 205)	__	Metelsky (1974)
gigas	M27	419[c,d]	__	__	Franzmann *et al.* (1978) &
	F148	367.6[c,d]	__	__	Franzmann (1981)
	M2	505(493,518)	__	__	Rausch (1958) cited by
	F11	375(263-452)	__	__	Blood *et al.* (1967)
andersoni	M6	527(475-570)[cc]	__	__	Haigh *et al.* 1980
	F12	422(325-515)[cc]	__	__	
	M42[d]	438(323-513)	219(162-257)	50%	Blood et al. (1967)[e]
	F61[d]	411(301-477)	206(151-239)	50%	
	M3-7	452(384-534)	267(237-316)	62%	Peterson (1955)[e]
	F1-2	347(331-363)	182	55%	
americana	M?	489	__	75%[f]	Des Meules (1965),cited by
	F?	373	__	__	Blood *et al.* (1967)
	M29	453(260-542)[c]	__	__	Quinn and Aho (1989)
	F45	435(310-530)[c]	__	__	
	M273[d]	466[g]	__	72%[f]	Heyland (unp.), cited by
	F178[d]	368[g]	__	72%[f]	Peterson (1974)
shirasi	M20	405[g]	203(156-263)	50%	Houston (unp.), cited by
	F7	339[g]	170(136-194)	50%	Blood *et al.* (1967)
	M97	332[g]	187[g]	56.2%	Schladweiler & Stevans
	F70	303[g]	164[g]	54.1%	(1973)[e]
	M3	354(229-417)[cc]	__	__	Babcock (1977)
	F13	350(297-420)[cc]	__	__	
alces	M323[d]	__	257	__	Sæther & Haagenrud (1985)
	F339[d]	__	189	__	
	M1460[d]	__	206	__	Nygrén (1986)
	F649[d]	__	185	__	
	M177	__ (267-484)[d]	__ (147-266)	55%	Skuncke (1949), cited by
	F177	__ (264-293)[d]	__(140-155)	53%	Peterson (1955)[e]
pfizenmayeri	M3	408(385-440)[cc]	280 (235-365)	68.6%[d]	Egorov (1965)
	F1	340[cc]	235	69.1%[d]	

a. M: male, F: female.

b. Viscera 57 kg (content 27 kg), hide 25 kg, feet 30 kg, head 20 kg.

c. Include live weights; cc. Only live weights.

d. Converted according to data of original paper.

e. Original data presented in pounds.

f. Percentage by field dressed (eviscerated) weight.

g. Estimated weight, whole wt. from dressed (carcass or field) wt., or inverse.

Table 3. Comparison of adult skull size (in millimeters) of Manchurian moose with three other subspecies.

Subspecies	Sample size[a]	Skull length	Basal length	Cheek width	Nasal length	Upper tooth	Source	X^2-test[b]
cameloides	M2	594	536	213	105	152	Wang (1986), Wang	
	F5-6	564	502	188	99	141	& Liu (1989)	
	Both sexes	579	519	200	102	146		
Theoritical size								
	87.6% of *gigas*	507	455	175	89	128	(114%)[c]	P<0.001
	90% of *alces*	486	427	178	86	131	(117%)[c]	P<0.001
	87% of *pfize.*	515	458	202	91	132	(109%)[c]	P<0.001
gigas	M7	616	549	220	__	148	Youngman (1975)	
	F3	601	542	205	__	147		
	Both sexes	611	547	216	__	147		n.s.
alces	M20-206	550	471	206	97	145	Nygrén (1986)	
	F29-94	529	478	190	93	145		
	Both sexes	540	475	198	95	145		n.s.
pfizenmayeri							Egorov (1965)	
	M(6)	592	526	232	105	152		n.s.

a. M: male, F: female.

b. Chi-square test for skull size, df=4; "n.s.": no significant difference.

c. Average of (actual/theoritical)%.

This conclusion is also supported by Wang (1983) who reported that the antlers of 3 yr old Manchurian moose branched into 2 tines with a tray appearing at the antler base; 4-yr-olds had 3 tines (sometimes only 2); 5-yr-olds had 4-5 tines. After 6 years of age, antler branching was more variable with different numbers of tines in moose of the same age. Antler weight increased steadily until 7 tines were present. Palm area remained small until antlers had more than 4 tines (Fig. 3A). This indicates that even though an antler is considered to be in the prime size category, great variation in antler weight and palm size exists.

Antlers of *cameloides* from northeast China differ from those of *gigas, andersoni, americana, shirasi*, and *alces* but are similar to samples of *pfizenmayeri* (Table 5). Manchurian moose may differ in antler morphology from American moose, with the exception of *shirasi* in Utah that shows a greater tendency toward cervicorn antlers (Babcock 1977).

The number of antler tines on Manchurian moose is much less than on other subspecies and may reach a maximium of 9 (Wang and Liu 1989); however, 3 antlers were found with more than 14 tines (Xu 1989). Data on tine number presented in Table 4 differ somewhat from that of Heptner *et al.* (1961) who reported that fully grown *cameloides* bulls have only 3 to 4 tines on each antler, reaching 5 in rare cases.

Cervicorn antlers are said to be common

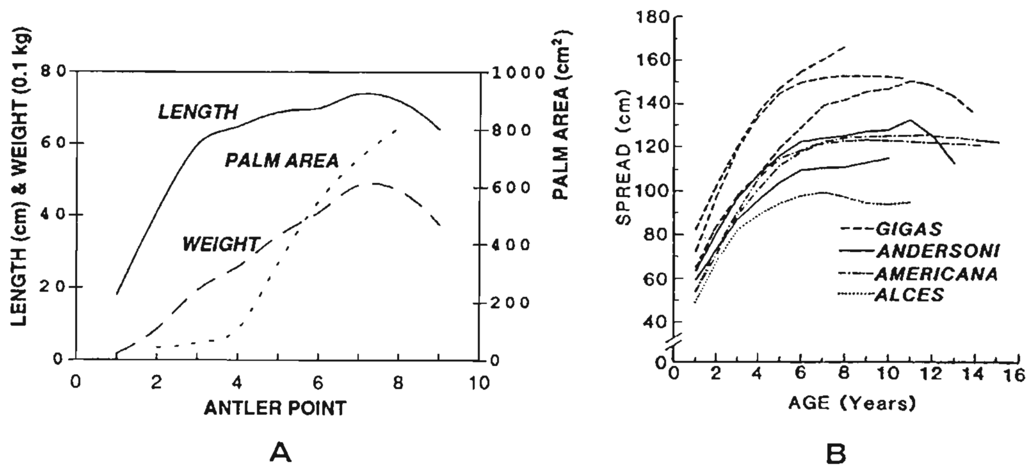

Fig. 3. Comparison of moose antler growth patterns using different measuring methods. A. Manchurian moose, antler length, weight and palm in relation to number of antler points (tines)(after Wang 1983). B. North American and European moose, antler spread (maximum width) in relation to age (after Gasaway *et al.* 1987).

Table 4. Antler measurements of Manchurian moose[a]

Number of tines on one antler	1	2	3	4	5	6	7	8	9
Sample size	10	20	20	20	20	20	10	10	1
Length	18	41	60	65	69	70	74	72	64
(cm)	14-30	31-56	39-82	36-78	57-87	61-80	65-85	59-81	
Weight	180	846	1940	2586	3436	4086	4850	4693	3750
(g)	150-	350-	750-	750-	2350-	3000-	3500-	3750-	
	240	1400	6300	3500	4500	6000	6250	6000	
Palm		44	59	105	336	552	700	808	
areas		12-	11-	24-	30-	35-	407-	585-	
(cm^2)		96	240	281	648	1160	1064	1156	

a. After Wang & Liu 1989.

in northeast China, especially in the Lesser Khingan (Lesser XingAn) Mountain area. Palmicorn antlers occur only when more than 3 tines are present. Some have only a small triangular web. Even the larger antlers with more tines have relatively long tines and small palms (Fig. 4). The palm shape is similar to the "butterfly" style described by Bubenik (1973); no "shell-type" antlers (after Bubenik 1973) were recorded.

It has also been noted (Piao pers. comm.) that the first tine on adult antlers from animals in the area of the Greater Khingan Mountains often branches into 3 points. The distance from the base to the point of branching between the first tine and the beam was similar in most cases (18±1 cm; n=37).

Using antlers with the ten biggest palms

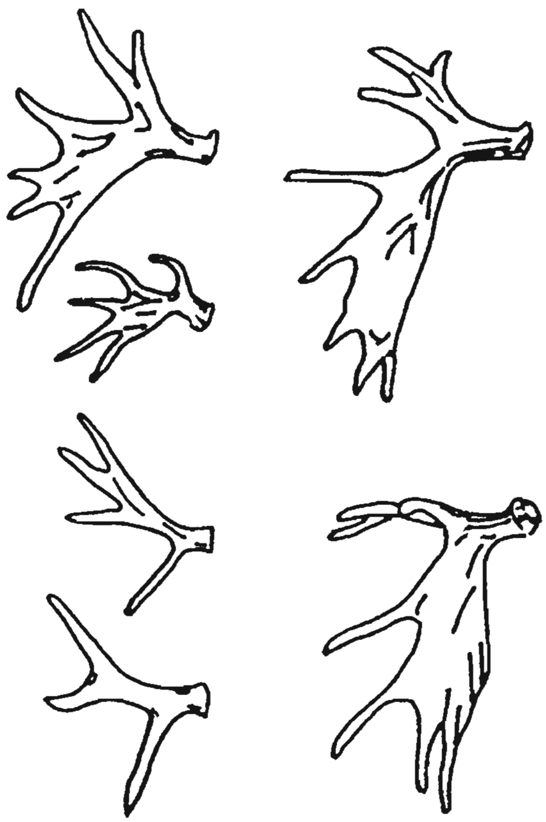

Fig. 4. Appearance of Manchurian moose antlers (drawn according to photos in Wang 1983).

(8 tines, Table 4), mean palm size of Manchurian moose was only 24.7-68.5% that of other subspecies (Table 5). However, Manchurian moose have a similar antler length to samples of *americana* and *shirasi*.

Antlers are usually shed from mid-February to late March in China. New piloses become completely ossified by late August or early September. The colour of the antler is white just after the velvet is shed, with obvious traces of blood vessels (Wang 1983). In Sikhote-Alin, Russia, young males with velvet remnants have been sighted as late as September 17, while the antlers of older animals were clean in some years by August 26 (Kaplanov 1948). Cervine piloses (antlers with velvet) are traditional medicine in China, and those from moose are no exception. They were used to cure neurasthenia (Wang and Liu 1989). The chemical contents of the pilose from a 6 year old bull kept in captivity included 15 different minerals and 18 amino acids (Piao pers. comm.).

Morphology of the Bell

The moose bell is believed to serve as a disseminator of urinary pheromones facilitating a short and economic mating strategy (Bubenik 1983). A bell is found on all seven subspecies of moose and a great variety of shapes and sizes is seen among sexes, ages and locality (Timmermann *et al.* 1985 and 1988). The longest bell measured was 60.7 cm (excluding hair) on a bull in North America (Timmermann *et al.* 1985). According to a description by Wang and Liu (1989), the Manchurian moose has a bell 10-40 cm long and 5-20 cm wide. Sac-shaped bells also exist, being similar in length and witdth about 25 cm.

Pelage

Pelage of *cameloides* shows considerable individual and geographic color variation (Sokolov and Chernova 1987). The hair is dark brown at the mane, mouth and rump, and darker brown or black around the hooves. In the inguinal area it is dirty white or grey (Wang 1986). While the North American moose has a coat with greater color contrasts, the dark area often being black, the European moose is brown, never black (Geist 1987).

Hair length of *cameloides* varies over the body and is shorter than that on other subspecies. According to Wang (1986), hair on the nose of *cameloides* was 15-30 mm, head 15-29 mm, side of neck 60-89 mm, rump 40-170 mm, belly 35-90 mm, extremities 12-35 mm and mane 130-190 mm long. In North America, guard hairs on the shoulder hump of *gigas* attained a length of 254 mm (Franzmann 1981). In Russia, the guard hair on the neck, chest and mane of *alces* can be up to 200 mm long (Sokolov and Chernova 1987).

Hair density on Manchurian moose was

Table 5. Comparisons of numbers of antler tines, antler length (cm) and palm areas (cm^2) of cameloides with other subspecies (data in means).

Subspecies	Sample size	Numbers of tines	Antler length	Palm area	Source
cameloides[a]	60	6.2	67.4	808	Wang and Liu (1989)
gigas[b]	693-838	11.1[c]	98.9[c]	3270.5[c]	Gasaway *et al.* (1987)
(c./g.)%[d]		55.9%	68.1%	24.7%	
andersonie	240-249	9.2[c]	73.3[c]	1865.1[c]	Gasaway *et al.* (1987)
(c./an.)%[d]		67.4%	91.9%	43.3%	
americana[f]	111-159	9.0[c]	61.9[c]	1521.5[c]	Gasaway *et al.* (1987)
(c./am.)%[d]		68.9%	108.9%	53.1%	
shirasi[g]	30-33	9.1[c]	66.9[c]	1604.6[c]	Gasaway *et al.* (1987)
(c./s.)%[d]		68.1%	100.7%	50.4%	
alces[h]	147	9.1	89.1	2176.7	
(c./a.)%[d]		68.1%	75.6%	37.1%	
pfizenmayeri	3	7.6	78.4	1180.2	Egorov (1965)
(c./p.)%[d]		81.6%	85.9%	68.5%	

a. Samples from antlers more than 3 tines for antler length, more than 8 tines for palm size (Table 4).

b. Samples from 6 regions.

c. Converted according to data of original paper.

d. Percentage ratios do not represent the situation in subspecies, only in the case of our comparison.

e. Samples from 4 regions.

f. Samples from 2 regions.

g. Samples from 2 regions.

h. Samples taken from Finnish trophy shows of last 20 years.

lower in summer but greater in winter than that on European moose (*alces*). In August, the average density of the guard hair was measured at 105/cm^2; in November it was 347/cm^2 (Wang and Liu 1989). In Russia, the summer guard hair density was 166/cm^2 and in winter 250/cm^2 (Sokolov and Chernova 1987). This could serve as an adaptation to the typical continental climate of northeast China which has a hot summer and a very cold winter.

The onset of molting in Manchurian moose is in early April. It peaks in mid-May and terminates by the end of June. Occasionally, molting in some individuals continues until mid-July. During molting, all black or dark brown colour disappears and the remaining hair is light brown without lustre and is easily broken. New hair is usually of a deeper, darker color. Molting proceeded in the same manner as described by Sokolov and Chernova (1987). However, the first signs of molting by *cameloides* was earlier than that of the Yakutian moose (*pfizenmayeri*), which has a similar longitudinal but more northerly distribution and begins molting at the end of April (Egorov 1965).

Rutting Behavior

Manchurian moose commonly reach

sexual maturity at 3 years. The rut extends from late August (some bulls begin in early August, Zhao 1980) to early October, peaking in mid-September (Wang and Liu 1989). The latter authors observed bulls courting cows along the forest edge, felled areas, clearings, marsh lands or river banks, while mating took place in the forests. According to observations on captive Manchurian moose (Wang and Liu 1989), bulls in rut are aggressive and excited and spend most of the day hitting and rubbing shrubs or young trees with their antlers. Cows with delayed estrus, irritate the bulls. The mating process, from mounting to breeding, is rapid, lasting only 2-3 minutes.

Parturition

The gestation period for moose is similar in different regions of the world, 226 to 244 days in Sweden, 240 to 246 days in North America (Peterson 1974) and 240($\pm$10) days in China (Wang and Liu 1989). April is the earliest recorded birth date of a calf moose in the wild in China. In one special case, a fetus observed in a cow killed in July would have been born in November if carried to term (Wang and Liu 1989). However, most wild cows give birth in late May or early June, similar to the period described by Franzmann (1981) for other subspecies. Manchurian moose usually have a single calf but twins are also observed (Wang 1981). In a sample of 9 calves captured in May-June of 1979, in the Denger Mountains of west northeast China, only 2 were twins (Yang *et al.* 1982). Kaplanov (1948), during a three-year study in Sikhote-Alin, observed 23 cows each of which had only one calf.

As parturition approaches, the pregnant cow seeks seclusion with no special selection of a site. *Cameloides* calves weigh 10.5-12 kg at birth and nursing lasts 90-150 days (Zhao 1980, Wang 1981).

Calf Development

Calves in China grow rapidly during their first 5 months, at a rate similar to the 1 kg gain per day reported by Franzmann (1981) in North America. In the first six months, calves reach up to 58% of adult weight (Table 6) and attain adult size in about 18 months. Little growth occurs after the age of 3 years (Wang and Liu 1989).

Body Temperature, Respiration Rate and Pulse Rate

Data on physiological parameters of *cameloides* are scarce. According to Wang and Liu (1989), normal body temperature (rectal) for Manchurian moose ranges from 37.7C° to 38.8°C. This increased 0.3 to 0.4°C for every 10°C increase in air temperature between -15°C and 18°C. This compares to a body temperature for adult European moose (*alces*) which ranges from 37.4 to 39.7°C from winter to summer (Chermnykh 1987).

Table 6. Development of moose calves in China (measurements in millimeters)[a].

Ages (mon.)	Sample size	Weight (kg)	Total length	Shoulder height	Chest girth	Fore leg	Hind leg
new born	4	11	770	795	610	600	640
1	1	27	980	929	792	720	750
6	2		1390	1300	1350	1100	1150
			41%[b]	58%[b]	63%[b]	67%[b]	65%[b]
18	2		1840	1520	1790	1210	1280

a. After Wang & Liu (1989).

b. Contributions to adult size within first six months.

Forty-seven, xylazine-immobilized adult *alces* in Finland had rectal temperatures between 35.5 and 40.2°C (mean±S.D., 38.25±0.94°C) when air temperatures were -16 to -3°C. Franzmann *et al.* (1984) reported that body temperatures of *gigas* in Alaska averaged 38.4±0.3°C and 38.9±0.3°C in winter and summer, respectively, and increased with excitability.

When air temperature changed from 20 to 34°C, the respiration rate of Manchurian moose increased from 68/min to 90/min (Wang and Liu 1989). The respiration rate of moose in Russia was reported as 7-16/min in the winter and 16-128/min in the hot summer (Chermnykh 1987). The respiration rate of *gigas* in Alaska increased from 19±5/min in winter to 40±16 in summer and varied with immobilization (Franzmann *et al.* 1984).

In Manchuria, the pulse rate of a yearling was 84-90/min in April (Wang and Liu 1989). Acoording to our measurements on an adult *alces* in Finland, pulse rate ranges from 30 to 68/min (n=24) at air temperatures of -16 to -3C°. Reports from Russia (Chermnykh 1987) recorded a rate of 40-50/min in winter and 78-81/min in summer for adult moose. In Alaska, the pulse rates of *gigas* immobilized with succinylcholine chloride increased from 75±13/min in winter to 91±15/min in the summer (Franzmann *et al.* 1984).

DISCUSSION

After reviewing the literature we are amazed at the diversity of published data and the paucity of comparable figures. Almost all of the measurements and observations on each of the 7 subspecies differed from study to study. The data on *cameloides* in China also differs from that on the same subspecies in Russia. Some of the variance might be due to disorganized population structures, or hybridization, as suggested by Bubenik (pers. comm.), or, more likely, is due a variety of measuring methods used in various studies.

During the past 5 decades, a large number of published moose studies took place in North America, northern Europe, and the European part of Russia (Fig. 2). They focus mainly on *gigas, alces* or *andersoni,* with few studies on *cameloides* and *pfizenmayeri.*

Taxonomy and Evolution

Peterson (1952, 1955) classified moose into 7 subspecies. However, this is not universally accepted. Bubenik (1986) questioned the subspecies classification, especially those of the moose in Russia. Sher (1987) believed there were 3 to 5 subspecies in the territory of the former USSR. Heptner *et al.* (1961) reported that the moose inhabiting western Siberia were significantly larger, heavier, and had larger antlers than those in Europe and suggested that *A. a. alces* might actually represent two subspecies. He proposed the name *uralensis* Matschie or *tymensis* Zukowski for the western Siberian moose.

Buturlin (1934) was the first to notice that moose in the Kolyma-Indigirka and Anadyr regions (northeastern Siberia) were the largest in Russia and were similar or identical to the Alaskan moose. Heptner *et al.* (1961) also suggested that the cranial features of the eastern Siberian moose was closest to *gigas*. Egorov (1965) stated that measurements and weights of the Yakutian moose were far less than those of east Siberian moose while Kistchinski (1974) made a distinction in northeastern Siberia between two kinds of moose which he believed were *pfizenmayeri* and *gigas*. Zheleznov (1993) argued for 3 subspecies of moose in eastern Russia, *pfizenmayeri, cameloides and buturlini*. This lack of agreement suggests that uncertainty exists about the status of *pfizenmayeri* and we agree with Heptner *et al.* (1961) who suggested that an independent study of moose subspecies in northeast Siberia is needed.

From our comparisons, we suggest that *cameloides* is probably closely related to *pfizenmayeri* and hybridization may have occurred. Transitional characters in morphophysiology between these two subspecies have been found in the Cis-Amur Territory and the Trans-Baikal region (Ditsevich 1990). There are also geographical differences among populations of moose in China. Cervicorn antlers are more frequent on moose of the Lesser Khingan Mountains than in the Greater Khingan Mountains. Hence, it has even been suggested that these two types should be considered different subspecies (Xu 1989).

We favour the hypothesis of reverse recapitulation in *cameloides*. According to Xu (1989), moose fossils were found in Manchuria in the Late Pleistocene period. In Europe, moose appeared near the end of the Middle Pleistocene period (Bubenik 1986) or the Riss Glaciation (Geist 1987). Manchurian moose may have been driven by ice from Europe to Manchuria in the same age, such as the late Riss. If this is true, it is possible that Manchurian moose, after settling down, also participated the first invasion of America before the Sangamonian Interglacial period. These travelling ancestors might have shared some morphological traits with modern *cameloides* and other small North American descendants.

Distribution and Current Population Size

The range of *cameloides* is clear in all directions except in the west where it extends from China into Mongolia (Fig.1). Ditsevich (1990) indicated that the morphological characters of the moose in Trans-Baikal region did not differ significantly from the moose of Cis-Amur region, which suggests that the range of *cameloides* in Russia may extend further westward than 123° E longitude as reported by Heptner *et al.* (1962).

The south edge of *cameloides* range has fluctuated during this century. In Sikhote-Alin, it extended up to 43°30' N latitude in the 1860's (Przewalski 1870, cited from Heptner *et al.* 1961), receeding to 44° 45' N lat. in the 1940's (Kaplanov 1948) and at about 46° N lat. since the 1950's (Heptner *et al.* 1961). Myslenkov and Voloshina (1992) suggested that the range of moose in the Sikhote-Alin Reserve extended south to within 30 km of the sea coast in 1958, but dwindled in the 1970's, and at present is rarely found on the eastern slopes. The southern limit of distribution in China has receeded northward 3° latitude since the beginning of this century (Jia 1992). Moose disappeared from the Wanda Mountains of China, part of its former southern range, (Jia 1992).

Unlike other moose populations in the world, *cameloides* has declined in the past several decades. In 1957, the Russian population was estimated at 12,000 in the Amur Territory, 4,000 in Primore (Sikhote-Alin), and 10,000 in Khabarovsk (Heptner *et al.* 1961). Adding the Chinese population, the total number of *cameloides* in the 1950's would have been 40,000 to 50,000. There were an estimated 18,000 *cameloides* in China in 1976. However, a recent census based on snow trails (Piao *et al.* 1993) revealed a population of 9,955 in 1986-87, a possible decline of 53.4% in China. We believe human interference, including heavy hunting pressure is the main reason that the range of *cameloides* has changed in China and Russia. Its overall distribution is probably shrinking rather than simply moving northward. If the same decline has occurred in Russia, a program of conservation for *cameloides* is seriously needed.

Future study of *cameloides* may help to better our understanding of the history of North American taiga moose (Bubenik 1986). It has lived for an extended period in a glacial refugium (Geist 1987), but clearly shares features with North American moose. In this regard, several questions can be asked. What is the real relationship between *cameloides* and other moose subspecies? What are the exact differences in morphological and ecological features between *cameloides* and other moose? Was *cameloides* involved in the migration to the New World or is it just an independant branch?

Kurtén and Anderson (1980) said, "Since

we are living in an interglacial, it behooves us to learn more about past ice ages for another one may be on its way, and knowledge of Pleistoncene environments, faunas, and species may be a key to mankind's future". The Manchurian moose provides an excellent opportunity to investigate this perspective.

Cameloides is poorly studied in comparison with other moose of the world. There are three reasons for this.

1. Lack of researchers and programs - In Russia, studies of *cameloides* were mainly carried on before the 1970's. In China, almost nothing was done before the 1980's. During the last decade, only a few scientists in China (probably less than 5 people) have taken the study of moose seriously. The history and recent status of moose in China was revealed to the western world for the first time by Jia (1992).
2. Lack of funds and facilities - Even in the 1990's, wildlife studies in China, which are encouraged by the government, are extremely difficult because of limited funds and facilities. *Cameloides* has been on the list of National, second-class, protected animals for 20 years in China, and hunting is forbidden. Permission to hunt or live-capture for special purposes must be obtained from the Provincial Government (first class protected animals can only be live-captured, and permission of the National Government is required).
3. Lack of suitable research methods and timely international communication - Most publications on *cameloides* are either in Russian or Chinese making it difficult for international reviewers. Furthermore, international moose conferences have been limited to locations representing all moose subspecies with the exception of *cameloides* and *pfizenmayeri*.

Suggestions for Future Study

From our literature review (Fig. 2) we conclude that genetics and world-wide comparative studies of moose are badly needed. There is also a need to standardize methods of measuring and recording moose morphology and ecology. Taxonomic revisions using techniques such as mitochondrial DNA analysis are needed. Population studies in Russia and China are needed to confirm the suspected decline and a conservation strategy for *cameloides* is seriously needed. Many theories and hypotheses remain to be tested.

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