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On the Relationship of Ecology and Behaviour in the Evolution of Ungulates: Theoretical Considerations

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ABSTRACT

It is possible to show from paleontological data that ungulates evolved in a predictable fashion. Lineages which evolved, changed in pre-Pleistocene epochs towards larger body size, larger and complex horn-like organs, and often greater dental specialization. Other forms remained frozen in evolutionary development over long geologic time spans. The Pleistocene accelerated evolution in the direction indicated and produced many large-bodied species with huge and bizarre horn-like organs unequalled in earlier times. An examination of the zoogeography of living and extinct forms, a consideration of bioenergetic factors impinging on the biology of periglacial and warm-climate ungulates, and a short examination of a theory explaining ungulate evolution during re-colonization of areas after glacial withdrawal, allow one to explain many aspects of ungulate evolution. It can be shown that evolutionary advancement is irreversible since breeding is the prerogative of dominant males, that evolutionary stagnation occurs in ungulates living at carrying capacity, that clines of races reflect not ecological gradients but the dispersal history of that species, that ecological and social specialization run parallel in the tropical climates but not necessarily in the periglacial zones, that longevity of species is related to ecological and social primitiveness, that rates of evolution were accelerated in the Pleistocene due to many glacial withdrawals which gave the opportunity to disperse, and that the bizarre, large horn-like organs are a product of the seasonal superabundance of forage in the short summer in temperate or arctic regions due to the high nutritional value of forage grown in the arctic or temperate regions as well as due to selection pressures for intense combat in colonizing, post-glacial populations.

INTRODUCTION

In the past decade the publication of such superb texts on the paleontology of mammals as the volumes by Thenius and Hofer (1960), Orlov (1962), Romer (1966) and Kurtén (1968), as well as the republication of Scott's (1937) excellent work on the history of land mammals in the western hemisphere, have placed the findings of paleontology in condensed and comprehensible form into the hands of other disciplines. The past decade also witnessed a blossoming of detailed field studies on the ecology and behaviour of large mammals. This has made it possible to begin a synthesis of the findings in these fields due to two fortunate circumstances. First, the remains of large mammals are better preserved and more numerous than those of small mammals. This has permitted the reconstruction of evolutionary lineages with adequate detail. Secondly, many large mammals possess conspicuous social adaptations in the form of antlers, ossicones, horns, tusks as well as skeletal structures apparently adapted to absorb severe impacts during intraspecific combat (Walther, 1958; Geist, 1966b, c and 1971a; Schaffer, 1968). Such structures are well preserved in the fossil record and provide considerable insight into social evolution in past epochs. This paper is a condensation of a theory linking ecological and social evolution elaborated in Geist (1971a) on the basis of studies of caprid and rupicaprid biology, and Geist (1971b) on the old-world deer, the genus *Bison* and several lineages of ungulates including proboscideans and perissodactyls. The theory, termed the *dispersal theory* was first proposed in simplified form in Geist (1966a). It was then termed 'glaciation theory', as well as in

Geist (1971a). In addition this paper will deal with aspects treated only peripherally in the earlier publications on this subject.

PALEONTOLOGICAL CONSIDERATIONS

If we examine the adaptations of living mammals as well as the fossil history of this class we can conclude that the evolution of mammals is generally a predictable process. We find that different stocks evolved into surprisingly similar animals, and we find that certain adaptive syndromes arose repeatedly. Such adaptive syndromes as 'sabre-tooth tiger', 'cat', 'wolf', 'mole' or 'mouse' evolved not only several times in therian mammals, but in the eutherian mammals as well. The adaptive syndrome 'rhino' appeared at least four times, if not more, in the Perissodactyla alone, namely in the rhinos proper, the aceratheres, diceratheres, brontotheres and maybe teleoceres; it appeared also in the embrithopods, Dinocerata and South American toxodonts. One can even make a case that the last of the dinosaurs, the ceratopsians, were good 'rhinos' also. Similarly the 'horse' was evolved in the perissodactyls twice, once in the familiar equid lineage and once in less perfect form in the cursorial rhinos (Hyracodontidae), as well as in the unrelated South American litopterans, in the family Proterotheriidae. In view of the great morphological similarities of the end products of convergent evolution that we encounter so often in mammals, the great behavioural similarities of convergent rodent lineages (Eisenberg, 1967), or the striking similarities in the behaviour of some African gazelles (Walther, 1964, 1965) with that of American pronghorns (*Antilocapra americana*) (Bromley and Kitchen, Papers 17 and 18 in this volume) should not be surprising.

An examination of individual ungulate lineages reveals that some have changed progressively in geologic time in a predictable, irreversible manner while others, illustrating Cope's rule, remained frozen in their primitive form and did not change markedly over long geologic time spans; some lineages show both processes. If lineages changed, the species evolved into ever larger forms with larger and more complex horn-like organs, and often—but not always—with more specialized dentition. The Dinocerata and the Brontotheriidae as illustrated by Flerov and Osborne respectively (see Thenius and Hofer, 1960) are examples of such change. Here ever larger species replaced each other in geologic time, changing in the manner indicated, but without noticeable specialization in dentition. The Protoceratines, a peculiar lineage of American ruminants, illustrate also progressive evolution, but here a specialization in cheek teeth from brachyodont to hypsodont types runs parallel with the evolution of horn-like organs and an increase in body size (see Scott, 1937). We notice the same in Pleistocene forms of *Dicerorhinus* when these adapted from forest to steppe to tundra (Kurten, 1968).

The best examples of lineages in which some forms froze in their evolutionary development and remained living fossils, while giving off lineages that evolved into larger and more bizarre forms, are the old-world deer and the rhino lineage represented by *Dicerorhinus* and *Coelodonta*. The Sumatran rhino of today (*Dicerorhinus sumatrensis*) appears to have changed little in size, cranial morphology and dentition from the Oligocene form of *Dicerorhinus* (Thenius and Hofer, 1960). In the northern, periglacial area *Dicerorhinus* evolved along expected lines to terminate in the large, heavy-horned woolly rhino (*Coelodonta*) that had a highly specialized skull and dentition. In the old-world deer, the Muntjacinæ, are essentially primitive deer, little changed since the early Miocene. While they remained essentially frozen in their evolutionary development, the Cervinini evolved in the direction outlined earlier to produce many huge-antlered giants. I have discussed the evolution of this group in some detail elsewhere (Geist 1971b). Both of these complex lineages also illustrate the great durability of generalized, primitive forms from the tropics and subtropics, and the susceptibility to extinction of specialized or bizarre forms. The same lesson can be learned by examining other lineages such as the Tayassuidæ, Suidæ, Tragulidæ, Rhinocerotidæ, Proboscideæ, Giraffidæ or Dasypodæ. Today we still find alive many primitive or generalized species while the fossil record is littered with extinct forms of large size odd horns and tusks, and specialized dentition and legs—the most striking being the horned armadillo *Peltephilus* (see Scott, 1937, p. 682), the horned and large-tusked pig

Stenocoerus (see Orlov, 1962, p. 487), the mid Pleistocene steppe rhino *Elasmotherium* or the giant sivatheres (*Sivatherium giganteum*) (see Orlov, 1962, p. 527). The durability of generalized forms versus the short-lived existence of bizarre forms requires explanation.

In addition to these observations we note that the Ice Ages accelerated the evolution of large mammals in an incredible manner and led to the appearance of grotesque forms unequalled in the complexity and size of horn-like organs by pre-Pleistocene mammals. The direction of evolution in individual lineages towards large body size, complex horn-like organs, and specialized dentition remained the same as in pre-Pleistocene epochs, but the rate of change increased. Such pre-Pleistocene lineages as the Dinocerata, Brontotheriidae or Protoceratidae lasted 10–20 million years; Pleistocene lineages like the true elephants, old-world deer, rhinos, caprids, bovids or even the Mastodontidae reached comparable evolutionary status and often extinction in usually less than two million years. It should be noted that antlers, horns, ossicones and tusks evolved during the Ice Ages in parallel towards large size and/or complexity in cervids, bovids, rhinos, giraffes and proboscideans. This is not surprising in view of the finding that these horn-like organs are used in a similar manner, and as such are analogous organs (Geist, 1966b).

These observations on mammalian evolution leave us with a number of questions. Why should most mammals converge into a lesser number of adaptive syndromes? For the present it is sufficient to answer that similar ecological professions probably require similar tools (in our case adaptations) for efficient exploitation of a given niche. The remaining questions cannot be answered that simply.

Why should evolution in some ungulates lineages invariably and apparently irreversibly proceed towards giantism, specialized social organs and often specialized dentition?

Why do some evolutionary stages in a lineage halt in their evolutionary advancement, stagnate and remain 'living fossils'? We find such stagnation within clines of living species such as in the genus *Ovis* or among old-world deer.

Why should ecological specialization as indicated in tooth structure parallel social specialization as indicated by form and size of horn-like organs in some lineages but not others?

Why should primitive, generalized forms have such great longevity compared to large and bizarre forms?

Why should the Ice Ages precipitate an acceleration of evolution in the same direction as in pre-Pleistocene times, and lead to the most bizarre ungulates ever to evolve?

1971a

ZOOGEOGRAPHIC CONSIDERATIONS

A first clue towards answering these questions comes from zoogeography. In the northern hemisphere, in the regions covered repeatedly by Pleistocene ice, we find ungulates of large size, bizarre horn-like organs and of recent evolutionary origin as indicated by the fossil record. In the tropics and subtropics we find many related, but relatively primitive and old species. This geographic distribution reflects Pleistocene and pre-Pleistocene evolution, as well as the complex dispersal of the animals.

Here we must deviate for a moment. A comparison of living forms considered primitive and advanced by modern taxonomic opinion, reveals that the advanced forms tend to be not only larger, have larger horns or antlers, and sometimes more specialized dentition, but also have larger rump patches, shorter and weaker tails, and occasionally enlarged skin glands. This is illustrated by the old-world deer (Geist, 1971b; Fig. 1, 2, 4), in the genera *Odocoileus*, *Ovis*—both in the Asiatic and again in the American sheep (Geist, 1971a; Fig. 43, 46), and *Capra*. We have here one of those silly correlations: in northern ungulates 'tail size' is inversely related to 'horn size'. Yet it is valid as can be seen not only in above forms but also in the living and extinct elephants, rhinos, and the genus *Bison*. Furthermore, in the genera *Ovis*, *Capra* and *Bison* there is in general an inverse relation between horn size and the amount of long hair on the body, such as manes, beards and robes (excepting *Capra falconeri*) (see Geist, 1971a).

b). It can be noted that the organs which change most, i.e. horn-like organs, hair patterns, rump patches and external skin glands, are intimately connected with the social behaviour of these ungulates. Since complex teeth and horn-like organs are often found together, this leads to the conclusion that somehow ecological and social evolution are connected, a conclusion which is not new. Eisenberg reached it earlier in his studies of rodents (1963, 1967) and more recently in tenrecs (Eisenberg and Gould, 1971). (The tenrecs, in particular, illustrate well that the ecologically most specialized form is also the most bizarre in appearance and most specialized in social behaviour.) Before that Cullen (1957) had drawn attention to the above relationship in a cliff-nesting gull. However, the conclusion was reached in a manner quite different from the above authors, and as such strengthens the hypothesis that ecological and social evolution are related. Again we turn to zoogeography. Examining the distribution of advanced and primitive races of northern cervids and caprids one notes that the primitive forms are found in glacial refugia and advanced races in glaciated zones (see Geist, 1971b: Table 1). A second examination reveals that the primitive races are at the geographic beginning of the dispersal of the species in post-glacial times and the advanced species are at the end point of the dispersal of that species. Races intermediate in physical characteristics between the primitive and advanced races occupy geographically intermediate positions. Put simply, the further a species moves, the larger the individuals become in body size, horn size, rump patch size, occasionally gland size, and the shorter the tail grows. We find such geographic clines and centres of post-Pleistocene dispersal in Asiatic sheep, American sheep, in the wapiti, the mule deer and to some extent also in the reindeer or caribou (Geist, 1971a, b). Clearly there is a close relationship here between post-glacial dispersal and social evolution.

One point needs to be raised: these living northern forms show little or no ecological specialization as indicated in tooth structure paralleling social evolution. There is precious little difference in the teeth of urials and argalis, thinhorn or bighorn sheep, red deer and wapiti, blacktail or mule deer. This runs counter to the apparent correlation found in the tropical and subtropical continents where tooth structure and such social adaptations as horns, or colouration appear to specialize in common, as is also confirmed by the fossil record, as well as by Eisenberg's studies on rodents (1963, 1965) and Eisenberg and Gould's (1971) study of tenrecs. It runs counter to a positive relationship between tooth specialization and tusk size in elephants or tooth specialization and wart and tusk structure in the living suidae, the positive relationship between ecological specialization and antler structure as found in the primitive deer of India, and the recent finding that the most specialized morphological species of baleen whales (*Megaptera*) has also the most complex song found among whales (Payne and Scott, 1971). We must now explain why the correlation between tooth structure (ecological) and social specialization is less pronounced in ungulates from the periglacial than from the subtropical and tropical zones.

BIOENERGETIC CONSIDERATIONS

The following may appear to deviate from the line of thought followed until now, but it is nevertheless relevant. The northern, temperate or periglacial regions are characterized by extremes in both forage production and availability to ungulates; it is an annual 'boom and bust' economy. The growing season is only 6-9 weeks in the north, but plant growth is intense. The winter is long, about eight months of the year, and the snow restricts ungulates to relatively small areas of favourable habitat. The life of ungulates in the northern zones is geared to these extreme conditions. The reproductive periods are timed with great precision. The rutting seasons are very short. Consequently the males are idle from sexual activity for all but a fraction of the year. Following winter, the individuals experience a superabundance of highly nutritious forage as they scatter over wide areas of new plant growth. Freed from the reproductive activity the males are free to grow, molt, fatten and store vitamins and minerals in preparation for the coming rut. Condemned to idleness and faced with a superabundance of food, the males are free to indulge in excessive horn growth as well as in the wasteful process of fat storage since nutrients are not limited. Lipogenesis is very wasteful of food energy (Blaxter, 1961), yet in the north the superabundance of forage makes the term wasteful meaningless. The fat is used advantageously by the

male during the short rutting season since it frees him from feeding in favour of engaging in courtship and dominance interactions; the large antlers or horns allow him probably to escape excessive combat since they tend to act as rank symbols. In the tropics, and in particular in the humid forests and savannahs, forage production does not fluctuate as severely as it does in the cold regions. The caloric density of plant tissues is much lower in the tropics and the fiber content of plant matter considerably higher than in the temperate and arctic regions (Jordan, 1971). Although in the tropics there is much more plant production than in the Arctic, the arctic plants have a much greater food value to a ruminant than the tropical ones. Since the maximum daily intake of energy for ruminants is directly proportional to the digestibility of forage (Blaxter *et al.*, 1961), it would appear that a ruminant from the temperate or arctic zones would have a much higher maximum daily energy intake during the vegetative season than would a tropical one. This suggests, assuming similar maintenance requirements, that a temperate or arctic zone ruminant would have a far greater surplus of energy for fat storage or antler-horn growth than would a tropical one. Therefore, not only a superabundance of forage, but also higher forage quality would generate an energy and nutrient surplus for cold climate ruminants in excess of that expected for tropical forms. As expected we do find that tropical deer and bovines have generally smaller antlers or horns than those from temperate zones, as I have discussed in detail elsewhere (Geist, 1971b).

Whereas in the cold climates breeding seasons are sharply limited, this need not be the case for tropical ungulates. Breeding seasons may be year round, or last for several months (see Schaller, 1967). The males are therefore not free to idle and grow fat in tropical forms; rather they must be on guard during territorial defense and courtship, or—if in bachelor groups—ready to take on a territory. The males must hence be ready to fight anytime, to better their rank in bachelor groups or to become territorial. The cost of social life should therefore be higher to tropical males than to those from temperate zones during much of the year. This would reduce still further the surplus energy and nutrients available for growth and fattening. Moreover, males which would forego lipogenesis in favour of direct use of the ingested energy for reproduction would have more energy to spend for reproduction. This would be so since lipogenesis is exceedingly wasteful of energy. We would expect, therefore, that ungulates from the humid tropics and savannah would have only a very small store of body fat. This is indeed found in the Uganda kob (Ledger and Smith, 1964), where the subject has been investigated.

Furthermore, if males and females roam over the same, limited home range, it becomes adaptive for the males to have food habits different from those of the females or to segregate males and females as much as possible. A reduction in food competition between the sexes during the female's gestation period would benefit the growing fetus, in that the female would have more net energy for foetal growth. This suggestion that males should feed on qualitatively poorer forage compared to females is less far-fetched than appears at first glance. We do know that Icelandic ptarmigan (*Lagopus mutus*) during the egg laying season have different food habits according to sex. Thus Gardarsson and Moss (1970) found that females fed on freshly growing herbs far more than did males, and thus consumed a more digestible and qualitatively better food. We also know that there are taste preferences in blacktailed deer (*Odocoileus hemionus columbianus*) (Crawford and Church, 1971). In view of the fact that exacting field studies on the food habits of ungulates of different ages and sexes during all seasons of the year are still outstanding, it is premature to discard the hypothesis that in some ungulates food habits may vary by sex and age, with the males feeding on the coarser, less digestible forage.

Another means of reducing competition for forage between sexes would be to segregate adult males and females spatially as much as possible. Some territorial systems, such as that of Thomson's gazelle (*Gazella thomsoni*), in which territorial males stake out large territories in the home ranges of females and regulate bachelor herds to secondary habitats at the forest edge (Walther, 1964), would serve the purpose. Assuming that both male and female would select for the highest quality forage possible, the reduction of males on the feeding ranges of females would clearly allow the females to feed more on high quality food. Whether the absence of non-territorial males indeed does free a noticeable amount of high quality food remains to be demonstrated.

The short rutting season in the north concentrates intense aggressive interactions between males. This puts a premium on mechanisms which clearly signal the combat potential of the dominant or breeding males. Every fight, chase or interaction saved necessarily saves fat from oxidation and allows the dominant male to use such fat to supplement his energy intake during winter. This should increase his life expectancy. At present it appears that natural mortality in males from northern ungulates is linked to the loss of body fat during rutting. That is, they go bankrupt into winter while males prevented from intensive rutting maintain fat stores and have an excellent chance of survival (see Flook, 1970; Geist, 1971a). Clearly, the better the male is at intimidating rivals the better his chances to live another year. This can be achieved not only by relatively large antler or horn size, but also by intensifying all signals that are used by the dominant males, be they sounds, odours or actions associated with dominance. This suggests that northern males should evolve not only larger antlers or horns than comparable forms from subtropical regions, but also that they should vocalize more, and spray more urine, distribute more dung or secretions and make themselves most visible during the rut. This prediction remains to be verified. Our present knowledge indicates that it will hold for old-world deer; in the caprids the horns alone increase in size.

In ungulate species living close to carrying capacity the year round and breeding the year round, mechanisms may evolve to ration rutting for each male. Theoretically this may take the form of males spending only a fraction of the year on the territories and recuperating from the strains of territorial life for the remainder of the year. One would note in such species that an individual male occupied his territory periodically and that in his absence other males occupied that territory. Leuthold's (1966) observations on the Uganda kob (*Adenota kob*) come close to this expectation.

This concept can also be applied to explain musth in Asiatic elephant bulls. Eisenberg *et al.* (1971) note that it is similar to rutting in ruminants and support this contention plausibly. According to the hypothesis suggested here, continuous rutting would place so heavy an energy drain on bull elephants as well as unduly expose the male to the hazards of intraspecific conflict, that the life expectancy of sexually mature bulls would be very short. A short annual rut coupled with continuous sexual activity throughout the year allows the male to dominate others for a short time annually, to breed uncontested females during any time of the year, as well as to recuperate from rutting and increase his life expectancy. This would, in the long run, allow a bull to sire more offspring than if the male were in rut continuously and died young. This viewpoint suggests that bulls can afford to rut only if they are in favourable energy balance and have sufficient energy available for rutting above those of maintenance. Eisenberg *et al.* (1971) support this view. First, musth appears mainly during rainy periods, that is when fresh, newly-sprouted vegetation is available that is of higher quality than old vegetation. Moreover, there should be more forage available than during the dry season. Second, to extinguish musth domestic elephant bulls are put on reduced rations by mahouts. Third, musth appears sporadically in bulls 14-20 years of age but more regularly in older bulls, implying that musth appears mainly in bulls whose growth processes are near completion and, hence, have more energy available in excess of maintenance. It is interesting in this context that African elephants may consume a much greater amount of forage per day than do Asiatic elephants (Sikes, 1971). If this is found to be valid, then it appears that Asiatic elephants may have evolved more efficient mechanisms of forage conversion in the face of chronic shortage. The predictions inherent in the above hypothesis explaining musth are as follows: musth should be found to occur most frequently in wild bulls from excellent habitats.

Bioenergetic consideration also helps in explaining why territories are found primarily in tropical and subtropical ungulates and only exceptionally in northern forms. A male can occupy a territory year round only in such regions in which the productivity and the diversity of plants is such that the male can find enough sustenance—and of the right kind—year round for himself as well as for his mates and offspring. The productivity in humid tropical climates, as well as the great diversity of plants on relatively small areas, appear to allow territorial behaviour. A territory cannot be held year round if the diversity of plants or the productivity of the territory is too low to supply the necessary sustenance, or if the productivity is highly seasonal and

adequate forage available for a short time only. Furthermore, fixed living or breeding territories becomes increasingly unadaptive the greater the movement of females during migration, the more unpredictable the availability of food, whether because food supply is determined by local rains—as it is on the African plains—or its availability is affected by snow storms, cold snaps and thaws. Thus a group of females faced with little or no forage on a territory is likely to escape from the territory holding male and head towards better pastures. A male holding a territory with favourable forage conditions may find himself the next day in territory covered by a deep blanket of snow, while the females have moved several miles to a more favourable area. A male holding a territory here may find himself alone as soon as strong winds have cleared specific ridges of snow. In short, if the rut is short and the animals must often move to different regions in order to feed, a male maximizes his reproductive success by sticking with the females. It is noteworthy that the roe deer (*Capreolus*) and the pronghorn (*Antilocapra*), both of which are northern forms in which the males form territories during the rut (Kurt, 1966; Bromley, 1969), mate during the summer or early fall when vegetation is still green, relatively abundant and the likelihood of snow storms minimal.

The foregoing illustrates how the availability of forage in the habitats of ungulates from cold and warm climates could, and apparently does, reflect itself in the biology of these animals. We now turn to the circumstances which accelerate social evolution in periglacial ungulates in preparation to answering the questions posed earlier.

THE DISPERSAL THEORY

Evolution in periglacial regions. The following is a short version of a theory discussed in detail elsewhere (Geist, 1971a, b).

After glacial withdrawal ungulates began to colonize the vacant habitat of the once glaciated zones. Individuals crossing or circumventing barriers, such as large melt-off channels or glacial lakes, formed colonizing populations. Until the population reached carrying capacity, the individuals would be confronted by a super-abundance of forage to which they would respond in a predictable fashion. Birthrates, birth weights and milk production would increase. Consequently neonatal survival and the growth rates of young would go up. The young would mature early and reach an adult size close to their genetic maximum. However, the adults would have a short life expectancy. Such animals would be lively, interact in play-like combat frequently, and fight intensely during serious combat at rutting time. Under such conditions large-bodied individuals as well as those with larger horns or antlers, which improved combat techniques and defense mechanisms, as well as sturdier skulls to absorb impact and stronger skull to spine connection, would have the advantage. The longer the population exists in the colonizing state, the longer selection continues for large males with improved combat techniques and adaptations.

Large body and horn size can be achieved by increasing the intensity and duration of growth. This can be done by enlarging the physiological mechanisms characteristic of juveniles. If this happened then ungulates should become not only larger, but also more juvenile-like during early post-glacial evolution. This hypothesis could be tested on American and Asiatic sheep (Geist, 1971a). It could be shown that in all parameters tested the behaviour of the advanced bighorn sheep (*O. canadensis canadensis*) was more juvenile-like than that of the more primitive Stone's sheep (*O. dalli stonei*); in Asiatic sheep evolutionary advancement was associated with the loss of the neck mane, a secondary sexual characteristic of males in primitive races.

Selection for large body size would come to a halt in the population at carrying capacity when the body size no longer reflects genotypic but phenotypic variation. Such a population is characterized by a low reproductive success, low vigour in its social interactions, but a long life expectancy of the individuals. However, the evolutionary advancement in weapons and defensive systems are maintained, since a reversal towards the primitive condition could only take place if males at the bottom of the dominance order, that is the subordinates and socially unfit, would do most of the breeding. This is most unlikely and has been reported as a rule for no species studied to date. Only if subordinates bred regularly and in the majority would evolution become reversible and thus contradict Dollo's law.

The foregoing exemplifies the simplest kind of evolution in which there is an advance in social adaptations without a concurrent advance in ecological ones, since the species only invades habitat to which it is already adapted. It explains why present-day ruminant clines from the north need not reflect ecological gradients, but reflect only the dispersal history of the species. It explains the correlation between evolutionary advancement and Pleistocene glaciations, as well as the irreversibility of evolutionary advancements. It explains why ungulates invading continents uninhabited by their kind evolved into grotesque giants such as *Bison latifrons*, or the large-tusked elephants (*Mammuthus jeffersoni*, *M. imperator*) that appeared in North America in mid-Pleistocene times. It also explains another mystery, namely why the oldest fossil forms of a genus or species of large mammal in any one locality tend to be the largest representative of that lineage.

Dispersal and social evolution in tropical environments. The same process as described above must also take place in the tropics, provided a species evolves which differs ecologically from the parent species. This new species dispersing across the continent and filling a new niche would also experience superabundance of resources during colonization. It should then respond in the manner described for Ice Age forms. However, it would be subject to an additional form of selection: since the parent species strongly resembles the new species, interbreeding is likely. Selection against hybrids would soon lead to a divergence in the external appearance, courtship and dominance behaviour of the new species from the parent species: since the new ecological species is relatively rare and hence outnumbered by individuals of the parent species, it is the new species which diverges from the old in external appearance and behaviour. Once the new species has colonized the land it will be characterized by individuals of larger body size, improved combat and display organs, and more distinctive colouration in hair coat and skin outgrowths than those of the parent species. Since each new species arising must go through the same process, the result is that the species most specialized ecologically will also be the most specialized socially and have the most bizarre external appearance. A corollary will be that the ecological specialists are more likely to extinction than the generalists and that the latter may survive over far longer periods than the bizarre, advanced forms. Secondly, it is evident that it is the ecological generalist that is most likely to disperse to new habitats while the specialized forms are more likely to remain in the land of their evolutionary origin and have a smaller geographic distribution. While this supports Darlington's (1957) views of dispersal, the previous example, using the periglacial example, supports Matthew's (1915) views of dispersal and evolution of mammals. These apparently contradictory theories are both correct, depending on where dispersal and evolution took place.

The dispersal theory and the antelopes. The predictions of this theory appear to be realised fairly well in the 'antelopes', although there are also a few exceptions. An examination of the Reduncinae, Tragelaphinae, Alcelaphinae, Hippotraginae and Antilopinae as described by Walther (1968a, b, c) shows the following. If we examine the obvious ecological specialists in those tribes such as the sitatunga (*Tragelaphus spekii*), mountain nyala (*T. buxtoni*), eland (*Taurotragus oryx*), the lechwe (*Hydrotragus lechwe*), or Lady Gray's water buck (*Onotragus megaceros*), we note that they are relatively large-bodied, have heavy or long horns and bizarre, striking colour, hair and skin outgrowths compared to the ecological generalists such as the bushbuck (*Tragelaphus scriptus*) and reed bucks (*Redunca*). In the Alcelaphinae the genus *Alcelaphus* contains the least strikingly coloured species of the tribe. The genus *Damaliscus*, however, which according to Walther (1968b) inhabits habitats either more mesic and forested, i.e. the topi (*D. imatus*) or more open and treeless, i.e. the blesbok and bontebok (*D. dorcas*), than does the genus *Alcelaphus*, is also more distinctly coloured. The most striking genus, *Connochaetes*, with bizarre hair outgrowths on face, neck and tail, and relatively heavy horns and specialised social behaviour (see Estes, 1969) should be ecologically the most specialised genus. This, however, is up to the specialists to decide.

In the Antilopinae we find the small-bodied gazelles of the subgenus *Gazella* to have the widest geographic distribution. This we expect from the most generalized subgenus. Quite in accordance with theory, members of this subgenus have a relatively small set of horns and a small rump patch. The subgenus *Nanger* contains larger

bodied gazelles with large rump patches and long horns; their distribution is contained largely within that of *Gazella*. The subgenus *Nanger* hence would be the higher evolved of the two subgenera according to the theory. The African ecological specialists among the Antilopinae such as *Litocranius*, *Antidorcas* and *Ammodorcas* differ from the small, generalized subgenus *Gazella* in more striking body shape, large or complex horns, specialized tails, specialized behaviours, larger body size and relatively small or even tiny geographic distribution. In Asia we find the ecological specialists adapted to the cold steppes or mountains differing from the small gazelles in the expected direction. Thus we find the saiga (*Saiga tatarica*) gazelle with an oddly shaped head, which in males becomes particularly grotesque during the rut. Next in relation to the high altitude form, *Panthalops*, larger in horn size than *Saiga* and with a rump patch. In the cold desert of Mongolia we find *Procapra gutturosa*, large-bodied for a gazelle with a 'mouth sack' as yet of unknown function. Moreover, *Procapra gutturosa* males have a swollen 'crop' during the rutting season. This species has a large rump patch and short tail. It can be noted that where data are available, they do follow the predictions that the ecological specialists have more complex or larger social organs than the generalists and are of larger body size.

If the Hippotraginae, in particular the genus *Oryx* and *Addax*, are indeed descendants of the Antilopinae, then the ecological and social adaptations of these desert antelopes are at once comprehensible following the predictions of the dispersal theory. These ecological specialists should be large horned and marked with striking body colouration, which indeed they are. Moreover, the largest oryx, (*O. gazella gazella*) is also the most colourful one. They should also have a social behaviour derived from that of the Antilopinae, but of an advanced form. If this is so, it remains to be discovered.

The dispersal theory does not predict correctly in a number of instances. In the reedbuck, it is not the largest horned and biggest bodied species (*Redunca arundinum*) which has the smallest geographic distribution, but *Redunca fulvorufula*, the smallest bodied and shortest-horned form. Horn size does not invariably enlarge with ecological specialization: thus the dama gazelle (*Gazella dama*) has rather modest horns, as does the saiga, Mongolian gazelle (*Procapra gutturosa*) and the springbok (*Antidorcas maurusipalis*). However, each of these species is highly distinct in some other attribute related to social behaviour. Note the striking body colour, the white face and large rump patch of the dama gazelle, the swollen proboscis, large preorbital glands and facial hair outgrowths of the saiga, the 'crop', rump patch, and 'mouth bag' of the Mongolian gazelle, and the facial colour pattern and dorsal display organ of the springbok. Horn size may remain conservative, but other social organs may compensate for horn size in their evolution.

The scarcity of hard ecological and behavioural data for African and Asian antelopes makes it difficult to test the dispersal theory adequately. It is tempting to suggest that *Tragelaphus scriptus*, *T. imberbis* and *T. strepsiceros* are an evolutionary lineage, leading from the small, primitive, brush-dwelling form to the arid-zone species in which social behaviour specializes with ecological specialization. Although Walther's (1964) work on the ethology of *Tragelaphus* is compatible with this view, there is insufficient ecological data to make a case. Similarly, the Cephalopinae are ill-known, and although the largest-bodied species (*Cephalophus sylvestris*) is the most strikingly coloured—as anticipated by the dispersal theory—its horn size is similar to that of other duikers, and we know nothing of its ecological differences from other duikers. Although our limited knowledge of the food habits, behaviour and zoogeography of duikers suggests that we are dealing with the most primitive of bovids, the paleontological record is as yet too inconclusive to clinch the argument.

Accelerated evolution during the Pleistocene. The acceleration in rate of evolution during the Pleistocene, as compared with pre-Pleistocene times can be explained by noting that frequent minor and major glaciations caused contraction and subsequent expansion of habitats upon melt-off. This would cause frequent dispersal of a species into vacant habitat, and frequent subjection to selection pressures typical of colonizing populations, hence a rapid change of the species towards large body size and sophisticated combat and display behaviour, as well as enlarged horn-like organs.

An association between specialized tooth structure and increased body and horn-like organs in Pleistocene forms can be explained as follows. If large body and horn, tusk,

etc. size is strongly selected for, then increasing digestive efficiency is also selected for. Hence males with improved mastication equipment benefit by having slightly more energy surplus to maintenance, for growth of body and combat organs. Over geological time one would notice an increase in specialization of masticatory apparatus, horn-like organs and cranial defense mechanisms. Such evolution, however, does not imply ecological specialization, but only increasingly efficient exploitation of forage within any niche.

Evolutionary stagnation. Lastly, how does one account for evolutionary stagnation in ungulates? The present theory suggests that this is due to the generalized ecological adaptations of long-lived species and the relative stability of the plant communities inhabited by these forms. Even if such plant communities contract and expand in response to the climatic conditions and fragment into geographically distinct units during maximum geographic contractions, the generalized ungulate species would nevertheless fail to find much opportunity to expand into identical habitat not occupied by its own kind. Under circumstances minimizing the opportunity for dispersal into vacant habitat, little or no evolutionary advancement would take place. I have explained evolutionary stagnation in the clines of sheep in detail elsewhere (Geist, 1971a).

BEHAVIOURAL CONSIDERATIONS

From the foregoing considerations it is evident that behavioural differences between northern ungulates and those from tropical continents can be expected. It has been noted that intense competition for females in the colonizing populations by large, relatively young and vigorous males would select for intense combat. It should not surprise, therefore, if northern species of ungulates are found to be far more damaged in intraspecific combat than African antelope or cervids from South-east Asia, for instance. Our present-day, meagre evidence is in line with this and we can say that severe wounding or killing in intraspecific combat is not uncommon in northern cervids or bovids. I have reviewed the evidence elsewhere (Geist, 1971a).

Secondly, we can anticipate noticeable quantitative differences in the social behaviour of ungulates from stagnant, poor quality populations, and high quality populations with access to adequate forage. It can be predicted that courtship, combat and display will be more frequent and intense in the high quality population. We have evidence to show that this is indeed so, but it is insufficient to demonstrate the point conclusively (see Geist, 1971a).

Thirdly, in a comparison between primitive and advanced races of a species (or species of a genus) the primitive forms should be found to have more generalized combat, a greater likelihood of body rather than weapon displays, and the less neotenous social behaviour. Data to show this exist today only for caprids (Geist, 1971a).

There are other relationships between the ecology of species and their social behaviour, but they are irrelevant to the present theme. I have discussed in detail elsewhere the impact of climax plant communities on the evolution of sheep and that of fluctuating ones on the evolution of moose (Geist, 1967; 1971a, c), as well as the many direct and indirect consequences of ecological adaptations on sheep biology (Geist, 1971a). Mention has also been made of Eisenberg's (1963, 1966, 1967) and Eisenberg and Gould's (1970) contribution to this subject. Of particular significance is Jarman's (1968) theoretical contribution which for the first time plausibly relates bioenergetics and feeding strategy to body size of ruminants, and considers the secondary effects of the anti-predator strategies and social systems of these animals. Recently Crook (1970) edited a volume that deals largely with the relation of ecology and the social behaviour of various mammals and birds. And, finally, of course, a considerable number of other papers in this volume discuss various aspects of the relationship of ecology to social behaviour in ungulates.

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Paper No. 11

The Influence of Foster Rearing on Adult Social Behavior in Fallow Deer (*Dama dama*)

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ABSTRACT

Many species of hoofed mammals are known to form strong social bonds to normal or surrogate parents shortly after birth. Despite the similarities of this process to imprinting in birds no study of the effects of early experience on the development of preferences for companions or the long term influences on social behavior has been reported.

In this study fawns were separated from their mothers between one and 48 hours after birth and were foster-reared by goats or bottle-fed either in isolation from other fawns or with fawn companions. When four to seven years old these foster-reared deer were compared with normally-reared deer for attachment to people and to other deer. The deer which were bottle-fed without fawn companions had the highest scores of attachment to people, lowest scores on three indices of gregariousness to deer and the highest scores for aggression toward other deer. In addition, the ranks of these measures of attachment to people and lack of gregariousness to deer were highly correlated with the age during the first 24 hours that the fawns were removed from their mothers. The data indicate that the differences in adult attachment resulted from processes initiated in the fawn's first day of life. Deer reared with other fawns ranked lower than isolate-reared deer in attachment scores to people and in aggression, and ranked higher in measures of gregariousness with deer. The normally-reared young of hand-reared does ranked lowest in attachment to people and in aggression, and highest in gregariousness with deer.

The degree of attachments to people or deer in both foster-reared and normally-reared animals was resistant to change and could be transferred to other individuals of the same species. The data suggest that the degree of attachment depends on social interactions during the first day of life.

Observations on the development of fear of people in the normally-reared fawn are presented. Exposures to people for 8 hours in the fawn's first day resulted in delayed withdrawal response during subsequent approach by people.

The major influence of foster-rearing was in establishing the social companion to which species-typical behavior was directed. The frequency of some behavior patterns was changed, e.g. aggression, but no change in the type of behavior was detected.

INTRODUCTION

The newborn young of hoofed mammals are characterized by well-developed perceptual and motor capabilities as compared with other orders of mammals such as carnivores and rodents. The neonatal wildebeest (*Connochaetes laurinus*) normally stands and follows its mother within 5 to 10 minutes after birth (Talbot and Talbot, 1963). Deer and antelope, although capable of standing within an hour of birth, remain lying in cover for a number of days (Bubenik, 1965; Walther, 1964). Experiments on visual perception in kids and lambs show that they are able to avoid the deep side of a visual cliff at one day of age (Hinde, 1966). At the other developmental extreme,

¹ This study was undertaken by the author in the Department of Zoology, Duke University.