hypothesis concerning the morphogenesis in moose antlers

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Abstract: From the evidence of fossil antlers in the Alcini, the morphological changes throughout ontogenesis of moose and the use of antlers in intraspecific communication, it is suggested that the genus Alces developed from smaller ancestors adapted to more dense cover than the present boreal taiga or open tundra. There is evidence that palmate antlers developed similarly to those of the palmicorn cervids from cervicorn types that have better "flight-form" (streamlined for flight) and better structural characteristics for encounters at short distances. Antlers with frontally oriented palms are probably for threat at long distances. The peak of this trend was reached in Alces latifrons. In recent Alces, in addition to the basic cervicorn antlers whose structure can be traced in the palm, we have two main palmicorn types: the shell-like palm and the split-palm. In the latter one the brow-tine is a more or less separated palm. It is hypothesized that the split or butterfly type is more recent than the shell-palm. Better documentation about ontogenesis and antler shapes would allow better insight into antlerogenesis in moose.

1 Portions of the studies on free living moose in Alaska were supported by the Swiss Foundation for Alpine Research. This paper is dedicated to the 70th birthday of Mr. Karl Weber (deceased), past-President of the Swiss Foundation of Alpine Research.
Until now little attention has been paid to the ontogeny of the construction of moose antlers in particular and to the relationships between antler constructions in the whole tribe *Alcini* (Simpson 1945) (or subfamily, *Alcinae* Jordan, Haltenorth 1963) in general. The attempts of Pocock (1933) and Beninde (1937) do not represent a satisfactory solution. They are not based on any direct studies with moose antlers. The construction schemes in Pocock's view (op.cit.) are based on the idea that all constructions are homologous and Beninde (op.cit.) homologized only those constructions which apparently have the same type of branching. From my previous studies (Bubenik 1959, 1962, 1966 and 1971a) it is evident that not all similar antler shapes have the same construction plane, that there are microstructural differences with species-specific characteristics and that the true dichotomous structure can be recognized only on the basis of two large channels vascularizing each of the future beam branches (Fig. 1).

We have no evidence that the evolutionary history of antler structures cannot be traced back in the ontogenetical steps in antler development. From our present knowledge we can follow the antler evolution in the pedicle history in the embryos and fetuses (Frankenberger 1951) of the species concerned.

The morphogenesis of antlers in *Alcini* can be traced back to the later part of upper Pliocene. Some further clues to the evolution of the antlers in this tribe are evident in
Figure 1. Cross-sections of beams of antlers with monopodial branching or dichotomous ramification. The large black dots represent the main blood supply channels.

The ontogenesis of recent moose (Alces Gray) (Fig. 2). In this genus we can distinguish three different antler forms:

the cervicorn type, which has to be considered as a construction form precedent to the other ones; the full-palmicorn type and the split-palmicorn type (Skuncke 1949, Kahlke 1956, Kaplanov 1948). Because the Cervicorn pattern is retained in the ontogeny, any palmicorn population can produce a variable number of specimens with cervicorn antlers if the environmental
or social pressure inhibits the hypertelical growth between the tines necessary for palmation. When searching for the distribution of antler patterns in moose, such variability must be taken into account.

By carefully eliminating incidental occurrences of cervicorn or other incompletely developed types we find that there are three where specific antler shapes are evident (Fig. 3). First there is the Manchurian "short-leg" moose (Alces alces cameloides) inhabiting N.E. China and the basins of the Amur and Ussuri Rivers. The moose populations here are reported to be only cervicorn. I agree with Heptner and Nasimovich (1967) that the Manchurian moose represents the most primitive form in Alces: It probably belongs in the assemblage of preglacial forms for which that area is known as a refugium. The full-palmicorn type or shell-type seems to be specific for moose of West Siberia and Europe; i.e., to the subspecies Alces a.alces. When the split-palm, which could be called butterfly-type, occasionally occurs the lobe is more or less poorly defined. Farther to the east, from Outer Mongolia through East and N.E. Siberia and over the whole of North America, the butterfly-palms are dominant. This is the distribution area for the subspecies of moose: A.a.pfitzenmayeri, A.a.gigas, A.a.andersoni, A.a.americana, and A.a.shirasi (Peterson 1955).
Figure 2. Typical shapes of antlers in recent moose.
Figure 3. Distribution of antler constructions in moose (Alces Gray).
COMPARISON OF ANTLERS OF RECENT ALCES WITH THOSE OF EXTINCT ALCINI

From the extinct genera Pseudalces (Flerov and Shevyreva 1963), Tamanalces (Vereshchagin 1967), Libralces (Azzaroli 1953) and Cervalces (Scott 1886) only the last two can be accepted as true Alcini. Pseudalces and Tamanalces are with distinct probability close to the Euctenoceros - Orthogonoceras (Kahlke 1956) group which includes only plesio-metacarpal cervids. These belong to the Old World group of Cervinae Baird. It is the view of Flerov (1950, 1952) and Vereshchagin (op.cit.) that Alces is of cervine and not neocervine (Neocervinae Carette) origin. But outweighing the cervine-close skull characteristics there are not only the metacarpal bones, but also the antler ontogenesis and antler construction and some behavioural elements like the "horse-shoe" posture during urination (Geist 1966, Bubenik 1973), and the use of brushes of tarsal glands in the neocervine-manner for trail marking (Bubenik 1971b). All these characteristics point out that Alces and Alcini must have Odocoileinae (Pocock) ancestors.²

Under such a view we have to deal only with two extinct genera, Libralces and Cervalces of which the first one is the older (Fig. 4). Its history can be followed up to the earliest

²Our recent macroscopical investigations on the structure of the core of some fragments of antler beams in Libralces from The British Museum, Department of Paleontology, London, gave no evidence to support one or two channels vascularizing the spongiosis. (see also, p. 209, Figure 9).
Figure 4. Antlers of two extinct members of the subfamily Alcinae.
Pleistocene, the Villafranchian (Azzaroli, op.cit., Kahlke op.cit., Kurten 1971, Reynolds 1934, Vereshchagin op.cit.). Cervalces is much more recent and most resembles the present and Middle Pleistocene moose. Remains of both appeared first in the Middle-Pleistocene, shortly before Libralces died out. The Libralces population inhabited nearly the whole Eurasiatic continent from England to the Aldan River in N.E. Siberia (Vereshchagin op.cit.). Cervalces is known only from Alaska, Canada and the northern part of the U.S.A. (Frick 1937).

The views about the evolutionary relationships between these three genera differ substantially. Dawkins (1887), Pohlig (1909), Soergel (1918), Hennig (1952) all cited by Kahlke (op.cit.) assume that Alces originated from Libralces. Thénius and Hofer (op.cit.) did not try to refute this view. Libralces evolved a shorter beam through its history. Furthermore, the shell-palm of the European moose is relatively similar to the crescent-like palm in Libralces: these factors could suggest a close evolutionary relationship. But Vereshchagin (op.cit.) considers (in free translation from Russian) that "there are serious reasons to doubt the evidence that the direct ancestor of recent moose was Libralces", but he suggests that "It is very probable that Cervalces and Libralces had a common ancestor".
ANTLER CONSTRUCTIONS IN ALCINI

By antler construction I refer to the basic pattern of beam ramification or branching in prime unstressed specimens (Beninde 1937, Bubenik 1966, 1971a, 1973, Pocock 1933, (Fig. 5). Palmated antlers often prevent the recognition of the structural pattern. In the palmated species, it is, therefore, necessary to compare antlers from young specimens and/or from those primes whose antlers were developed under inadequate trophic conditions. Moose antlers are in this category.

The most simple structural pattern in the Alcini is the cervicorn "monopodium" (Beninde 1937) with at least two true tines; i.e., the brow and trez (Fig. 6). These tines originate from the fronto-lateral edge of the beam similar to Rangifer or Cervus antlers. The burr or shaft is Neocervine-like; in the first one or two sets it remains relatively short but is bent upward (Fig. 7). In older specimens the shaft is longer and more or less horizontal. By secondary dichotomy of tines and beam-tips the cervicorn construction can easily become palmicorn.

The ramification pattern in Libralces antlers seems to be more obscure. From the oldest Libralces gallicus with the longest shafts up to the youngest L. latifrons with relatively short burrs (a woodland inhabitant?) (Fig. 8) we do not have large enough fragments of antlers from the first or second set, nor from prime antlers with simplified structure to identify,
Figure 5. Basic scheme of evolution of antler construction.
Figure 6. Ontogenosis of cervicorn antlers in moose (Alces alces).
Figure 7. Angle of palms in antler ontogenesis.
Figure 8. Trend of evolution in antlers of Libralces through the Pleistocene (Kahlke 1956).
with accuracy, the basic pattern of ramification. Neither do we know if the burr has one or two wide channels which is diagnostic of the basic construction pattern as shown in Fig. 1. We can only assume from Tables 1 and 3 in Kahlke (op.cit.) that the crescent-like palm of Libralces cannot originate from a monopodium, but only from dichotomous ramification (Fig. 9).

Figure 9. Probable branching pattern in two analogous palmate antlers.
This suggestion is supported by the knowledge that the majority of the oldest antler constructions is dichotomous. Following the scheme of evolution of antler structures (Fig. 5) the next evolutionary step can then follow from one or two possibilities: both of the ends can remain as equivalent beams, or one of them can degrade to a tine (Bubenik 1966). In the first case the dichotomous process will continue, in the other one a monopodium will result. Primary or secondary dichotomy is a general rule in antler development. It can be influenced temporarily by a surplus of nutrients but it belongs to species-specific patterns.

Building upon this argument we have to conclude that in the Lower or Middle Pliocene there was probably a group of neocervids with more horizontally than upright oriented pedicles, and relatively long but elevated burrs, with forks on the ends (Fig. 10 A_1-A_2). We suggest that in this group, which we could call "Eoalces" there must be populations in which either the dichotomous ramification or monopodial trend (i.e., with two or only one channel in the burr) in the forks was dominant (Fig. 10, B-E). Perhaps the first type inhabited more open, the other one more forested, habitats. Perhaps the monopodial construction could evolve through disappearance of one channel from the dichotomous one. The dichotomous pattern could in open habitats develop much faster because the antlers gained
Figure 10. Pattern of probable evolution of antler construction in Alcini.
more influence as optical and social releasers (Bubenik 1968, 1973). The burrs could be longer and dichotomy more luxurious. These descendants of *Eoalces* could also display two variants: one with forking points close together and the other ones with distant forking (Fig. 10, B, right and left). We could call them "*Plioalces*". They could be the ancestor for *Libralces* and *Cervalces* as is suggested by Vereshchagin (1967), (Fig. 10, C, D). The crescent-like palms of *Libralces* probably resulted from close forking; the double-split (triple-lobed) palms of *Cervalces* could be a variant with distant forking. The more flexible lobed construction of *Cervalces* permitted greater curvature of the tines and palms than is the case with the compact, crescent-like shape with short and thick points of *Libralces*.

In my opinion this hypothesis has at least two weak points: Why did the *Cervalces* group appear so late when it was so closely related to *Libralces* and why could *Cervalces* not be a species originating from hybrids between *Libralces* and *Alces* in the sense of Geist's theory (1971) on evolution in Cervids? The logical explanation could be that ancestors of *Cervalces* tended to be woodland inhabitants. They have shown the slower evolution of optical releasers which would be expected in a forested habitat. It is possible that in the Pliocene *Cervalces* could not compete successfully with the *Libralces* group or other more successful species.
The application of Geist's theory (op.cit.) seems unacceptable for reasons which we will discuss later.

The evolutionary trend toward Alces is easier to predict. As an intermediate stage we have to assume a "Proalces" group with brow tine and beam; i.e., with monopodial pattern of branching (Fig. 10, A2-E-F). From the "F-variant" the first Alces primigenius (Fig. 10, G-I), (equivalent or close to A.a.cameloides) had to be derived. We assume that in this group there were also variants with close and distant forking patterns (Fig. 10, F, right and left) which finally led to the full and butterfly palms, displayed in the recent moose (Fig. 10-H-J).

ENVIRONMENTAL AND BEHAVIOURAL IMPACT ON ANTLER CONSTRUCTION AND ARCHITECTURE

Our hypothesis concerning the evolution of moose antlers is based on knowledge about similar processes in other cervicor species. The main idea is that the antler evolution is controlled by structural genes with a very complicated code. For each new structural development there can be two or more interrelated changes. In the first, explosive phase of any new development, there must be displacement or suppression of other structural elements competing for function and space (Bubeník 1966). The following structural changes can evolve: reversal of
tines from frontal to dorsal orientation, switching to dichotomous forking, or to three dimensional features (Fig. 5).

The theory of Geist (op.cit.) that new cervid species evolved by hybridization is hard to accept. One of the fundamental laws in ethology (Lorenz 1965a, Wickler 1970) is that behavioural elements are not only very important taxons but also serve as isolating mechanisms. I have studied a male hybrid between sika (Sika dybowskii) and red-deer (Cervus elaphus hippelaphus). Conforming to the general rule that the primitive species dominates in hybrids between evolutionarily distinct species, this male was in appearance and behaviour closer to sika than to red-deer. The differences in behaviour were so great that this male chose to live in the herd of fallow deer (Dama dama). It is likely that sika deer and fallow deer are more closely related than sika are to red-deer. Moreover, the reference used by Geist in support of his theory in Heptner et al. (1961) is doubtful. Heptner quoted Menard (1930) who referred only to deliberate hybridization attempts in sika deer parks. Hybridization in free living populations in Manchuria is reported by Maak (1859) as quoted by Menard (1930). Maak did not see any hybrids and, furthermore, did not know which kind of deer lived there. He described the sika deer as fallow deer. Geist did not pay any attention to the footnote to this paragraph (p. 106) in which G.F. Bromlej
stated that hybridization is rare between the mentioned species in the Far East. This is also recorded from Europe (Wettstein 1931), from Ireland and New Zealand where sika deer has been introduced and is forced to live together with red deer (Delap 1967, 1968a,b, Gray 1966, Kiddie 1962, MacNally 1969, MacTaggart 1969, Mitchell 1972).

ENVIRONMENTAL PRESSURE ON ANTLER EVOLUTION

Antlers are organs that project from the body. It is to be expected that the antler construction should be adapted to the frictions to which the antlers are exposed. This means that the physical properties of the environment can modify size and structure to the extent that the flight of the animal will not be obstructed. Therefore, cervids originating and surviving in dense cover have never developed oversized antlers or complicated construction which do not have the necessary streamlined, cover penetrating "flight-form". Even if social pressures favour the largest possible and most sophisticated antler construction, they could develop only in environments in which at least the head of the animal was not exposed to any kind of hard objects. In open environments the antlers evolved as dominant optical releasers (Bubenik 1971a,b, 1973). They sometimes reached immense dimensions but regardless of the size the "fleeing-form" has always incorporated aerodynamic shape and architecture compatible with high wind velocities (Fig. 11).
A = *Libralces latifrons*,  
* B = *Dolichodoryceros süsennbornensis*,  
* C = *Euctenoceros sedgwicki*,  
* D = *Cervalces scotti*,  
* E = *Megaloceros hibernicus*.  

*From Bubenik 1966*

**Figure 11.** Spectacular diversification of antlers of extinct cervids inhabiting open landscapes during the Pleiocene - Pleistocene.
For many cervid species it can be shown that there are constant relationships between the physical properties of different habitat horizons and the body shape, colouration pattern, behaviour and antler construction. In Table 1, we chose some of these elements related to the antlers. Under the assumption that the different ontogenic constructions may reflect the evolutionary history of organs (Rensch 1972), Wickler 1970) we have to deduce that antlers and the antler selection by the environment in at least some of the species, developed and remained under the same environmental impact and others evolved under the pressure of two different habitats. It is most important that the penetrating "fleeing" architecture is well expressed in the first two sets of moose antlers (Fig.11). Beginning with the third set, the antlers start to be more and more open and aerodynamic. In full prime bulls between the 5th and 12th sets of antlers, the palms are nearly parallel with the head profile or perpendicular to the body axis and ready to display their size and shape when the head is lowered.

I have very few records of the uses of antlers for frontal threat in one and two year old bulls with cervicorn antlers. None of them have used their antlers in frontal display like the prime palmicorn bulls. It is difficult to generalize from these few observations. From the references available (Altmann 1959, Bromee 1940, Geist 1963, Heptner and Nasimovich op.cit., Kaplanov, op.cit., Markgren 1969, Seton 1953) it is not clear
Table 1. Physical Structure of Environment and Ontogenesis of Antlers.

<table>
<thead>
<tr>
<th>A) GRASS, BRUSH OR TREE COVER OVERTOPPING THE HEAD</th>
<th>B) GRASS OR BRUSH COVER UP TO THE HEAD HEIGHT OR HIGH FOREST WITH LOW BRUSH ZONE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) AS PRIMARY AND PERMANENT HABITAT</td>
<td></td>
</tr>
<tr>
<td><strong>Pedicles</strong> parallel, streamlined with head long or short; or horizontal and short</td>
<td><strong>Pedicles</strong> divergent, elevated from forehead, shortening with age</td>
</tr>
<tr>
<td><strong>Antler construction</strong></td>
<td></td>
</tr>
<tr>
<td>all antler parameters and characteristics stable throughout the ontogenesis</td>
<td></td>
</tr>
<tr>
<td>simple architecture streamlined (Flight-form) for penetrating plant cover</td>
<td>complicated architecture variable</td>
</tr>
<tr>
<td><strong>Dominant releaser</strong> is colouration pattern of body</td>
<td><strong>Dominant releaser</strong> is antler</td>
</tr>
<tr>
<td>Examples: muntjac, roe deer, axis, rusa, sika, Manchurian moose</td>
<td>Examples: Libralces, Megaloceros, Euctenoceros, red deer, wapiti, woodland caribou, mule deer</td>
</tr>
<tr>
<td>2) AS SECONDARY HABITAT</td>
<td></td>
</tr>
<tr>
<td><strong>Pedicles</strong> divergent; no adaptation to the new environment</td>
<td><strong>Pedicles</strong> parallel or horizontal, no adaptations to the new environment</td>
</tr>
<tr>
<td><strong>Antler construction</strong></td>
<td></td>
</tr>
<tr>
<td>follows the adaptation processes first sets and the lower part complicated upper part simplified</td>
<td>first sets and the lower part streamlined with &quot;Flight-form&quot; upper part complicated and aerodynamic</td>
</tr>
<tr>
<td><strong>Dominant releaser</strong>; colouration and antlers can compete</td>
<td><strong>Dominant releaser</strong> is antler</td>
</tr>
<tr>
<td>Examples: barren gr. caribou, Mesopotamian fallow deer, Atlas and Bocchara red deer, white-tailed deer</td>
<td>Examples: red deer, fallow deer, Barasingh deer, moose</td>
</tr>
</tbody>
</table>
if cervicorn bulls use the same kind of frontal display. It is difficult to decide if the frontal presentation of palmicorn antlers in moose is strictly connected to the architectural changes from cervicorn to palmicorn antlers in evolution or only in ontogenesis.

Nevertheless, the fact that the antler surface created by beam and tines in the first set of antlers is streamlined for dense habitat and the mature construction is aerodynamic, leads us to the conclusion that the evolutionary history of \textit{Alces} involved two habitats with different physical properties. We assume that the ancestors of \textit{Alces} inhabited dense cover overtopping their heads. Later they changed to parkland or tundra and the shape and architecture of the cervicorn type was modified to the palmicorn and aerodynamic one.

For this hypothesis we can offer further evidence. In typical Scandinavian woodland and Ontario taiga moose, the antlers represent an intermediate stage between an aerodynamic and dense-cover flight form. The burrs are shorter, the palms not divergent and the outer parts of palms cup together with the points bent foreward.

From the evolutionary history of \textit{Liberalces} we know that the nasal bones needed several hundred thousand years to shorten to a degree close to \textit{Alces} (Thenius and Hofer 1960). Long nasal bones are specific for ungulates whose noses have
to penetrate the cover. Short nasal bones are developed in species living traditionally in habitats in which the nose is not exposed to obstacles like in the saiga (Saiga tatarica) or tylopodes (Haltenorth op.cit.).

The bell of the moose raises another evolutionary question which could support our hypothesis. Sokolov (1964), referred to by Heptner and Nasimovich (op.cit.), found that the bell has no secretory function. Zschetsche (1959) disagreed and reported that the bell has a channel opening into the bell's surface and that it has secretory activity. He also refers to observations by Krott and Krott that the bell is used for olfactory marking and individual recognition in encounters. Following Knorre (1959), the change between the long bell of young bulls and the short one in primes is due to a partial atrophy which occurs in two year old males (in Ontario moose it may occur later) in the spring. Knorre points out that the bell is slightly developed in some fetuses. We could conclude that the bell might be a very old accessory organ which lost its importance during the evolution. Why should this occur?

If the bell is really an olfactory organ, at least in the first two or three years of life, then we can assume that it was used to leave an olfactory trace in the horizon closest to the nose; i.e., on plants surrounding the head and rubbed off on the nose and the bell. We could assume that when Alces adapted to a new open habitat the bell lost its importance.
There is another morphological change through ontogenesis indicating changes in habitats through the evolutionary history of moose. The interdigital glands of hind legs in calves and yearlings according to Heptner and Nasimovich (op.cit.) are more dense, and they cover larger areas, are deeper in the skin and more active than in prime animals. In comparison to significance, appearance and degeneration of olfactory glands in other boreal cervids (Bachnová 1957, Haltenorth op.cit., Schumacher 1939) we have to conclude that the earliest ancestors of Alces were inhabitants not only of dense cover but that they were relatively short legged animals like the Manchurian moose, for which it was not difficult to perceive the odours in the tracks. In connection with this it is interesting to note that the majority of moose lack the metatarsal gland (Haltenorth op.cit.) which plays an important role in the social life of the Nearctic bush-inhabiting cervids (Bubenik and Smith, unpubl. data, Hershkovitz 1958, Müller-Schwarze 1971).

THE SELECTIVE PRESSURE OF BEHAVIOUR ON THE ANTLERS

The construction and shape of antlers are not only influenced by the environment, but also by the behavioural demands of social releasers and offence and defence. The larger the antlers and tines the greater their capability for offense, but it is not the main goal of social interactions to evolve dangerous
weapons (Lorenz 1965b, Portmann 1953, 1960, Bubenik 1966, 1971a, 1973a). Thus forking in antlers permits a male to hold his opponent's antlers and prevent physical damage. Tines bent from the axis of attack can do less damage than straight ahead orientation. Palmate antlers make clumsy weapons but highly visible display organs. Thus antler structure incorporates defensive elements which outweigh their offensive capability. The brow and bez tines in _Cervus_ species function to shield the forehead, orbital region and parietal bone. In species with long burrs (_Odocoileinae_) either the coronets can shield the whole forehead as in _Capreolus_ (Bubenik 1971c) or long knobs, pearls and prongs are produced between the burrs, or the beams are bent together (_Odocoileus_) to lock the unprotected "window" to the parietals.

Some elements of this trend are also seen in the development of moose antlers. The first two sets, or the cervicorn antlers, in general have more offensive than defensive elements. The tines are long and the brow-tine is oriented foreward or sideways. Neither the forehead nor the parietals and eyes are especially protected. Because practically nothing is known about the use of such antlers we cannot say if in such specimens special courtship patterns exist which diminish their offensive structure. Rival wapiti (_C. canadensis_) whose antlers are extremely offensive, prefer to have a solid barrier, such as a wind-fall between them (Bubenik 1973).
In recent cervids the small cervicorn antlers are either of very low social significance or must be seen at relatively short distances to estimate the rank or individuality of the antler-bearer. Palms in general serve as long distance releasers, in which reflecting light plays a role (Bubenik 1966, 1972b, 1973).

In palmate moose the palms are used mainly in display by lowering the head or using a rocking, swaying gait (Altmann 1959, Bubenik 1972b). The full-palm antlers represent a relatively archaic structure. They are very efficient visual display organs with poor protective architecture. Their tines are relatively straight and the inner points in the lower part of the palm are too far apart to efficiently protect the face.

The butterfly or split-palm must be regarded as a more advanced architecture. By separating the lower part of the palm thus creating a great distance between the brow-palm and trez-palm an excellent shield is provided on either side of the eyes. The larger the palms and the closer the inner points the better the shield should be.

There are almost no data available on this point. I have seen a deep wound on the nasal bones of one moose which lacked efficient brow tines.

In red-deer it is well known that the loss or failure of the brow or trez-tine leads sooner or later to the loss of the
corresponding eye (Benzel 1967, Bubenik 1968). It would be of great importance to get some data about blind moose and their antler construction.

My own studies with North American moose in Alaska and Ontario lead me to believe that these species have in their antlers a potent optical releaser which overwhelms all others. Their antlers act as releasers for both sexes and my studies with moose dummies have shown that antlers in moose play an important role, not only as symbols of rank, but also as a sexual attractant (Fig. 12). To date I know of no other species in which the antlers have reached such a grade of importance in social relationships. I was surprised how accurately the bulls can estimate the individual rank of their antlers, and how precise their response is to antlers of lower, higher or the same rank. It was a pleasure to work with the dummy and communicate with bulls and cows like a conspecific because the releasing power of the antlered head overwhelmed all other releasers including the human scent.
Figure 12. Moose displaying towards a dummy.

CONCLUSIONS

We have submitted a hypothesis about the origin of the construction in moose antlers. We know well that our assumptions could be wrong because there is not enough comparative information on the evolutionary history of the Alcini and also not enough data about recent moose. For us the weak point in the hypothesis is the assumption that in moose, like in other cervids, the changes in ontogenesis of antlers recapitulates the evolutionary pattern and that the basic plan is really homologous to the monopodial branching in cervid construction. But it is the
destiny of any hypothesis to be refuted by new data or to be verified. Each hypothesis is in some manner a threat to longheld views; this one should mobilize attention to an organ which has been neglected. I hope that this hypothesis will attract attention and bring us closer to understanding the evolution and function of moose antlers.

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