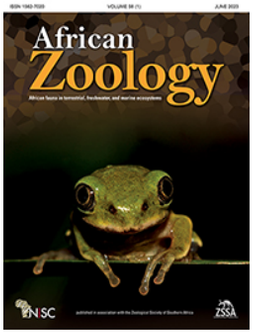

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SOCIAL BEHAVIOUR OF AFRICAN EQUIDAE

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ABSTRACT

Two basically different forms of social organisation have been discovered in the equids. Type one is represented by the plains zebra, *Equus quagga*, and by the mountain zebra, *E. zebra*, who live in non-territorial and coherent family groups and stallion groups. The young leave their original families in a set pattern. Type two comprises Grevy's zebra, *E. grevyi*, and the wild ass, *E. africanus*, species with stallions keeping large territories which they defend under certain conditions against their neighbours. There is no evidence for the existence of personal bonds between any two or more adults.

With the exception of a few small populations, equids live in areas where their food and water supplies change with the seasons. In the territorial species the females emigrate when living conditions deteriorate, whereas the territorial stallions stay behind until living conditions become critical. Thus there is a segregation of the sexes for part of the year, a factor which will certainly influence the reproductive rate. The non-territorial species, by contrast, can reproduce throughout the year.

The evolution of equine sociology is discussed.

Four species of equids inhabit the African continent: the wild ass, originally occurring over large parts of northern and north-eastern Africa, now reduced to a few localities in the Sudan, Ethiopia and Somalia; Grevy's zebra of northern Kenya and parts of Ethiopia; the plains or Burchell's zebra, ranging from the southern Sudan and southern Ethiopia to South and South West Africa; and the mountain zebra of South West and South Africa. During the last nine years we have, with intervals, investigated the behaviour of these species in the wild. This paper attempts to give a comparison of the social behaviour of the various species.

The equids are all very much alike; they belong to one genus only and can all interbreed with each other in captivity. So it can be expected that their behaviour is similar as well. In fact, a number of behaviour patterns are practically identical in all the equine species including the two Asiatic ones, the horse, *E. przewalskii* f. caballus, and the Asiatic wild ass, *E. hemionus*.

SOCIAL ORGANISATION

We have, however, discovered two completely different types of social organisation among the African equids. The plains zebra and the mountain zebra live in coherent family groups, consisting of one stallion, one to several mares and their young, and in stallion groups. These social units are non-territorial and move freely over rather large home ranges, the sizes of which depend on their ecological conditions and which they share peacefully with conspecifics (Figs. 1 and 2).

In both species the family groups were found to be permanent units as far as the adult members are concerned. Mares stay normally for their life times in the same group, even when they are very old or sick. Old and sick stallions may be replaced by younger and healthier ones; they then join stallion groups. The stallion groups are more variable in their composition, but some individuals may stay together for many years as well.

FIGURE 1
Plains zebra groups (Serengeti, Tanzania).

In the plains zebra we could study the mechanics of this social set-up in detail (Klingel 1967). In the mountain zebra we obtained the same results even though we could not observe the actual processes leading to them (Klingel 1968a ; 1969).

Mating takes place only between a family stallion and his mares and there is no competition among stallions for adult mares. Adolescent mares, however, during oestrus attract stallions in the vicinity of their groups. Family stallions and bachelors surround the group and try to separate such a mare from her group. The family stallion defends by attacking individual stallions, but eventually the young mare will be separated from her group because of the large number of suitors. Usually the young mare does not stay with the stallion who abducted her, as the fight over her continues until the end of her oestrus. With the next oestrus it starts all over again up to the age of two to two and a half years when she becomes a permanent member of a group.

The different attitude of stallions towards adolescent and adult mares is caused by the conspicuous oestrous posture of the younger mares, whereas in adult mares the oestrous is optically inconspicuous.

FIGURE 2
Mountain zebra family group; stallion guarding (Etosha, SW Africa).

What I have described here is one way in which stallions start a family or increase the number of their mares. In the other one a stallion replaces an old or sick family stallion or takes on a group of mares whose stallion has died. Even in this case the group formation stays intact and the new stallion takes on the group as a whole.

The young stallion stays with his family even up to the age of four years. He leaves at an earlier age when his mother has a new foal and when there are no playmates, stallions of similar age, in the family. There is no evidence of family stallions chasing their adolescent sons away. The colts eventually join stallion groups and from the age of five to six years they start to compete with other stallions for adolescent mares.

This type of social organisation with non-territorial coherent stallion groups and one-male families, which has also been discovered in the horse (Tyler 1969), has no parallel among other mammals nor in any other species.

The social organisation of the two other African equids, Grevy's zebra and the wild ass, is completely different from the above. In these species there are no permanent bonds between any two or more adult animals, which are found solitary or in a variety of different associations: stallion groups, mare groups, groups of mares and foals, and mixed herds (Fig. 3). All these groups are variable and their composition may change within hours. The only bonds existing are those

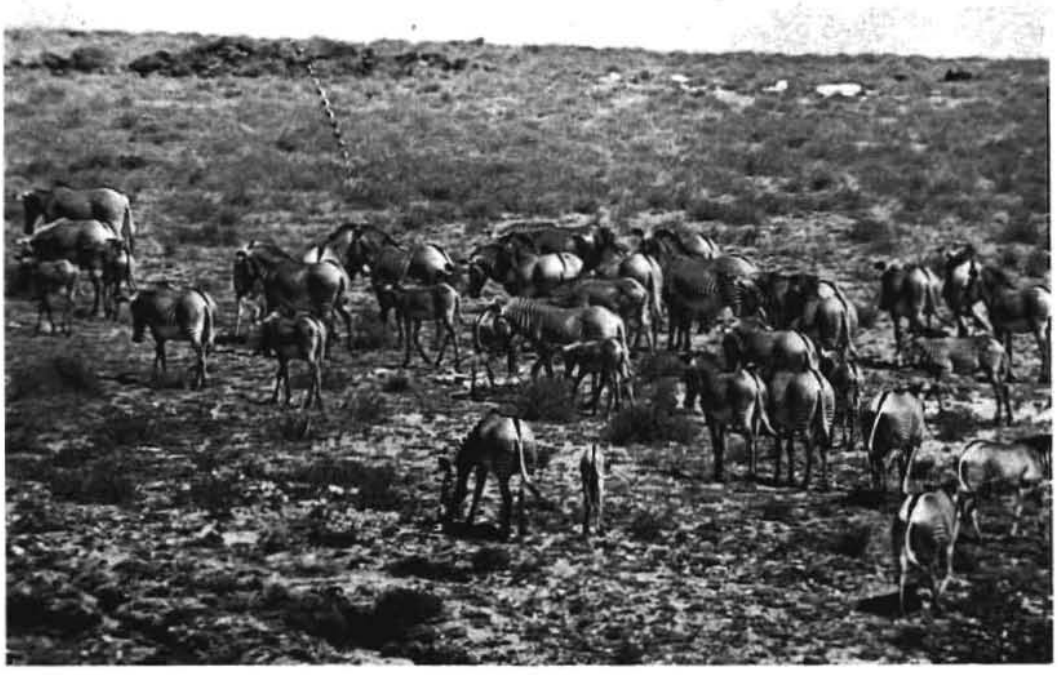

FIGURE 3
Grevy's zebra herd of mares with foals (NFD, Kenya).

FIGURE 4
Wild ass mare with yearling and two-year-old male foals (Danakil, Ethiopia).

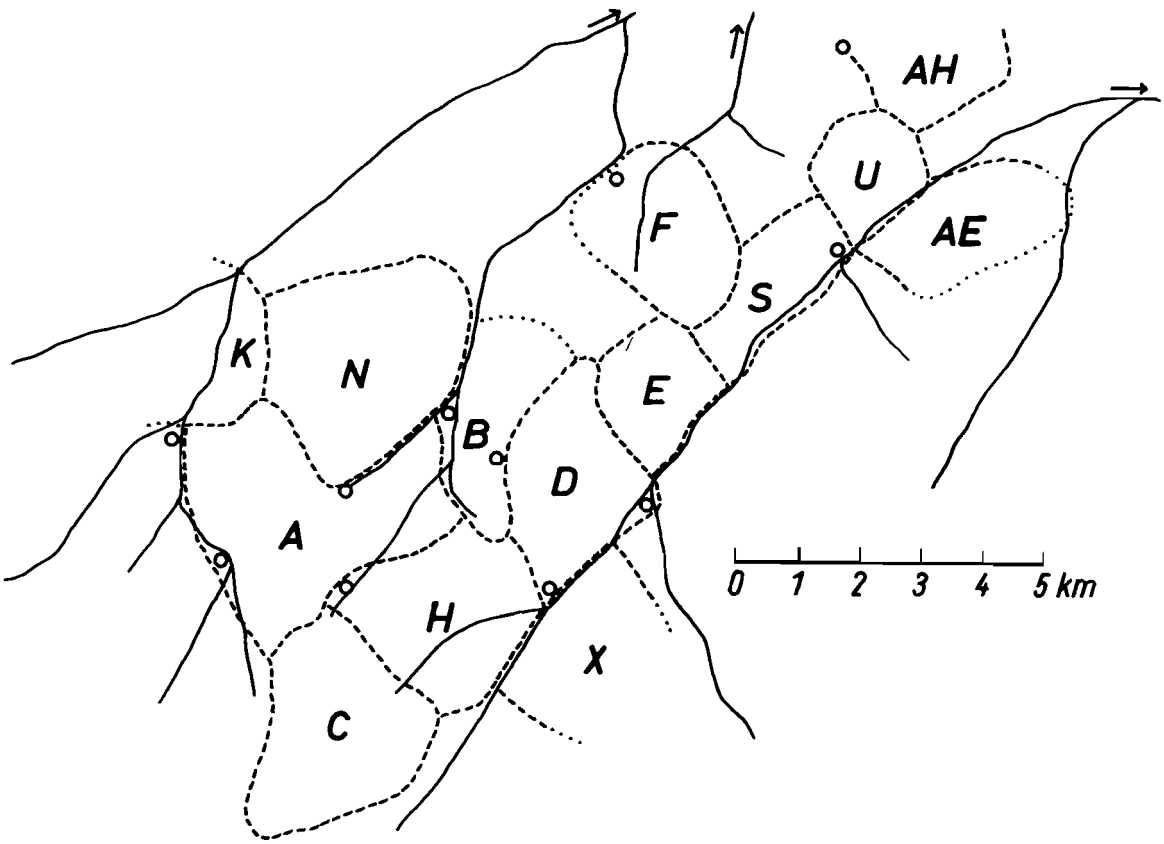

FIGURE 5
Grevy's zebra territories (Wamba, Kenya). —— known; . . . . . assumed boundaries; ------ dry river beds; o dung piles.

between a mare and her foal (Fig. 4). Some of the solitary stallions are territorial.

Of the two species, we have been able to study Grevy's zebra in detail, whereas our observations on the wild ass are still fragmentary because of the shyness of the animals and the fact that we had only very little time for this work. The observations strongly suggest, that the social organisation of the wild ass is identical to that of the Grevy's zebra (Klingel 1970). The territoriality of these species is of particular interest. There is firstly the extraordinary size of the territories. Ten territories of Grevy's zebra stallions in our working area near Wamba in northern Kenya measured from 2,7 to 10,5 km² with an average of 5,75 km². The territories of the wild ass near Tendaho in the Danakil region of Ethiopia seem to be even larger, averaging at least 10 km²; we have, however, no accurate figures on this. The territories of these two species are the largest male territories ever recorded in a herbivore (Fig. 5).

The second important feature is the tolerance of the territorial stallion towards conspecifics

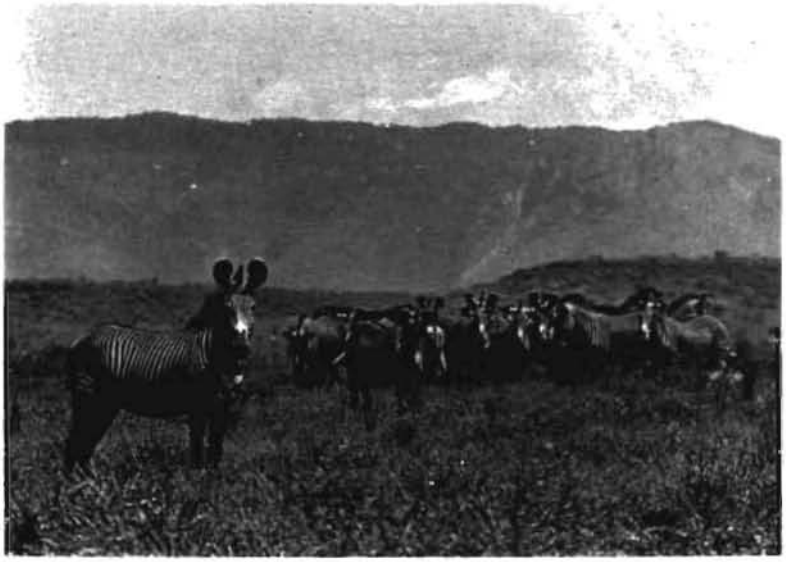

FIGURE 6
Grevy's zebra stallion (in front) with mixed herd of conspecifics in his territory (NFD, Kenya).

including other males which means that he does not prevent them from entering his territory. Within the territory these males respect the territorial stallion and they do not interfere when he is engaged in mating activities. If they happen to get near a mare in oestrus the territorial stallion chases them away. We have never observed him to be challenged (Fig. 6).

The territorial boundaries are, with rare exceptions, defended only when there is an oestrous mare near the boundary. Then the territorial neighbours will fight with each other and at the same time each of them will try to make the mare walk towards the centre of his territory. As soon as one of them succeeds, the fighting ceases and the successful stallion follows his mare, whereas the other one waits at the boundary. Some of the boundary points we found by recording the places where fights between territorial neighbours took place. In order to find more of them we made oestrous mares walk towards the boundaries by driving them with the vehicle. Since territorial stallions move with their mares, and as the neighbours are usually alerted by the precopulatory activity of that pair, we could induce the stallions to fight anywhere along the boundary and thus determine it accurately. Territories are mainly marked by the mere presence of the owner. In addition he signals his presence acoustically. The dung piles found mainly along the territorial boundaries and probably used for years by the territorial stallion may also serve to mark the territory, not so much for potential intruders, but for the territorial animal itself.

The function of the territorial system in these species became clear when we observed an oestrous mare in a non-territorial area. For two hours she was courted by up to nine stallions at a time. These stallions were fighting each other almost continuously and therefore none of them succeeded in copulating with the mare. The group eventually moved into a territory where the

territorial stallion took over. The other stallions moved away while he copulated with that mare undisturbed. The territories of Grevy's zebra and of the wild ass are therefore mating territories. Due to the territorial system only one particular male, i.e. the territorial stallion will court a mare at any one time, since all the other males are subordinate to him.

There is no explanation for the immense size of the territories, which do not seem to have any other function. The tolerance, however, of the territorial stallion toward other stallions can be considered to be a consequence of the size of the territories: a stallion could not possibly fend off intruders from his boundaries, which are, in larger territories, over 10 km long.

The stallions leave their territories for short periods of time in order to walk to their drinking places. At least Grevy's zebra stallions keep their territories throughout the year and probably for many years, even during the dry season when mares, foals and non-territorial stallions leave the area because of the shortage of food and water. Only in extremely dry seasons do the stallions leave their territories. In 1971 almost all the stallions in our study area emigrated, but returned to their territories at the beginning of the rains and before the arrival of the rest of the population.

This type of social organisation, characterised by the instability of the groups and by the existence of non-exclusive male territories, is not altogether restricted to the equids: Owen-Smith (1972) has recently discovered an interesting parallel in the white rhinoceros, where the territorial bulls are tolerant to subsidiary bulls. In this species, however, the subsidiary males live permanently in one particular territory, whereas in Grevy's zebra and in the wild ass all males may enter all territories.

SOCIAL BEHAVIOUR

As I have mentioned above, some behaviour patterns are identical or similar in the various equine species. This is true for fighting, social grooming, mother-child relationship and largely for greeting and mating behaviour (Klingel 1971). Other patterns, however, are quite different and can be correlated with social organisation.

In the non-territorial plains zebra and mountain zebra we discovered a stable order of dominance among the members of the families, the stallion being the α-animal. He also occasionally leads the group when they are migrating. Normally, however, the highest ranking mare leads the group and the other mares follow her in the order of their dominance. Whenever a mare walks in front of a higher ranking one, she will be attacked and threatened by that animal until she takes her right place. The young of a given mare follow her in reversed order of age, the youngest first. A foal near its mother has the rank just below her in the dominance order. The stallion usually brings up the rear or moves parallel to the group (Fig. 7).

In bachelor groups there is an order of dominance among the subadult members, whereas all the adult stallions seem to be of equal rank. The leader in these groups is always an adult stallion.

No stable order of dominance could be found in the territorial Grevy's zebra and wild ass, in which a territorial stallion is dominant over all conspecifics in his territory. The adult members of the various associations all seem to be of equally low rank. There is also no order of leadership. Any member, male or female, of such a group may start walking and thereby induce the others to follow it. When the others do not react, this animal may continue on its way or return to the group. During migration the leading animal may be replaced even after distances of only 20 to 30 m,

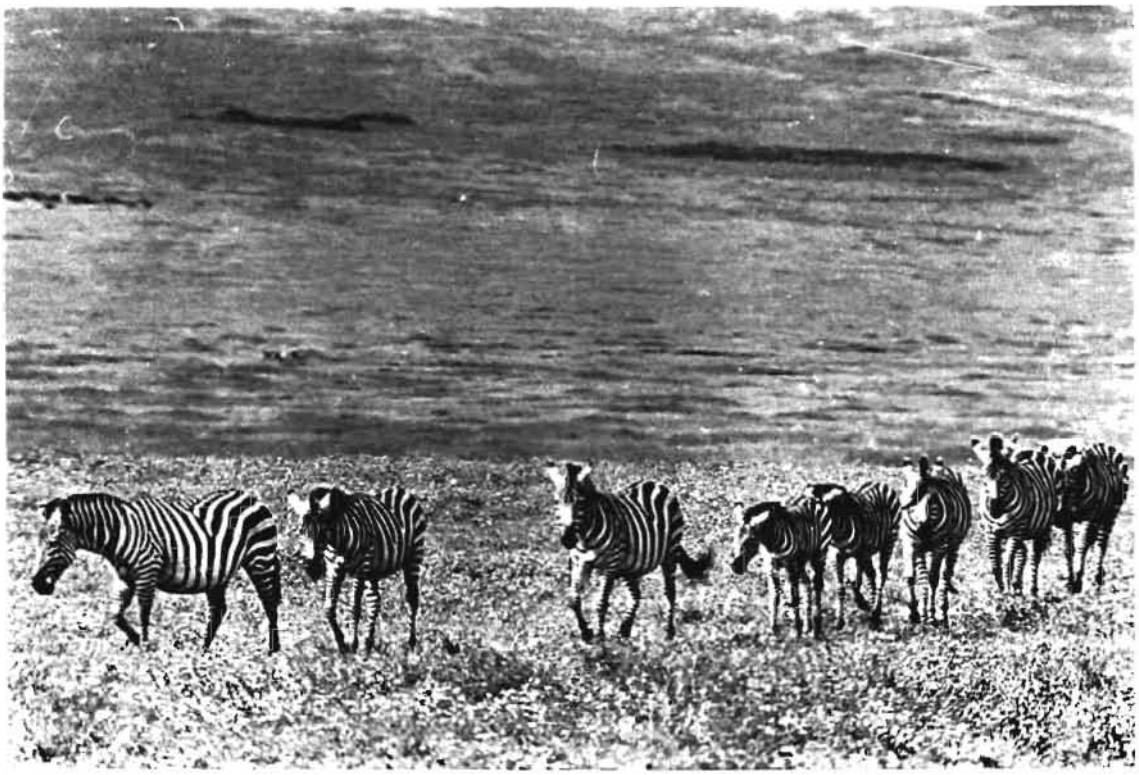

FIGURE 7
Plains zebra family migrating (Ngorongoro, Tanzania).

FIGURE 8
Plains zebra family sleeping, stallion watching (Ngorongoro, Tanzania).

and no antagonism has been observed to occur in such instances.

Searching for lost members of the group is another feature of group behaviour restricted to the non-territorial species. We have observed it in the plains zebra only, but it can be assumed to occur in the mountain zebra as well. When one animal has lost contact with the rest of the group, e.g. while sleeping, it searches for the others and is looked for by them. We could observe this in detail during our immobilisation programme (Klingel 1968b), when stallions, mares, and foals became separated from their groups. We found that all family members search for each other, with the exception of mares which do not search for other mares or for colts older than two years (Klingel 1968b). In Grevy's zebra and in the wild ass it is of course only the mare and her foal who search for each other.

Three further behaviour patterns demonstrate again how strongly plains zebra family groups act as units. Whereas in all the equine and some other ungulate species a female will wake her young when she is disturbed, in the plains zebra even other members of a group will do so quite frequently, e.g. when the mother is too frightened to go close to the foal or when she is not aware of the danger. When resting by day or by night there is always at least one adult or subadult member of a family standing and alert, while the others are sleeping in a recumbent position (Fig. 8). We observed two instances of a stallion grabbing with his teeth a still sedated mare by a fold of skin on her neck and thus leading her back to the rest of the family. In the mountain zebra we have in several instances observed stallions guarding their families at water holes (Fig. 2).

Marking behaviour consists in all the equine species of defecating and/or urinating onto the faeces and/or urine of their conspecifics. This pattern is displayed mainly by stallions and foals, but to some extent also by mares. Grevy's zebra and wild ass stallions also have the habit of defecating preferentially onto their own faeces to build up enormous piles which cover several m^2 and are up to 40 cm high. Only in these two species does the marking behaviour serve an obvious purpose, namely to produce prominent marks for the orientation of the stallion in his own territory.

An earlier explanation for the marking behaviour of the plains zebra was given by Trumler (1958). He claimed that a stallion, by marking the droppings of a mare, altered their smell and thus hid from other stallions the fact that the mare was in oestrus. Our own observations show clearly, that this is not the case. A stallion does not mark all the faeces and urine of an oestrous mare, and even when other stallions come across such unmarked droppings they do not approach the mare but respect the presence of the family stallion. The marking behaviour of the non-territorial equids has, as far as we have observed, no function. Its existence must therefore be explained otherwise.

ECOLOGICAL ASPECTS

African equids, with the exception of a few small populations, live in areas where their food and water supplies change drastically during the year because of the climatic conditions. This forces them to migrate either regularly where there is seasonal rainfall, or irregularly, where the rainfall is unpredictable.

It is obvious that the non-territorial species have an advantage over the territorial ones in that

they are not restricted in their movements and the population as a whole can make use of good grazing anywhere within reach. The population can potentially reproduce throughout the year, as males and females are permanently together.

In the territorial species, at least in Grevy's zebra, territories are only established in the rainy-season grazing areas; in the dry season, mares and non-territorial stallions emigrate while territorial stallions stay behind. Migratory stallions do not establish new territories in the dry-season areas and are therefore unable to mate with the mares. This means that the sexes are segregated for much of the year. Reproduction is therefore limited to the rainy seasons.

In regions with regular seasons this is no great disadvantage to the species. Since all equids have a gestation period of about a year, the foals will all be born during a rainy season. However, both Grevy's zebra and the wild ass live to a large extent in areas with irregular rainfall, where their segregation during the dry season will certainly reduce their reproductive rate.

EVOLUTIONARY ASPECTS

Of the two different types of social organisation, either one has evolved from the other, or both have evolved from an original one. As the ancestry of the equids is well known, it is challenging to speculate on the evolution of social organisation. As far as we know (Simpson 1951), *Eohippus* was a browsing, bush-dwelling animal whose habits may well have been similar to those of small antelopes, like the dik-dik, steenbok or klipspringer. These species are all territorial and their type of social organisation seems to be well adapted to their habitat. If we conclude, that *Eohippus* was territorial as well, then the territoriality of Grevy's zebra and the wild ass must be considered to be the original form of social organisation adapted to these species living in semi-arid and arid grasslands. The plains zebra, mountain zebra and horse are, according to this hypothesis, much more highly evolved, having abandoned territoriality and having become unrestricted in their movements.

It is interesting to note, that some primitive equids possessed a concavity in their nasal bones in front of the eyes. According to Simpson (1951) these animals may have had pre-orbital scent glands like most of the antelopes. If so they would most probably have used them for the same purpose, i.e. for marking their territories. Modern equids have neither concavities nor scent glands. However, they all display marking behaviour, using their faeces and urine. Only in the territorial species does this behaviour serve a purpose, as I have mentioned. In the non-territorial species the existence of the marking behaviour can be explained as a vestigial pattern inherited from territorial ancestors.

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