Key note address:

Population dynamics of reindeer

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Abstract: Five types of reindeer populations are distinguished in terms of population dynamics, population density, social structure and migration distance. Differences in the biological rhythms of the populations result in calving occuring 20 days before snow melting in all populations as well as maximal utilization by the deer of young green vegetation in summer. The growth of antlers may serve as a regulatior of biological rhytms. Populations differ in the level of social motivation. Formation of groups of not less than 30-35 animals ensures cooperative protection from insects and management of the group by man. The fidelity to the calving sites, summer ranges and constant migration routes is based on the common orientation reactions of the animals and social attraction. The direction and migration routes are detemined by obligate learning. The dynamics of populations depends on the fertility of 2 and 3 year old females which is determined by feeding conditions in summer and the activity of males during the rut. Migration plays an important role in the population dynamics.

Key words: populations, rhythms, spatial

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The large amount of information collected from different populations of reindeer from various parts of this species vast range has helped to provide new insight concerning the dynamics of *Rangifer* as well as to improve our evaluation of the adaptive potential of individual populations.

Populations are named after their localities, a practice which emphasises the significance of adaptation to local conditions. It is important to understand that a population which settles down in a particular locality has adapted itself to the complex of conditions actually existing here. Such as view helps both in estimating the potential of not yet occupied ecological niches and in understanding co-existence of different populations in the same winter ranges. Their differences may concern migration traditions, the phenology of deer from another population is a limiting factor for forage reserves, which distracts predators. A characteristic example is furnished by a co-existence in the same locality for wild and domestic deer. It should be emphasized that some ecological and behavioural properties of populations require a minimum of at least a single generation before they can change. For instance when tundra deer are transported to the forest zone, only their taiga-

born calves become fully adapted to local conditions (Druri, 1952). It took about 10 years for migration routes to change in Taimyr (Pavlov et al, 1985), and about 20-25 years passed before lichen-eating reindeer changed their foraging habits to become essentially herbivorous as lichen pastures became depleted in Chukotka (Arefyev and Chechukov, 1981)

Biological rhythms

In numerous populations of reindeer the relative proportion of protein carbohydrate and vitamins in the diet is seasonally highly variable. Feeding conditions during the summer season determine the rates of calf growth and the rates of antler growth, moulting and the restoration of body tissue after winter. The principal objective of entire annual foraging in adult deer is to follow the "wave" of new growth of vegatation for as long as possible and thereby to maximize their intake of green vegetation, which is richest in proteins, vitamins and salts.

The welfare of calves and their ability to survive their first winter is enhanced by a matching of the time of appearence of the first vegetation with the calves' ability to consume it. The date of the birth of the first calves is constant on any locality and is a function of the dates of snow melting. Most births occur 10-30 days before snow melting. The timing of the rut is regulated accordingly (Baskin, 1970). According to Klein (1985) the purpose of migration in spring is to ensure that the peak of lactation occurs when the animals have acces to high- quality feeds. In addition, Klein related migration to the search for ranges where the numbers of the wolf and blood-sucking insects are low.

Antlers apparently play an important role in the humoral regulation of seasonal biological rhythms in reindeer. Their growth is regulated by the level of consumption of young vegetation and the time of shedding of the velvet determines the time of the onset ot the rut and, hence, also calving. Reindeer are seasonally polyoestrus. Their oestral cycle and ovulation occur only in autumn and is induced by the males. Thus, the activity of males may regulate the timing of conception. (Mashdovtsev, 1940; Wislocki, 1943; Baskin, 1970).

Pronounced differences in seasonal cycle of growth and fattening exist between males and females but these have so far attracted little attention. Sex differences in fattening may be the reason for differences in the dates and distances of migration in males and females. Big males can dig deep snow more easily and males of tundra populations are therefore able to move further south and to penetrate the taiga more deeply in winter.

Social structure

Reindeer populations display considerably variability in their social structure. Differences are thought to be related to reproduction (rutting and calving) and to represent adaptations to environmental conditions. Reindeer are gregarious but although this behaviour is innate, most other social behaviours are formed through obligate learning. Social behaviour is intimately related to defense behaviour and defense behaviour is likewise a characteristic of particular populations. The level of defense behaviour can be judged by the flight distance, while social behaviour can be estimated by the frequency of visual contacts between neighbours, by the coordination of alarm behaviour and by group size. The level of social motivation depends not only on the conditions of obligate learning but also on environmental conditions (Baskin, 1989).

Sociality may depend directly on environmental conditions. For instance, if reindeer are driven out of the forest and into the alpine zone, their behaviour becomes more coordinated and the animals follow the leader more obediently. Such an effect must be associated with sharp changes in communication conditions. Sociality is highly seasonal in tundra reindeer. Analysis of the sociality of reindeer in Taimyr (Yakuskin, 1976) demonstrated that the group

size is the largest in July (mean group size = 83.7) due to the abundance of blood sucking insects, and in October (mean group size = 308.2). Large accumulations of animals occur at obstacles during autumn migrations. Group size is smallest during the calving season (mean group size = 12.5 - 18.6) and in late June - early August after the fly-season (mean group size = 18.7). In the latter case 26.5% of the animals occur singly or in pairs.

Forest reindeer live in small groups. In a population which lives on the left bank of the middle reaches of the Yenisei river the mean group size is 13 in marshes and 4.3 in pine and leaved forests. In the montane taiga in the upper reaches of the Lena river the mean group size is 3.2 (Zyryanov, 1976). Quite a number of males in these populations are solitary. The group size of reindeer, which are generally thought to be highly social, is close to that of the moose, which lives singly or in small groups. But group size is a poor measurement of sociality. Reindeer are highly sociable even when found in small groups as indicated by their highly synchronized pattern of grazing, and the way in which the group follows the leader rather than dispersing as moose or roe deer.

It is believed that females' tendency to congregate on relatively small calving grounds is an adaptive strategy against predators (Geist, 1971, Bergerud 1974). Geist (1971) designates reindeer as "swampers", animals in which females congregate in dense aggregations at calving, thereby heavily outnumbering their predators. This view can be endorsed, with reservation, only with respect to tundra populations. Forest reindeer calve alone and Geist (1971) correctly designates these as "mountant followers" (i.e. the mother and the calf remain at one site for 2-3 days before social bonds are established, whereupon she leads her calf away). Tundra reindeer do not form such dense aggregations as many other typical "swampers". Species and such aggregations are not always successful in defence. For instance, brown bears occasionally inflict much damage, killing many reindeer calves.

Blood-sucking insects penetrate no more than five rows of reindeer and consequently the animals form large aggregations in summer when insects are active. The full protective effect of group formation is attained with a minimum of 31 animals in group. (Baskin 1970).

In 1931-1938, when numbers of reindeer in the Kola Peninsula were low, an the mean size of groups in summer was approximately 3 individuals (Semenov-Tien-Shansky, 1977). The deer protected themselves from insects by running about slowly in the forest for most of the day. When numbers increased (1958-1972) the animals began to aggregate and the mean size of groups in summer rose to 55. The size of groups during rut increased from 15-25 to 18-35 animals over the same period.

Spatial dynamics

The females of each population retain fidelity to particular calving sites (Dau and Cameron, 1986; Gunn and Miller, 1986) In addition, it has been established that populations are characterized by fidelity to particular summer ranges (Cameron et al., 1986). When several populations use the same wintering grounds they migrate in spring, each in its own direction (Azarov, 1976; Carruthers and Jakimchuk, 1986). Presumably, populations use traditional migration routes. Despite this "spatial fidelity" the animals evidently display a certain degree of lability in their movements. When reindeer first confront artificial barriers on their migration routes (a gas pipline, a road, ice broken by ice breakers) they hesitate but eventually find a detour to new ranges. Another step towards the understanding of population management will be elucidation of the significance of spatial fidelity in adaptation to changing conditions in the environment.

Reindeer females show fidelity to calving sites. They return there even from a distance of

200-500 km (Brown et al. 1986, Valkenberg and Davis, 1986). According to Brown et al. (1986), cows calve no farther than 10 km from the calving site of the preceding years and sometimes even use the same site twice. Similar fidenlity is found on other ungulates, e.g. camels and moose.

The question arises how traditional calving sites are formed. One could agree with Bergerud (1974) that there exist some laws of orientation which guide the deer. Rindeer move towards the sea in spring and inland in autumn following familiar routes.

Young females tend to calve with other females. This social effect described by Allee (1939) is well known for reindeer (Pruitt, 1960; Baskin, 1970). This is may be a peculiar form of transmitting tradition (Gunn and Miller 1986).

Presumably obligate learning accounts for the traditional use of particular migration routes. The direction of migration is determined by lichen conditions as stated by Sokolov, (1983), who monitored migrations in the mountains of Southern Siberia. In winter, reindeer travel from upland tundras to the upper edge of the taiga. In April and May they move to south-facing slopes and in summer they move to the mountains where there are no blood-sucking insects.

Population dynamics

The possible limits of change in demographic parameters of reindeer populations are well-known now. Parameters from some of the best reindeer breeding farms of the USSR are as follows: barreness of females of all ages = 6% number of calves per 100 females = 88%; survival of adult animals = 96%; maximum annual harvest = 40%.

Analysis of the dynamics of some individual populations provides examples of both sharp falls and increases in numbers as well as the existence of some stable populations. The latter included five isolated populations in the montain massifs of southern Siberia: 1000 - 1400 reindeer in Altai, 3000 in Tuva, 1200 - 300 in the western Sayans and approximately 6000 - 7000 in the eastern Saynas (Sokolov, 1983). Is it only the balance between reproduction and death that determines the stability of these populations? Or are there some internal mechanisms of population homeostasis?

Changes in female fertility and survival of calves account for the large changes in rates of increase of a population. In caribou over 50% of yearling females (12-23 mo. old) may be infertile (Parker, 1981): Fertility depends of their physical development: at 53 kg the probability of pregnancy is 8%, at 57 kg it is 75% and all females weighing over 67 kg will normally be pregnant (Thomas, 1982). Pavlov *et al.*, (1985) found 53.7% barren individuals among 3 year old females. Among the females of 4 years and older infertility was low and changed little between years, varying form 12.3 to 17.4%. These authors believe that many female calve at intervals so that on the average a female gives birth to 4 - 11 calves during her lifetime.

There is no doubt that the number of males born is larger than that of females, but males are less likely to survive. Young and old males do not participate in the rut and the male: female ratio in mating groups in 1:5.3 (range = 1:2 to 1:8) (Fil, 1976). In domestic tundra reindeer the male: female ratio in rutting groups is 1:18 and the majority of females are covered, since the animals keep in compact groups. The average percentage of barren females in reindeer populations is 8.45 (Baskin, 1983).

It is often thought that nomadism can, in some critical situations, be a major component in population regulation. Reindeer move when food is in short supply. The greater the lack of food the more they are likely to move. The question of whether the frequency of contacts with conspecifics may, in accordance with Wynne-Edwards' (1962) hypothesis, be one cause of migration still remains controversal. We can now distinguish at least 5 types of reindeer populations: (1) Forest montaine - the size

of populations is small, their numbers are constant, migrations are both vertical and horizontal, sociality is low and variable; (2) Forest sedentary populations - population density is low, migrations are short and associated with seasonal change of habitats, sociality is minimal; (3) Forest migratory - population fluctuations are minimal, population density is relatively high, migrations are consederable, sociality is moderate; (4) Forest-tudra migratory - large populations (up to several hundred thousand animals), density is moderate, population fluctuations are small, ingrations are small, sociality is considerable. Populations on Arctic islands can be considered as a variant of this type (Kuprijanov *et al.*, 1985): numbers usually remain low on account their poor habitat but may occasionally increase at which time a tendency to migrate appears.

References

Allee, W.C. 1939. - *The Social Life of Animals. London,* 293 pp.

Arefyev, A.A. and Chechukov, Yu. V. 1981. On changes of lichens proportions in winter diet of reindeer. - *Magadansky olenevod,* 33:18-19. (in Russian).

Azarov, V.I. 1976. On migrations and changes in wintering grounds of wild reindeer in the basin of Konda river. - *Byulleten Nauchnoissledovalentskogo institute selskogo khozyaistva krainego severa* 12-13:3-5. (in Russian).

Baskin, L.M. 1970. - *Reindeer: Ecology and Behavior.* (Severnyi olen: Ekologia i povedeniye). Moscow, Nauka Publication, 150 p. (in Russian).

Baskin, L.M. 1983. The causes for reindeer mortality. - *Acta Zoologica Fennica* 175:133-134.

Baskin, L.M. 1989. Pastoral husbandry. - In: Hudson, R.J., K.R. Drew and L.M. Baskin (Eds). *Wildlife production systems.* Cambridge, Cambridge Univ. Press (in press).

Bergerud, A.T. 1974. The Role of the Environment in the Aggregation Movement and Disturbance Behaviour of Caribou. - In: Geist, V. and F. Walther (Eds.). *The Behaviour of Ungulates and its Relation to Management.* IUCN Publ., New series, 24 (2), Morges, Switzerland, pp. 552-548.

Brown, W.K., Hout, J., Lamothe, P., Luttich, S., Pare, M., St. Martin, G. and Theberge, J.B. 1986. The distribution and movement patterns of four woodland caribou herds in Quebec and Labrador. - *Rangifer Special Issue No.1:* 43-50.

Cameron, R.D., Whitten, K.R. and Smith, W.T. 1986. Summer range fidelity of radiocollared caribou in Alaska's Central Arctic herd. - *Rangifer Special Issue No.l* 51-56.

Carruthers, D.R. and Jakimchuk, R.D. 1986. Caribou of the Central Arctic Region of Alaska in relation to adjacent caribou herds. - *Rangifer Special Issue No. 1* 65-72.

Dau, J.R. & Cameron, R.A. 1986. Effects of a road system on caribou distribution during calving. - *Rangifer Special Issue No. 1* 95-101.

Druri, S.M. 1952. Transplantation of tundra reindeer into the forests zone. - *Summary of Candidate Dissertation* Leningrad, 14 p. (in Russian).

Fil, V.T. 1976. Some properties of ecology and of exploitation of reindeer in the south of Kamchatka. - In: *Dikiy severnyi olen'.* Norilsk, NIISKh drainego severa, pp. 99-102 (in Russian).

Geist, V. 1987. On the reproductive strategies in ungulates and some problems of adaptation. - In: Scudder, G.G.E. and Reveal, J.L (Eds.) *Evolution today. Proceedings of the Second International Congress of Systematics and Evolutionary Biology,* pp. 111-132.

Gunn, A. and Miller, F.L. 1986. Traditional behaviour and fidelity to caribou calving gorunds by barrenground caribou. - *Rangifer Special Issue No. 1* 151-158.

Klein, D.R. 1968. The introduction, increase and crash of reindeer on St. Matthew Island. - *J. Wildlife Management* 32:350-367.

Klein, D.R. 1985. Population Ecolgy: The interaciton between Deer and their Food Supply. - In: Fennensy, P.F. and Drew, K.R. (Eds.) *Biology of Deer Production. The Royal Society of New Zeeland, Bulletin.* 22:13-22.

Kupriyanov, A.G., Belikov, S.E., Randle, T. 1985. Reindeer on Arctic islands. - *Priroda* 3: 46-51 (in Russian).

Mashdovtsev, A.A. 1940. Biological and physiological significance of sex dimorphism in vertebrates (a neuro-emotional theory of sex cycles). - *Doklady AN SSSR* 27 (1):91-94 (in Russian).

Pavlov, B.M. Arsentyeva, N.F., Borzhonov, B.B., Dorogov, V.F. and Kuksov, V.A. 1985. Demographic structure of the Taimyr population of wild reindeer. - In: *Ekologia, okhranai khozyaistvennoye ispolzovanye dikikh severnych olenei. Novosibirsk, Sibirskoye otdeleniye Vaskhnil,* pp. 71-89 (in Russian).

Parker, G.R. 1981. Physical and reproductive characteristics of an expanding woodland caribou population in northern Labrador. - *Canadian J. of Zoology* 59 (10):1929-1940.

Pruitt, W.O., Jr. 1960. Behaviour of the barrenground caribou. - *Univ. of Alaska, Biological papers, 3.* 44p.

Semenov-Tien-Shansky, O.I. 1977. - *Reindeer.* Moscow, Nauka Publ., 94 p. (in Russian).

Sololov, G.A. 1983. The wild reindeer of the mountains of the south of Siberia. - In: *Dikiyi severnyi oleni Sbronik trudov CNIL Glavohoti RSRSR,* pp. 122-130. (in Russian).

Thomas, D.C. 1982. The relationship between fertility and fat reserves of Peary caribou. - *Canadian J. of Zoology,* 60:597-602.

Valkenberg, P. and **Davis, J.L.** 1986. Calving distribution of Alaska's Steese-Fortymile caribou herd: a case of infidelity?. - *Rangifer Special Issue No 1.* 315-324.

Wislocki, G.B. 1943. Studies of growth of deer antlers. - In: *Essays in biology.* Los Angeles, Berkeley, pp.629-653.

Wynne-Edwards, V.C. 1962. *Animal dispersion in relation to social behaviour.* London, Oliver, Boyd, 653 p.

Yakushkin, G.D. 1976. Characteristics of herding of wild reindeer of the Taimyr population. - *Byulleten Nauchno-issledovatelskogo instituta selskogo khozyaistva krainego severa* 12-13:106-109 (in Russian).

Zyryanov, A.N. 1976. The state of the population by commercial explotation of the wild reindeer in the upper Lena taiga. - *Byullenten Nauchno-issledovatelskogo instituta selskogo khozyaistva krainego severa* 12-13:17-19 (in Russian).