THE HABITAT OF *ALCES ALCES CAMELOIDES* - A REVIEW

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ABSTRACT: *Alces alces cameloides* inhabit a region of Pleistocene ice-edge with numerous mountains and rivers. Living in a continental and monsoon climate, which covers four climatic zones, *cameloides* have probably developed morpho-physiological adaptations. The habitat is characterized by a rich flora. However, *cameloides* was supposed to suffer from malnutrition during both the Pleistocene and in modern time. *Cameloides* are subjected to predation by tigers, a phenomenon unique to this subspecies. The effect of tiger or other carnivores is limited at present because of their rareness. It is human activities that have a notable impact on moose. The current knowledge of habitat preference and food habits of *cameloides* since 1940 are also summarized.

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Alces alces cameloides (the Manchurian moose) are presently distributed in an extensive region of northeast China (Manchuria), far-east Russia and the eastern-most corner of Mongolia, 46°-56° N latitude and 110°-140° E longitude, with the total area being about 1.7 million km^2 (Fig. 1). The western edge of the range is not definitive because of a possible mix with the Yakutian moose, *A. a. pfizenmayeri* (Ditsevich 1990, Jia *et al.* 1994). Historically, the range was larger. Its southern edge has fluctuated several times (Heptner *et al.* 1961) and receded northward three latitudinal degrees during this century (Heptner *et al.* 1961, Jia 1992).

Increasing attention has been given to *cameloides* in the past decade for its morphological similarity, and therefore implied relationship, with moose in North America (Telfer 1984, Bubenik 1986, Geist 1987). It has been suggested that *cameloides* would specifically have both evolutionary and ecological adaptations to the glacial-refugium habitat (Geist 1987). Their smaller body and antlers, and relatively large head (Jia *et al.* 1994), were considered to be a result of poor nutrition in the refugium during glaciation (Geist 1987). It is speculated that the evolution of a smaller, heat-dissipating form of moose may have permitted a higher survival or reproduction during warmer interglacial periods and encouraged moose to invade warmer regions (Telfer 1984).

Unlike other moose populations, *cameloides* may have declined in recent years along with a range shrinkage (Piao *et al.* 1993, Jia *et al.* 1994). There is a paucity of knowledge about *cameloides* habitat due to few studies being done. Early efforts were made by Kaplanov in Sikhote-Alin in the 1940's and more recently (1980's) by researchers in northeast China, but these works have been published in Russian or Chinese and generally not available in western countries. This paper summarizes current knowledge on *cameloides* habitat and habitat use including food habits. Further research concerning *cameloides* and their habitat is urged.

HABITAT CHARACTERISTICS

Topography

Within the *cameloides* range, there are six large mountain ranges; four in Russia, i.e. Sikhote-Alin (SA, in Fig. 1), Bureinskiy (BU), Tukuringra (TR) and Stanovoy (ST), and two in China, i.e. Greater Khingan (GK) and Lesser Khingan (LK). The Sikhote-Alin is the southern most limit of present-day moose in Eurasia. The Stanovoy is the northern limit of *cameloides* (Ellerman and Morrison-Scott

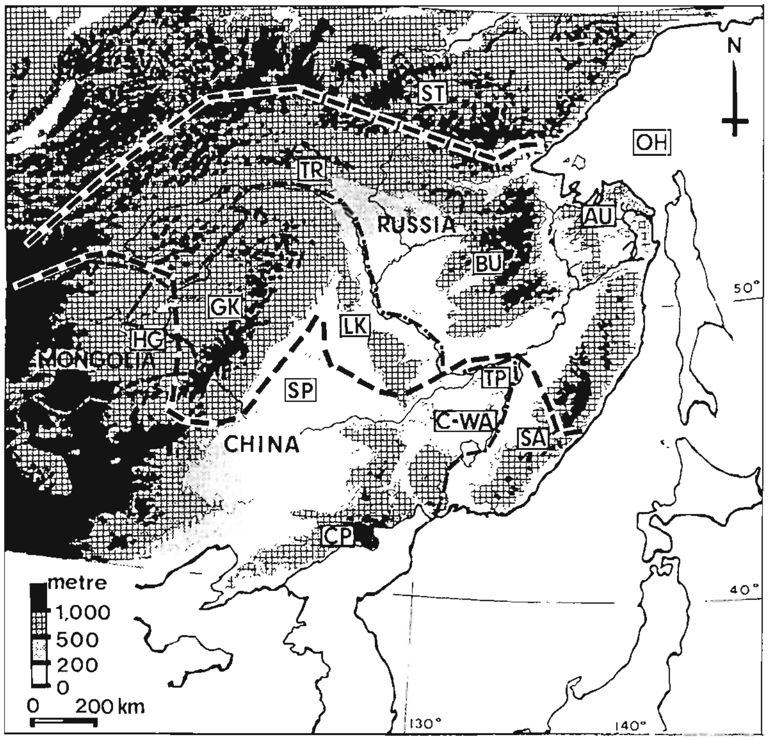


Fig. 1. Topography of *cameloides* range in China and Russia. (According to "The Times Atlas of the World", John Bartholomew & Son Limited 1977).

AU:	Amgun Basin;	OH:	Okhotsk Sea;
BU:	Bureinskiy Mountains;	SA:	Sikhote-Alin Mountains;
CP:	Ch'ang-Pai Mountains;	SP:	Sunglen Plain;
C-WA:	Chang-kuang-ts'ai Ling & WanTa Mountains;	ST:	Stanovoy Mountains;
		TP:	3-River Plain;
GK:	Greater Khingan Mountains;	TR:	Tukuringra Mountains;
HG:	Hu-lun-bay Grassland;	— —:	Moose range.
LK:	Lesser Khingan Mountains;		

1951, Ma 1986). The Greater Khingan is characterized by gentle slopes with rounded peaks and wide valleys, which form a suitable wildlife habitat. The Lesser Khingan is characterized by fewer but undulating mountain peaks and wider valleys on the western slopes where the land is more cultivated. These mountains do not have high relief. Areas with elevations above 1000 m a.s.l. (above sea level) represent less than 15% of the whole range, with 75-80% ranging from 200 to 1000 m a.s.l.

Lowlands (<200 m a.s.l.) occur only in the Amur and Amgun basins, and comprise less than 10% of the whole area. The Amgun Basin (AU in Fig. 1) with its' Nimeleno-Chukchagirskaya lowland has the forests comprising 53% of the land and vast steppe-like plains (Metelsky 1974).

Outside the current *cameloides* range in the south is another mountain region - Mt. Chang-kuang-ts'ai Ling & WanTa (C-WA, Fig. 1). It is a northern connection of Mt. Ch'ang-Pai (CP) and is characterized by low, even, squared mountain tops. Moose were present there at the beginning of the 19th century (Jia 1992). Between the Lesser Khingan and WanTa is the 3-River Plain (TP), an intersection of the Amur, Ussuri, and Sungari rivers. This land is low (<200 m a.s.l.) with many marshlands. Similar marshy features can also be seen in the Sunglen Plain (SP), located between the Greater and Lesser Khingans. West of the Greater Khingan is a high plateau prairie (>600 m a.s.l.), the Hulun-bay Grassland (HG), which is a fertile pasture.

There are few lakes in the region. But, numerous springs, high-land ponds, streams, and small branch rivers exist on every mountain. The Amur river (4370 km long) originates from both the Argun river in the south and the Shilka river in the north, and flows to Tatarskiy Strait in the Okhotsk Sea (OH in Fig. 1). Frequent flooding of these rivers results in large quantities of early succession vegetation and a heavy growth of forage plants such as willows (*Salix* spp.), which are used extensively by moose.

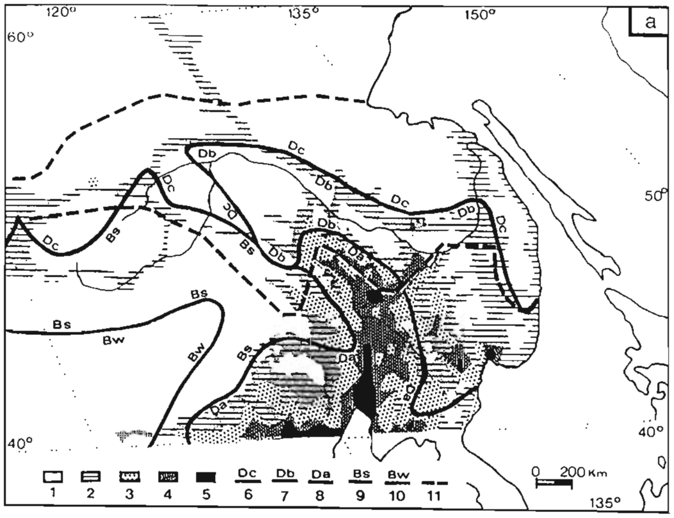
Manchuria, with the exception of the northern mountains, i.e. the Greater Khingan, was not covered by Pleistocene continental glaciers (Burger and Zhao 1988). In places of lower than 300 m altitude, the mineralogical composition of soil materials is mainly the Quartair alluvial deposits, which are rich in clay, less leached and more fertile. Above 300 m altitude, soils are closely related to the underlying bedrock type. Soil profiles of the forests in the south of the region are deeper, and this is attributed to the longer periods of weathering without glaciation (Burger and Zhao 1988).

Climate

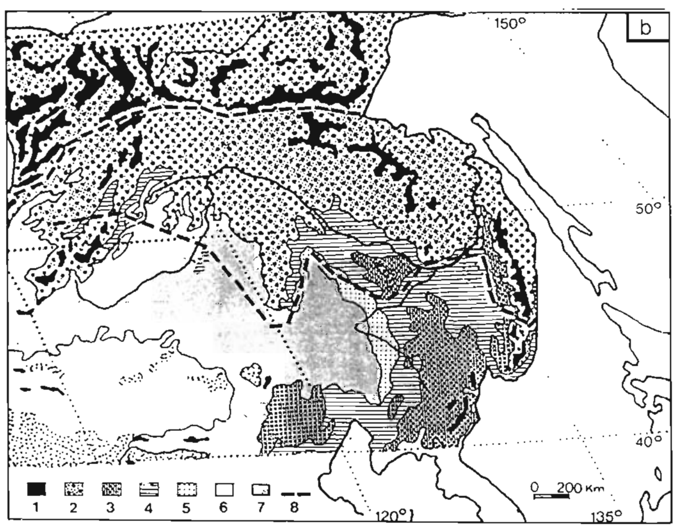
The climate in *cameloides* range is best expressed as continental and monsoon. Strong, dusty winds occur in April and May with speeds as high as 10 m/s., and in July and August southeasterly winds from the Pacific Ocean bring heavy rain. From October onwards, the prevailing strong northwesterly winds from the high, dry Mongolian Plateau and Siberian Plain, cause a fast drop in temperature and a long, bitterly dry-cold winter. Temperatures less than 0°C can last for 5 months in most places, and up to 7 months or longer in the northern Greater Khingan and further north. Average annual temperatures vary from 1 to 4°C with an annual temperature difference reaching 40°C.

Rainfall occurs primarily from June to September, with 50-70% of the annual precipitation in July and August. Rainfall amount decreases from southeast to northwest, depending on distance to the sea and local topography. Higher rainfall can be as much as 1000 mm along the coast. The annual ratio of evaporation/ precipitation is 1 to 3.5 from east to west, which indicates the western region is much drier. The growing season is 80-160 days, with up to 180 days along the coast. In the Greater Khingan, snow cover lasts from the end of November to April. In the Sikhote-Alin, snow cover can last from the beginning of October to June, and ranges from 90-240 days. Snow depth averages 40-50 cm, with extremes of up to 200 cm at high elevations. Rivers are frozen for 150-200 days. The Amur river is generally frozen from November to April, averaging 140-150 days, with surface ice as thick as 1-1.5 m. But, the fast flowing sections of the Amur are never frozen.

According to the Köppen classification (Trewartha 1954) which is based on temperature and precipitation, *cameloides* range covers four climatic zones (Fig. 2a), i.e. (1) Dc climate (subarctic): severe in winter, with the coldest month below -30°C, the warmest month above 10°C, the cool summer lasting for less than four months, and mean annual precipitation (MAP) averaging 430 mm; (2) Db climate: warmer than Dc with the coldest month below -20°C, the warmest month below 22°C, and MAP averaging 550 mm with >700 mm along the coast; (3) Da climate: hot in summer, with the warmest month above 22°C, the coldest month below -10°C, and rainy with MAP averaging 700 mm; and (4) Bs climate: a semi-arid steppe, dry and cold, with the warmest month above 20°C, the



a: Human population density and climatic zones
1: 0-2 person/km²;
2: 3-20 person/km²;
3: 21-100 person/km²;
4: 101-200 person/km²;
5: >200 person/km²;
6: rainy, severe winter, coldest month <0°C, warmest month >10°C but less than four months;
7: rainy, severe winter, coldest month <0°C, warmest month >10°C but <22°C;
8: rainy, severe winter, coldest month <0°C, warmest month >22°C;
9: steppe, semi-arid;
10: desert, arid;
11: moose range.



b: Vegetation zones
1: mountain vegetation;
2: boreal forest;
3: mixed forest;
4: broadleaf forest;
5: prairie (long grass);
6: steppe (short grass);
7: desert vegetation;
8: moose range.

Fig. 2. Natural conditions in *cameloides* range.
(According to "The Times Atlas of the World". John Bartholomew & Son Limited 1977)

coldest month below -15°C, and MAP only 300 mm. Further westward, out of moose range, is a dry cold desert (Bw) climate.

Vegetation

The rich Manchurian flora is another feature of *cameloides* range. It is composed of Changpai, Mongolia and Dahuri vegetation, and primarily refers to those plants found in areas outside the boreal forest. In an area that includes the Greater Khingan, the Lesser Khingan, Mt. Chang-kuang-ts'ai Ling & WanTa, the 3-River Plain and the Sunglen Plain, i.e. Heilongjiang Province of China, more than 2300 species of plants have been recorded (Zhou 1985). About 800 plant species grow in the Greater Khingan (boreal), 1400 in the Lesser Khingan, and 500 in the Sunglen Plain (Zhou 1985). For commercial trees, i.e. those >15 cm dbh (stem diameter at breast height) and up to 5 m in height, there are 15 species of coniferous trees in 8 genera, and more than 110 species of deciduous trees in 39 genera in all of northeast China (Burger and Zhao 1988). Five general types of vegetation can be seen in *cameloides* range (Fig. 2b).

1. Mountain Vegetation

The altitudinal vegetation occurs mainly in the Sikhote-Alin, Bureinskiy, and Stanovoy regions. The vertical distribution of plants is not clear in the Greater Khingan because of its gentle and rounded topography. In the Lesser Khingan, mountainous forests are above 1000 m a.s.l., dark coniferous forests at 700-1000 m a.s.l., mixed forests at 300-700 m a.s.l., and deciduous forests below 300 m a.s.l. In the Sikhote-Alin, western slopes (0-600 m a.s.l.) have the Manchurian flora. Above 1200 m a.s.l. in the Sikhote-Alin are subarctic alpine plants with tree species being mainly *Pinus* spp. and other shrubs (Kaplanov 1948).

2. Boreal Forest

Boreal forests are the primary habitat for *cameloides*. They occur throughout the Russian side and the Greater Khingan area of China. In the Greater Khingan, the dominant virgin forest is *Larix gmelini* mixed with some *Pinus sylvestris* var. *mongolica*. The *Larix* domination rather than *Picea* or *Abies* is attributed to the drier winters (Burger and Zhao 1988). At higher elevations (820-1100 m in the north and 1050-1380 m in the south), *Larix-Picea jezoensis* forests occur. *Pinus pumila*, a dwarf tree with a maximum height of 3 m, is common in the high sparse larch forests. Scots pine (*Pinus sylvestris* var. *mongolica*) are mainly distributed on the south bank of Hai-la-erh River, the northern Greater Khingan, and interspersed with a mosaic of grasslands. At lower elevations (300-600 m) such as in the eastern Greater Khingan, forests of *Quercus mongolica*, *Larix gmelini* and *Betula dahurica* occur with additional co- or sub-dominants of *Populus davidiana*, *Tilia amurensis*, *Fraxinus mandshurica*, *Phellodendron amurense*, *Vaccinium* spp., *Empetrum nigrum*, *Ledum palustre*, etc. In the Lesser Khingan, boreal forests are limited to a small area, and consist primarily of larch forests. In the Sikhote-Alin, boreal forests cover most of the eastern slopes with the main coniferous trees being *Picea* and *Abies*. In the Amgun Basin, besides the steppe-like plain of the lowland, and dwarf shrubs with *Betula nana* in alpine areas, five forms of forests are described (Metelsky 1974), i.e. mountain taiga; dark coniferous forests (with *Picea*, *Abies*, *Pinus cembra*, *Pinus sibirica*, etc.); rosemary larch forests; grass larch and mossy larch forests; and mountain taiga mixed with larch, birch and aspen.

3. Mixed Forest

Mixed forests mainly occur in the Lesser Khingan of China and the western slopes of Sikhote-Alin. The characteristic forest in the Lesser Khingan is composed of *Pinus koraiensis*, mixed with *Abies holophylis*, *Taxus cuspidata*, *Thuja koraiensis*, *Maackia amurensis*, *Populus ussuriensis*, *P. koreana*, *Tilia amurensis*, *Betula costata*, *Fraxinus mandshurica*, *Ulmus japonica*, *Acer mono*, *Juglans mandshurica*, *Phellodendron amurense*, *Vitis amurensis*, *Schizandra chinensis*, etc. Pioneer species are *Betula platyphylla* and *Populus davidiana*. Floristically, the Lesser Khingan is rich in plant species including some pre-Pleistocene relics such as *Phellodendron amurense*. Korean pines (*Pinus koraiensis*) often exist locally in pure forests. At the higher elevations of the Lesser Khingan, more boreal species, i.e. *Abies*, *Picea* and *Larix*, occur.

4. Deciduous Forest

Deciduous forests with more complex plant composition occur mainly on the lower plain or the base of mountains. The dominant plant species include *Populus*, *Betula*, *Quercus mongolica*, *Tilia amurensis*, *Tilia mandshurica*, *Phellodendron amurense*, *Acer mono*, *Juglans mandshurica*, *Fraxinus* *mandshurica*, *Deyeuxia angustifolia*, *Carex*, *Salix rosmarinifolia*, etc. Forests of *Populus davidiana* - *Betula platyphylla* are common.

5. Steppe

The southwestern part of *cameloides* range is located in the lower Greater Khingan and Inner Mongolian plateau, which is covered by forest-steppe habitat. Meadow-steppe is scattered with light forests of *Populus davidiana*, *Betula platyphylla* and *Quercus mongolica*. Plant species are mainly *Filifolium sibiricum*, *Stipa baicalensis*, *Aneurolepidium chinensis*, *Carex*, *Suaeda*, *Cyperus*, *Arundinella hirta*, *Puccinellia tenuiflora*, *Calamagrostis epigeios*, etc.

Vertebrate fauna

There are at least 97 mammal species distributed among 19 families in 6 orders recorded (Ma 1986) in Heilongjiang Province, China. The family *Felidae* includes tiger (*Panthera tigris*), leopard (*P. pardus*), lynx (*Lynx lynx*), steppe cat (*Felis manul*) and leopard cat (*F. bengalensis*). The family *Ursidae* includes black bear (*Selenarctos thibetanus*) and brown bear (*Ursus arctos*). The *Canidae* includes wolf (*Canis lupus*), fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*) and jackal (*Cuon alpinus*). Mustelids include wolverine (*Gulo gulo*), badger (*Meles meles*), otter (*Lutra lutra*), and other weasels and martens. Ungulates include wild boar (*Sus scrofa*), musk deer (*Moschus moschiferus*), sika deer (*Cervus nippon*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), reindeer (*Rangifer tarandus*), goral (*Naemorhedus goral*) and moose (*A. a. cameloides*).

There are more than 340 bird species representing 57 families in 19 orders recorded in Heilongjiang Province of China (Piao 1990), 41% of them being perching birds (*Passeriformes*). The range has no special locally distributed bird, but it is an important breeding area for many birds such as cranes (*Grus*), ducks (*Anas* and *Aythya*), and other migratory species. Eleven species of amphibians in 2 orders and 6 families and 16 species of reptiles in 3 orders and 4 families have been recorded (Piao 1990).

Cameloides may have more potential predators than moose subspecies in other parts of the world. Furthermore, only *cameloides* are subjected to predation by tiger. At the beginning of this century, the Siberian tiger could be found in several mountains of Manchuria such as the Greater Khingan (Zhao 1911). However, tigers have disappeared from the Greater and Lesser Khingans since the 1970's and 1980's (Ma 1983). At present, they only survive in Sikhote-Alin Preserve and some small areas in Chang-kuang-ts'ai Ling & WanTa Mountains (Kaplanov 1948, Wu *et al.* 1994) with a total population of approx. 300-500 individuals (Wu *et al.* 1994). In 1962-1969, moose mortality from tigers accounted for only 9% in Sikhote-Alin Preserve (Myslenkov and Voloshina 1992). The main predator of *cameloides* is wolves. But, wolves have disappeared from most areas of this region. The scenario is the same for bears. Wolf-kill and bear-kill were once recorded as 27% and 64%, respectively during 1961-1969 in Sikhote-Alin (Myslenkov and Voloshina 1992). To date, no precise estimation has been made for the entire *cameloides* range. Additionally, lynx and wolverine possibly prey on moose calves (Kaplanov 1948), but there is no direct evidence of this.

Besides predators, *cameloides* have other cervid competitors to contend with. Red deer and roe deer both compete with Manchurian moose for forage and living space. It has been reported that roe deer have a niche overlap with moose, from November to March, which averaged 59% on forage, 69% on habitat, and 45% on foraging height. Red deer have a niche overlap with moose of 49% on forage, 64% on habitat, and 90% on foraging height (Li *et al.* 1992).

Human influence

Human population growth and agricultural development in Manchuria began in the 18th century. A 190% increase in the human population occurred from 1771 to 1781. Farmland in local areas such as Hulan and Payen had a 52-fold enlargement during five years from 1878 to 1883 (Xu 1989). Most recently, human population increased 50% from 1978 to 1994 in the whole of China. The southern edge of *cameloides* range is clearly defined by a lack of human settlements during the current decades (Fig. 2a).

Agriculture and forestry are the two major human activities in northeast China. Farmlands are dominant in the Sunglen Plain where agriculture has been dominant for centuries because of favorable climate and soil. In the Amur Basin and 3-River Plain, more and more marshes have been converted to cropland since the 1960's. All mountains in this range are included in the productive forestry region. With the discovery of gold, along the upper Amur River in the 19th century, forests of *Pinus sylvestris* and *Larix* suffered from destruction by logging due to increased human settlement. During 1896-1949, valuable forests of pine and tolerant hardwoods such as *Pinus koraiensis*, *Fraxinus mandshurica*, *Tilia amurensis*, *Juglans amurensis* and *Phellodendron amurense* were extensively harvested for the construction of railways. Cutting and forest fires that took place along the railways and the interior, resulted in many forests becoming dominated by *Quercus mongolica*, *Populus davidiana* and *Betula platyphylla* (Burger and Zhao 1988). Logging continued until the 1980's, and since then much reforestation has been underway in both the Greater and Lesser Khingans.

In *cameloides* range, ancient people using fire for agriculture was recorded in the 17th century (Xu 1989). Burned land is common in Sikhote-Alin (Kaplanov 1948) and other forest regions. The largest forest fire occurred in 1987 (6 May - 20 June) along the Amur river of the northern Greater Khingan and burned 1,140,000 ha. This fire measurably affected the resident moose population. According to a census performed in 1988, eight months after the fire, the moose population (0.04/km^2) was 54% of 1985's (0.074/km^2). However, a census performed 1.5 years after the fire in 1989 (0.061/km^2) indicated a subsequent 50% increase from 1988 to 1989 (Ma *et al.* 1993).

The heaviest human pressure on *cameloides* may come from hunters. A long history of hunting and non-rational harvest were two features in this region. The Amgun Basin has been famous for moose hunting since the 18th century because moose were known to gather there in winter (Metelsky 1974). Hunters either relentlessly hunt when moose have no legal protection or poach when hunting is forbidden. Some minorities such as Owenk and Olunchun in the Greater Khingan, historically do have some traditional hunting methods with probable rationality. Unfortunately no studies have been made to reveal what hunting methods the minorities used.

HABITAT UTILIZATION

Habitat preference

Cameloides habitat in the Greater and Lesser Khingans consists mainly of six types, i.e. (1) *Larix*-deciduous mixed forests, (2) *Populus-Betula* forests, (3) *Quercus* forests, (4) *Betula platyphylla* forests, (5) *Salix*-bushes and steppe dominated by *Betula-Quercus*, and (6) marshland plants (Xu 1989). Further detailed, 9 types (Xu 1989), and 15 types (Yu *et al.* 1993), of the habitat have been classified. Habitat preference by moose varied obviously with season and place (Xu 1989, Yu *et al.* 1993).

In the Sikhote-Alin, *cameloides* occurs primarily in five types of habitat, i.e. (1) coniferous forests located on eastern slopes, (2) *Larix* forests on western slopes,

(3) marshland along rivers occurring on western slopes, (4) birch-spruce meadows in high alpine areas, and (5) all burned areas (Kaplanov 1948). The western slopes of the Sikhote-Alin have remained the main habitats of moose. On the eastern slopes, moose inhabit only the upper reaches of rivers (Myslenkov and Voloshina 1992).

The Amgun Basin is regarded as highly valuable moose habitat due to the availability of favorable wintering grounds (Metelsky 1974). This basin is characterized by larch, peat-moss bog forests interspersed with dwarf shrubs and light forests. There is generally shallow snow cover. Moose in the Amgun Basin primarily inhabit river-bottom lands (preferred), lowland with spruce forests, larch peat-moss bog forests with forest regeneration (preferred in winter), larch peat-moss bog forests with shrubs, and mixed taiga on mountain slopes (Metelsky 1974).

Movement

Cameloides make regular altitudinal movements in mountain areas. In China (Piao, pers. comm.), they move in spring (March) to lower wetlands to take advantage of new growth and remain here for 1 to 2 months. They then move (males first) to higher elevations (1000-1200 m a.s.l.) for the summer. In the autumn (October), they move down to the base of the mountains (300-400 m a.s.l.) for winter, followed by an upward movement in December to 500-700 m a.s.l. The horizontal movement is as long as 150-200 km, and follows the river corridors. In areas where food and water sources are abundant, such as the northern Greater Khingan, moose migrations are not evident. Additionally, when snow cover is over 60 cm, moose moved less than 2 km/day.

In the Sikhote-Alin, moose were observed during winter on mountain tops when snow depth was not too extreme, but usually remained at elevations of 700-1200 m a.s.l. and somewhat lower on eastern slopes. They move to winter areas in September and to summer areas in March. *Cameloides* spend the summer at different elevations of Sikhote-Alin: abundant in pine-spruce-deciduous forests at 500-800 m a.s.l., fewer in spruce forests at 800-1100 m a.s.l., and abundant again in alpine meadows at 1100-1300 m a.s.l. (Kaplanov 1948). Summer habitats of *cameloides* are numerous on alkali soils along the Kolumbe river of the Sikhote-Alin (Myslenkov and Voloshina 1992).

In the Amgun Basin, moose were seen everywhere in the summer, but during winter they concentrate on certain areas such as river bottoms of the Amgun, Kerbi, Omal and Im rivers (Metelsky 1974).

Food habits

There is not a complete record on how many different plant species *cameloides* consumes. Table 1 lists at least 160 species of *cameloides* forage plants observed by five authors in different regions (Kaplanov 1948, Yang *et al.* 1982, Wang 1983, Xu 1989, Yu and Xiao 1991). According to the microhistological analysis on moose feces by Yu and Xiao (1991), from December 1987 to November 1988 in Heihe, a forest area between the Greater and Lesser Khingan, more than 70 plant species in 54 genera were consumed by moose. Among those, 87.4% were browse (tree and shrub), 4.9% forbs, 3.3% grasses and sedges, and 4.4% leaf litter. The staple browse species consisted of *Salix* (18.7% of total forage), *Corylus* (15.8%), *Betula* (12.2%), *Populus davidiana* (9.4%), *Pinus koraiensis* (7.6%), *Tilia amurensis* (5.2%), and *Quercus mongolica* (5.1%). The study also revealed a seasonal change in moose feeding (Fig. 3). Grass, sedges and forbs were consumed primarily in summer and autumn with the highest diet proportion of 34.7% in August. Moose bite diameter was 2-4 mm in winter browsing, and increased 17-47% from November to April. The winter preference order was *Populus*

Table 1. Recorded food-plants eaten by *cameloides*

Plant name	Season	Author
Coniferous		
Abies coreana	4	Ka
- *nephrolepis*	4	Ka
Picea koraiensis	2 3 4	Yu
Pinus koraiens	1 2 3 4	Ka,Yu
Taxus cuspidata	4	Ka
Deciduous		
Acanthopanx senticosus	2 3 4	Yu
Acer spp.	2	Wa
- *mono*	1 2 3 4	Yu,Yg
- *tegmentosum*	2 4	Ka
- *triflorum*	2	Yg
- *ukurunduense*	2 4	Ka
Aconitum kirinense	2	Yg
- *kusnezoffii*	2	Yg
- *villosum*	2	Yg
Adenophora tetraphylla	2	Yg
Agrimonia pilosa	2	Yg
Agrostis mongolica	2	Yg
Alnus spp.	4	Ka
- *fruticosa*	2	Ka
- *hirsuta*	2	Ka
- *japonica*	2	Yg
- *sibirica*	1 2 3 4	Yu
Aquilegia oxysepala	2	Yg
Artemia spp.	2	Yu
Aster scaber	2	Yg
Astragalus spp.	2 3	Yu
Athyrium spp.	2	Yu
Batrachium trichopyllum	2	Ka
Berberis amurensis	2 3 4	Yu
Betula spp.	1 2 3 4	Yu
- *costata*	1 2	Yg
- *dahurica*	2	Wa
- *ermanii*	4	Ka
- *fruticosa*	1 2 3 4	Yg
- *middendorffii*	4	Ka
- *manshurica*	2 4	Ka
- *platyphylla*	1 2 3 4	Ka,Xu, Yg
Brachybotrys paridiformis	2	Yg
Bromus inerrnis	2	Yu
Cacalia hastata	2	Ka,Yg, Yu
- *firma*	2	Yg
Calamagrostis langsdorfii	2	Ka
Campanula punctata	2	Yg
Carex spp.	1 2 3 4	Xu,Yu
Carpesium macrocephalum	2	Yg
Chamaenerion angustifolium	2	Xu,Yg, Yu
Chenopidium spp.	2	Xu
- *album*	2	Yg
Chosenia macrolepis	2 4	Ka
Cirsium setosum	2	Wa
- *intricata*	2	Yg
- *segetum*	2	Yg
Clematis aethusi	2	Yu
Commelina communis	2	Yg
Convallaria keiskei	2	Yg
Cornus alba	2 3 4	Yu
- *tatarica*	2 4	Ka
Corylus spp.	1 2 3 4	Yu
- *heterophylla*	2	Wa,Yg
Crataegus pinnatifida	2	Wa,Xu
Deutzia spp.	1 2 3 4	Yu
Deyeuxia angustifolia	1 2 3 4	Yu
Diervilla middendorffiana	2	Ka
Dioscorea nipponica	2	Yg
Echinochloa spp.	2	Yg
- *crusgalli*	2	Wa
Epilobium palustre	2	Yg
Equisetum spp.	2 3 4	Yu
- *silvaticum*	1 2	Yg
Erigeron komarovii	2	Yg
Erodium stephanianum	2	Yg
Evonymus sacrosancta	1 3 4	Yu
Filipendula intermedia	2	Yg
Fraxinus mandshurica	2 3 4	Yu,Yg
Galium verum	2	Yg
Gentiana macrophylla	2	Yg
Geranium spp.	2 3	Yu

Table 1. Continued...

Plant name	Season	Author
- maximowiczii	2	Yg
Geum aleppicum	2	Yg
Gymnadenia conopsea	2	Yg
Halenia corniculata	2	Yg
Hippuris vulgaris	2	Wg
Hypericum ascyron	2	Yg
Impatiens nolitangere	2	Yg
Ixeris denticulata	2	Yg
Ledum hypoleucum	4	Ka
Leonurus japonicus	2	Yg
Lespedeza spp.	1 2 3	Yu
- bicolor	2	Wa,Yg
Ligularia fischeri	2	Yg
- speciosa	2	Ka
Lilium distichum	2	Yg
Lonicera spp.	1 2 3 4	Yu
- caerurea	2	Yg
- edulis	2	Ka
- japonica	2	Yg
Lycopus lucidus	2	Yg
Lysimachia dahurica	2	Yg
Malus pallasiana	2	Wa
Medicago sativa	2	Wa
Malus baccata	2 3 4	Yu
Menyanthes trifoliata	2	Ka
Nymphaea micrantha	2	Yu
- tetragona	2	Yg
Onoclea sensibilis	1 2	Yg
Oxalis corniculata	2	Yu
Padus asiatica	2	Yg
- maackii	2	Ka
Pedicularis resupinata	2	Yg
Persicaria orientale	2	Wa
- hydropiper	2	Wa
Phellodendron amurense	2	Wa
Philadelphus schrenkii	1 2 3 4	Yu
Plantago depressa	2	Yg
Poa annua	2	Yg
Polygonum spp.	2	Yu
- avicalare	2	Yg
Populus davidiana Wa,Xu,	1 2 3 4	Yg,Yu
- tremula	2 4	Ka
Potamogeton tepperi	2	Yg
Potentilla spp.	2	Yu
- chinensis	2	Yg
- conferta	2	Yg
Pteridium aquilinum	1 2	Yg,Yu
Primula fistulosa	2	Yg
Prunus asiatica	1 2 3 4	Yu
- padus	2 4	Ka,Xu
Pyrola spp.	2	Yu
- rotundifolia	1 2	Yg
Quercus mongolica	1 2 3 4	Wa,Yg, Yu
Ranunculus baudotii	2	Yu
Rhododendron chrysanthum	2	Ka
- mucronulatum	2 4	Ka
Ribes mandshuricus	1 2 3 4	Yu
- dikuscha	2 4	Ka
- maximoviczianum	2	Ka
- ussuriensis	2	Ka
Robinia pseudo-acacia	2	Wa
Rosa spp.	1 2 3 4	Yu
- davurica	2	Wa
Rubus crataegifolius	2	Yg
Rumex acetosa	2	Yu
- crispus	2	Wa,Yg
Sagittaria trifolia	2	Yg
Salix spp.	1 2 3 4	Wa,Xu, Yg,Yu
- caprea	2 4	Ka
- maximowiczii	2 4	Ka
- rorida	2 4	Ka
- viminalis	2 4	Ka
Sambucus spp.	1 2 3 4	Yu
- latioinna	2	Wa
- williamsii	2	Yg
Sanguisorba officifolia	2	Yg
Saussurea japonica	1 2	Yg
- serrata	1 2	Yg
Schizandra chinensis	3 4	Yu
Sedum aisoon	2	Yg
Setaria viridis	2	Yg
Silene repens	2	Yg
Solanum nigrum	2	Yg

Table 1. Continued...

Plant name	Season	Author	Plant name	Season	Author
Solidago virga-aurea	2	Yg	*Ulmus macrocarpa*	2	Yg
Sorbaria sorbifolia	1 2 3 4	Ka,Yu	*- propinqua*	1 2 3 4	Yu
Sorbus spp.	4	Ka	*- pumila*	2	Wa,Yg
- pohuashanensis	1 2 3 4	Yu	*Usnea barbata*	4	Ka
- sambucifolia	2	Ka	*Vaccinium* spp.	1 2 3 4	Yu
Spiraea spp.	1 2 3 4	Yu	*- uliginosum*	4	Ka
- salicifolia	2 4	Ka,Yu	- vitis	4	Ka
Syringa amurensis	1 2 3 4	Yu	*Valeriana officinalis*	2	Yg
Taraxacum spp.	1	Yg	*Vallisneria asiatica*	2	Wa,Yu
Thelypteris palustris	1 2	Yg	*Viburnum sargentii*	1 2 3 4	Yu
Tilia amurensis	1 2 3 4	Ka,Yg,Yu	*Vicia* spp	2	Yu
			- baicalensis	2	Yg
- mandshurica	2	Wa,Yg	*- cracca*	2	Yg
Torilis japonica	2	Yg	*- unijuga*	2	Yu
Typha orientalis	2	Yg	*Xanthium strumarium*	2	Wa

1: spring, 2: summer, 3: autumn, 4: winter,
Ka: Kaplanov (1948),
Wa: Wang (1983),
Xu: Xu (1989),
Yg: Yang *et al.* (1982),
Yu: Yu and Xiao (1991).

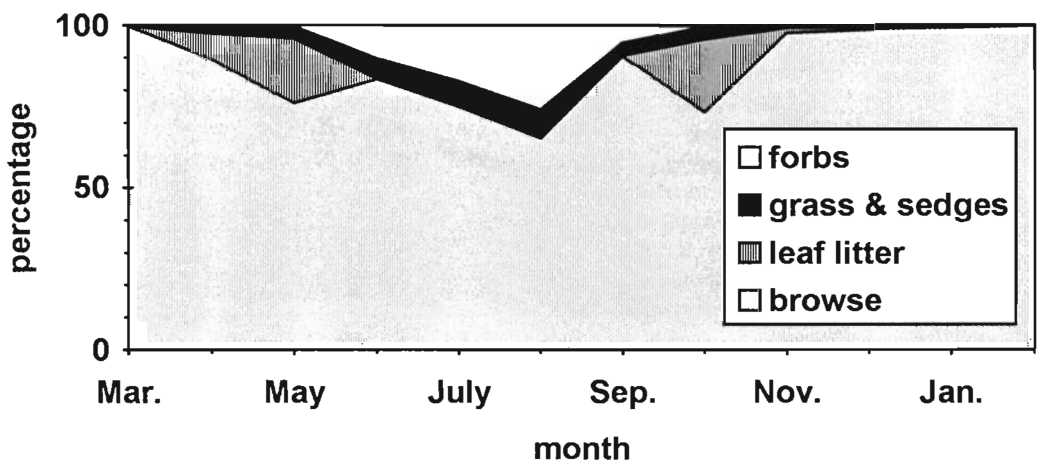


Fig. 3. Annual variations in diet composition of moose in Heihe - a region between the Greater and Lesser Khingans (after Yu and Xiao 1991).

davidiana > *Salix* spp. > *Pinus koraiensis* > *Tilia amurensis* > *Corylus* spp. > *Betula* spp. (Yu *et al.* 1992). Winter forage use (ratio of browsed to encountered) was highest for *Salix*, followed by *Populus*, *Tilia*, *Pinus*, *Corylus* and *Betula* (Yu *et al.* 1993).

In the Sikhote-Alin, *cameloides* were found consuming large quantities (36% in the diet) of lichen (*Usnea barbata*) in winter. In one case, a moose killed in 1938 was found with 50% of the rumen content being lichens (Kaplanov 1948). It was found that moose in the Sikhote-Alin never had their stomachs full year-round. Males were found with empty stomachs during the rut for 5-10 days.

It was also observed that *cameloides* prefer *Epilobium angustifolium*, *Chenopidium* spp. (Xu 1989) and juicy plants (Wang

1986) during the rutting season. Plant twigs consumed in a whole winter have been observed on moose in captivity and calculated to over 3 tons per moose, 30-40 kg per moose per day in summer, and 20 kg per moose per day in autumn (Wang 1986). They also bark strip willow, aspen and oak, and prefer the bark of aspen that grows on sunny slopes. *Cameloides* took bark from trees with a dbh of 10-15 cm, at a height of 100-150 cm (Wang 1986), or 160-200 cm (Piao, pers. comm.).

DISCUSSION

Landform, climate, vegetation and animal community including humans were regarded as major limiting factors to moose distribution (Telfer 1984). The only seldom inhabited landforms by moose are crags or other precipitous terrain (Telfer 1984). In *cameloides* range, the Stanovoy mountain peaks seem to have formed a natural barrier to separate this subspecies from *pfizenmayeri*. These mountain peaks are usually higher than 1200 m a.s.l. and not suitable for moose habitation due to lack of vegetation. Historical records have shown the landform did not limit *cameloides* from occupying habitat further south. Lack of lakes in *cameloides* mountain habitat has been compensated for by numerous rivers and streams. On the other hand, *cameloides* may have benefited from mountains because the mountains limited human activities and settlement.

Snow thickness, density and hardness are affected by wind or temperature to form crusts, and thus influence moose movement and foraging (Telfer 1984). *Cameloides* have shorter legs compared to other subspecies (Jia *et al.* 1994), which, combined with thick snow cover, has caused *cameloides* to adopt a seasonal sedentariness. In most areas, they spend winters on the lowlands because snow cover increases with elevation. Concerning the ambient temperature, extreme warmth may become a problem for moose heat-dissipation (Telfer 1984). *Cameloides* are exposed to a continental climate where temperature variation from warmest to coldest can be up to 40°C. However, *cameloides* once inhabited an even warmer southern climate. This suggests they may have an ability to adapt to warmer temperatures. A small body may be one adaptation that allows them to dissipate heat rapidly. Other evidence of adaptiveness might be the seasonal hide hair density. *Cameloides* in the Greater Khingan have a winter hair density of 347/cm^2, but in summer only 105/cm^2 (Wang and Liu 1989). Similar figures for moose in other areas of Russia are 250/cm^2 in winter and 166/cm^2 in summer (Sokolov and Chernova 1987).

Boreal forests did not strongly limit *cameloides* distribution because the Manchurian moose historically occupied a wide spectrum of vegetation types. *Cameloides* should have more nutritional opportunities if one considers the rich flora available within the range. On the other hand, they were thought to suffer from malnutrition as far back as in the Pleistocene (Geist 1987), and as recent as in the 1940's (Kaplanov 1948). The hypothesis of plants having more chemical defense against herbivore foraging in glacial refugium due to an intensive browsing by Pleistocene megaherbivores (Bryant *et al.* 1989, Bryant *et al.* 1994), may provide a possible explanation. However, evidence from moose forage to demonstrate the hypothesis is not presently available. To acquire a definitive explanation, more studies on plant nutrition and chemical defense on *cameloides* and other moose subspecies forage are needed.

Historically, *cameloides* suffered predation by tigers. However, moose and tigers have a very limited distribution overlap at present, and thus tiger predation is not a major concern. Wolves and bears are still the main natural enemies, but neither are abundant in *cameloides* range. The only serious threat to *cameloides* comes from man. Al-though numerous mountains separate moose from high human densities, and moose hunting is forbidden, *cameloides* still suffers from poaching throughout its' range. Continuous human encroachment of remote mountains will increase the difficulty for the continued survival of *cameloides*. In addition, though no detailed studies exist on *cameloides* diseases in the wild, parasites are certainly another potential mortality factor to be considered.

In conclusion, mountain topography forms the northern limit of *cameloides* distribution and slows human settlement. Climate and vegetation are not limiting moose distribution but can be of potential significance for moose ecological adaptations. Humans have had and will continue to have an impact on *cameloides*.

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