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TRANSFER OF GROUP MEMBERS IN PLAIN ZEBRAS (Equus burchelli) IN RELATION TO SOCIAL ORGANIZATION

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ABSTRACT

Social organization of plain zebras (Equus burchelli Gray, 1824) was studied in the Isiolo National Park in Kenya from June 1978 to June 1980. Their society is composed of one-male groups (consisting of one adult male, several adult females and their offspring) and all-male groups (consisting of full adult and young adult males). All the individuals which appeared in the study area were thoroughly identified throughout the study period, and the membership of each group was confirmed. The main data analyzed in the present paper are (a) moving range of the study groups and movements of nonresident groups, (b) group transfer of individuals during the two years and (c) observation of behaviours in relations to the group transfer. Based on these analyses the cluster of several one-male groups and an all-male group living in the study area was concluded to be a social entity which is one level higher than a one-male group or an all-male group. Such social organization was compared with social organization of other species, especially with that of baboon species. Finally, it was noted that 'neighbourhood relationship' plays an important role for the formation of a two-layered social group such as the band in gelada baboons and the cluster in plain zebras.

INTRODUCTION

Numerous studies on social organization in mammals have revealed that the one-male group (harem) is usually territorial in terestrial and arboreal species. But a few species have one-male groups which are not territorial; mountain zebras, plain zebras, hamadryas baboons and gelada baboons are included in the latter type. Precise studies of these two baboon species mentioned above revealed multi-layered social organization, where plural one-male groups constitute a high-level social unit which is called 'band' (Kummer, 1968; Dunbar & Dunbar, 1975; Kawai, 1979). In zebra species, however, such a high-level social unit has not been found.

Development of such a multi-layered social organization was reffered to by Imanishi as 'neighbourhood relationship'. He adovocated this term in order to express inter-individual relation in the society of semi-feral horses where each member of a horse group does not always aggregate in a group, though all of them or a part of them can easily aggregate in a group (Imanishi, 1949). The neighbourhood relationship is applicable also to interrelation among family groups which have continuous and overlapping territories to each other and then can easily aggregate in a bigger group (Imanishi, 1950). The idea was followed by Itani (1972) and Morishita (1974): Itani pointed out its importance in the development of the relationship among social unit of some prosimian primates, and Morishita adovocated an aggregation pattern based on the neighbourhood relationship. Furthermore, Ohsawa (1979b) applied this to the explanation of the multi-layered society of gelada baboons.

As for the zebra society, detailed studies by Klingel revealed its social organization, especially of the one-male group and its social behaviour, though the higher-level social organization than that of the one-male group and the all-male group (bachelor group) were denied in his study (Klingel, 1967). The denial of the higher-level, however, must be in the sense that no higher-leveled social unit so closed as the one-male group in membership.

The present study aims to reveal the social organization of plain zebras in an area where several one-male groups and all-male groups are living together, and to clarify the interrelation among one-male groups and/or all-male groups through analysis of changes of group members, their behavioural shift and ranging behaviour. For this purpose all the individuals in a definite area were completely identified throughout the study period. Individual behaviours on the group transfer will be discussed in relation to the multi-layered social organization.

SUBJECTS AND METHODS

The study of plain zebras (Equus burchelli Gray 1824; nomenclature based on Churcher 1978) was conducted in the Samburu and the Isiolo National Parks in the middle northern part of Kenya, mainly at Isiolo area (formerly the Buffalo Spring Game Reserve) alongside the southern bank of the Ewaso Nyero River (0.5 North and 37.5 East). The parks are located about 50km apart from the cliff of the central highland of Kenya, in the transitional zone from savanna to arid area (vegetation type: mixture of bushed grassland and wooded grassland) with the mean annual rainfall of 255-510 mm (information supplied by the East African Meteological Department; Survey of Kenya, 1970). The plain zebras at Isiolo are one of the population inhabiting the most arid area in the distribution of plain zebras (based on the distribution map of plain zebras in Kenya: East African Wild Life Society, 1977). On the other hand this area is one of the moistest and southernmost area of the distribution of Grevy's zebras (Dirshl, 1978), which were also common in the study area (Fig.1). Other mammalian fauna also shows such transitional phase as of zebras; waterbucks and impalas which prefer rather moist, for example, environment commonly inhabit this area as well as gerenuks and oryx which have a wide distribution in arid areas. The mammalian species which prefer the wet area were found mainly in the riverine forest along the Ewaso Nyero River and around the Buffalo Spring. Plain zebras live only in the vicinity of the Buffalo Spring and travel everyday between the spring and the fertile plain nearby. In the western part of the Isiolo Park there was no resident group.

All the resident groups of plain zebras in the park, which consisted of five one-male groups (harem) and one all-male group (bachelor group), were thoroughly investigated. Their total number was 69 including animals which disappeared during the study period. Besides these six groups, four one-male groups, two all-male groups and one pair (a male and female), all of which occasionally wandered into the study area, were observed, and their data were also analyzed as nonresident groups.

All of them were completely identified based on differences in their stripe patterns by the aid of field sketches and photographs. Additionally, characteristics of body shape, posture and locomotion were also used for a rapid identification during the observation of behaviour of the resident groups.

Field observations started with a preliminary survey in June 1978. Then every member of all the resident groups was identified within a week.

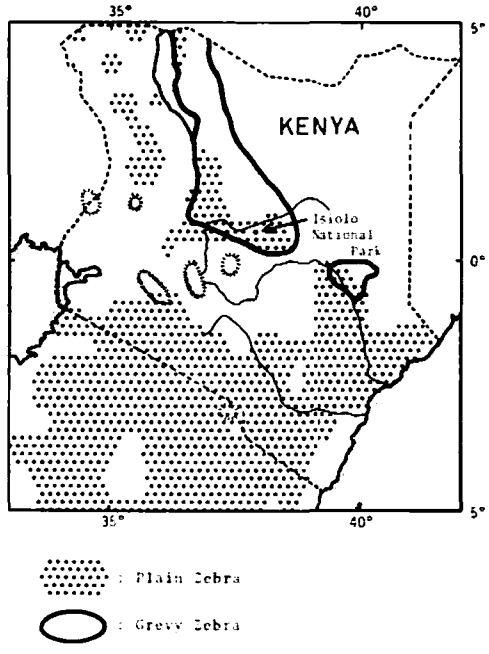

Fig. 1. Distribution of plain zebras and Grevy's zebras in Kenya (after Dirshil et al., 1978 and EAWS report, 1977).

Since then until the end of February 1979, field observation was carried out seven times. This was the first study period. After a blank of one year, the second investigation started in March 1978, and lasted until June 1980. Direct observation of zebras was made for 45 days in the first period and for 80 days in the second period. Some extra days were spent for the distribution survey in the neighbouring areas and the environment survey. Main data in this report concern group transfer of identified animals during two years from June 1978 to June 1980. Observation of behaviours in relation to group transfer and survey of moving area were conducted mainly in January and February 1979 and from March to June 1980.

RESULTS

Group Composition

The one-male group (OMG) investigated in this study consisted of one adult male (stallion), three to eight full adult and young adult females and their offspring. The members are shown in Table 1. The age class was divided largely into two, Adult and Offspring (Non-Adult). Offspring which is defined as individuals accompanied by their mothers are divided again into three classes according to body size; Young, Juvenile and Infant. Their actual ages were confirmed by tracing each identified animal in the course of the two years' study period: those from birth to two months are termed as Infant, those to one year as Juvenile, and those to two years as Young. Even at the age of two they have not reached full size. Therefore, individuals which were more than two years old but still had a smaller body size than full grown adults were distinguished

Table 1. Members of plain zebra groups in the Isiolo National Park

Group	Adult Male	Adult Female	Offspring I	II	III	IV	V	VI	VII	VIII
Moja	MJ	Kz	——[Kz1M]							Kz3M
		Mr	——[Mr1F]						Mr2M	
		Ec	——[Ec1M]						Ec2F	
Bili	BL	Fz	——					Fz2M		
		St	——							St3M
		Fy	——[Fy1M]					Fy2M		
		Fw	——[Fw1F]				Fw2M			
		Fx								
		(Tf)								
Tatu	[TT]	Yc	——[Yc1F]							Yc3M
	(XN)	Vd	-[Vd1F]							
		We	——[We1M]							
		Xb	——							Xb3M
		Za								
		(Uf)								
Nne	NE	Aa	——[Aa1M]						Aa2F	
		Dc	——			[Dc1F]				
		Bd	——[Bd1M]				Bd2M			
		Cb	——				[Cb2F]			Cb3F
		Ee	——					Ee2F		
		(Ff)								
Tano	TN	Az	-[Az1M]					Az2M		
		Ay	-[Ay1M]			[Ay1F]				
		Az	-[Ax1F]							
		(Ye)								
		(Wd)								
Mume	[XN]		(Az1M)							
	WM			(Kz1M)						
	[TJ]			(Ec1M)						
	[ZP]			(Fy1M)						
	[SI]			(We1M)						
	VL									
	[YO]									
	UK									
	(AO)									

[ ] means disappearance from the group during the study period. ( ) means join to the group during the study period. Roman numerals indicate the period of birth in offspring; before June 1978 (I-III), from June 1978 to Feb. 1979 (IV), from March 1979 to March 1980 (V-VII), after March 1980 (VIII) (see text). Lines (——) connect siblings which are the offspring of the adult female in the same level of the line.

from Full Adult and termed as Young Adult.

The age classes of Offspring were determined in July 1978 and in March 1980, and thereby the month of birth of each individual offspring was estimated. Then the birth period of offspring was classified into eight group; in Table 1, offspring are arranged from the left to the right

according to birth periods.

The average group size of five one-male groups (OMG) was 8.2 in July 1978 and became slightly bigger (9.0) in July 1980, ranging from 7 to 11. The group size of nonresident OMGs was 14 at its maximum and 2 at its minimum, although the minimum one was during the formation of a new OMG as will be mentioned afterward. On the other hand, the resident all-male group (AMG) had 8, later 9 members; one nonresident AMG had 11; another nonresident AMG had 3. The total number of resident animals belonging to the six resident groups was 49 in July 1978 and 54 in 1980; therefore the population growth during two years was 5 animals (ca. 5% growth rate per year). This growth, however, was not due to birth, but mainly to the female immigration. As will be shown in the later section, almost all the female offspring emigrated from the natal area and many of young bachelor males disappeared from the study area. Hence the birth of infants itself did not contribute to the growth of the population. The number of birth was exactly the same as that of emigration plus death (see Fig.7).

The number of females in OMG increased by immigration. The overall average number of adult females in a OMG was 4.7, the number ranging from 3 to 6, throughout the two years. Although there was a OMG with eight adult females (the Nane group) among the nonresident groups, three of the females were new immigrants to the Nane from the resident groups during the interval between the two study periods.

The above figures present the general feature of the one-male group in the Isiolo Park: it was a group with one adult male, 4 to 5 adult

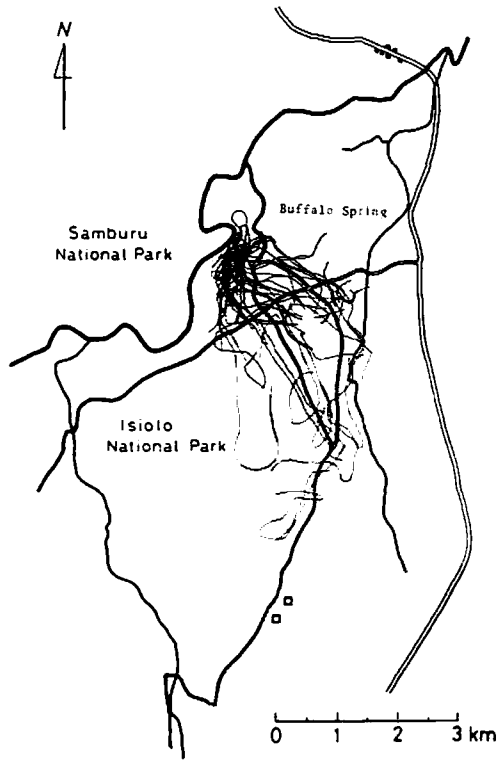

Fig. 2a. Daily moving routes of plain zebras in the Isiolo National Park (the Moja group during the first study period for 45 days).

females, and 3 to 4 offspring. Almost every adult female in the cluster had one offspring, though a few had none.

Moving Area

The daily moving pattern of one-male groups (OMG) and an all-male group (AMG) in the Isiolo National Park did not much vary much. The average home range was 10.5km; they moved around the spring where they drank water almost every day (Fig.2a). The sleeping sites were fixed at three locations, although each group used them in slightly different ways (Fig.2b). All of three sleeping sites were large and unobstructed plains with short grasses. The choice of this type of sleeping sites can be explained by the fact that the zebras have to protect themselves from predators by running quickly away rather than by hiding themselves.

Their typical daily movement starts by grazing at the sleeping site before dawn. It lasts about half an hour until they make the first movement to the Acacia forest nearby. Then they graze for several hours with slow movement. In the daytime they usually take a rest for about one hour at the grazing field. They go to the spring to drink water once a day around noon. The six groups including the AMG had movement patterns similar to this, and each group aggregated and separated among each other in the process of daily movement. They get together at the spring and sleeping sites. On the other hand, they disperse when they

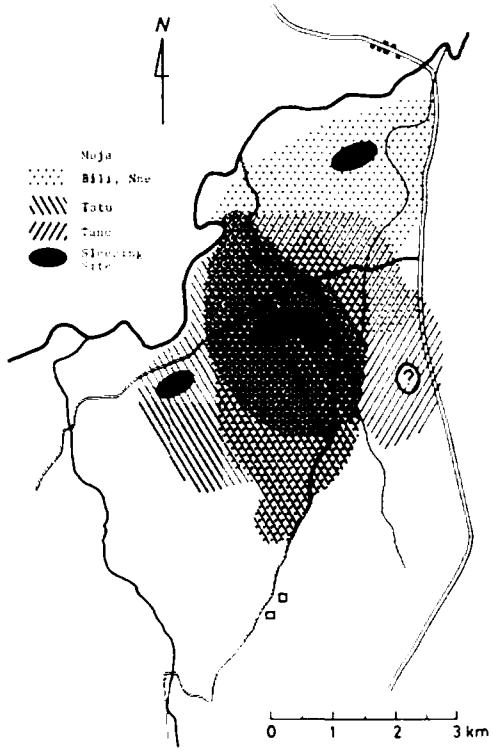

Fig. 2b. Moving ranges of each OMG of plain zebras in the Isiolo National Park. Each range was drawn by surrounding daily moving routes during the first study period as in Figure 1. The moving range of the Mume AMG is covering all the range of these OMGs.

move from the sleeping site to the grazing field in the morning or from the spring to the sleeping sites. Although each group occupied different areas in some parts, the fact is that these six groups of OMG and AMG had no exclusive territory to each other but shared the same moving range.

Their unity can be explained in terms of formation of group association. The Moja OMG, one of the five OMGs, for example, was found alone 154 times, and in association with other groups. Other groups, Bili, Tatu, Nne and Mume (AMG) showed a similar tendency. Therefore aggregation of groups was rather frequent. Only Tano tended to be alone more frequently than others, and its moving range extended toward the eastern border of the park.

The number of days on which other groups, Sita, Nane, Tisa, Kumi, Wageni (AMG) Jirani (AMG) and Jozi (pair) were observed was 3, 5, 4, 12, 8, 1, and 9 of 130 days respectively. They were groups which wandered into the study area. The Sita and the Tisa groups appeared only in the first study period; the Nane, the Wageni, the Jirani and Jozi groups appeared only in the second study period; the Kumi group appeared in both periods. Although the usual moving ranges of these nonresident groups were not confirmed through direct observation, the route of entry to the park was found for some groups. They (the Kumi, the Nane, the Wageni and the Jozi groups) were observed to progress slowly from the south east to the Buffalo Spring. In the south-eastern direction there is a large fertile grassland where some groups of the BS cluster stayed for several days in the rainy season in 1980. It was suspected that the usual home range of those nonresident groups was in the vicinity of this plain. Fig. 3 shows the distribution of plain zebras around the Isiolo National Park. The data is based on the survey in neighbouring areas. A few groups were found to inhabit near the park though they were

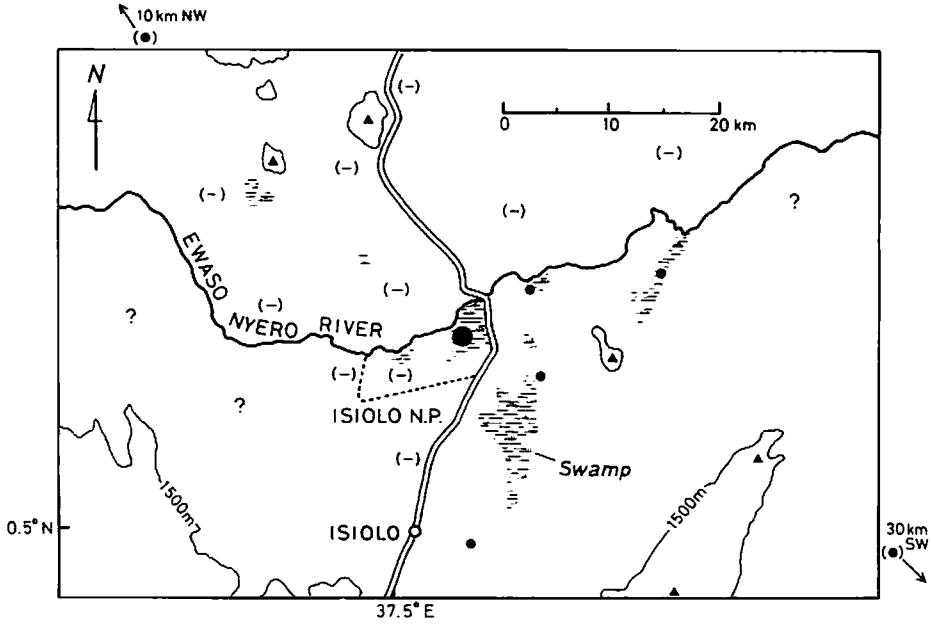

Fig. 3. Populations of plain zebras around the Isiolo National Park. Solid circles: Population observed. (–): not observed. ?: no information.

scattering and the density was low.

As shown in Figure 3, there was no resident group of plain zebras either in the western part of the Isiolo National Park or in the Samburu National Park which are located along the northern band of the Ewaso Nyero River, while another species of zebras, the Grevy's zebra, were abundant in both areas. In the north of the Ewaso Nyera, plain zebras were found near Wamba about 60km to the north west of the Isiolo Park. The Grevy's zebra have a wide distribution extending from the Ewaso Nyero River to Wamba or even furthermore to the north as well as covering all areas around the Isiolo Park in the south of Waso Nyero River. In contrast to this, the plain zebra has only a local and patchy distribution. The reason for this phenomenon is that plain zebras extend less freely to the arid area than Grevy's zebras, and the most favourable area around the Samburu and Isiolo Parks for plain zebras is around the Buffalo Spring.

The six resident groups in the park did not move over a long distance through the whole year, though they sometimes left the original home range. Some of the groups moved to the south-eastern plain outside the usual home range for a short period amidst the rainy season in April 1980. Within a few days they returned to the Isiolo Park one by one. On the other hand, nonresident groups appeared frequently in the Isiolo Park at the beginning of dry season in June 1980, though they did not appear much in dry season from June 1978 to February 1979.

The moving pattern of the resident groups clearly indicated that the groups formed a cluster. The analysis of the moving pattern only, however, is not enough to clarify whether this cluster organization is based on some definite social behaviour or is forced by the environmental factor, namely, discontinuity and patchness of the environment. Nevertheless, it is notable that only these six groups had preference to this area in the park, while other group merely passed there in spite of no inhibition from staying there. The cluster of these six groups will be called the BS cluster therein after.

Group Transfer of Individuals

The membership of the one-male group (OMG) and the all-male group (AMG) of plain zebras is so rigid that members of a group are easily distinguished from others after a short period of observation. Therefore the member change of a group was usually very clear except some cases in which the transfer was not completed. Figures 4, 5 and 6 show transfer of individuals between groups, disappearance of members, and immigration of newcomers. The movement of members differed according to age and sex, so that the data were separated to three figures. In this section the age-sex category was divided into five: Adult Female (including full adult and young adult) in OMG, Adult Offspring in OMG and Adult and Young Males in AMG. Offspring includes Young, Juvenile and Infant.

(a) Adult Females

Parous females (full adult) and nulliparous adult females (usually young adult) were 21 altogether in the BS cluster in June 1978. The parous females were distinguished from nulliparous females by elongated nipples. None of these adult females disappeared before June 1980 (Fig.4). On the other hand five nulliparous young adult females entered OMG during the two year study period. One of them moved from the Tatu group to the Bili group, while the natal groups of the other four were not known. All of them were estimated to be more than one year of age and none of them were found in the BS cluster in the first study period. Therefore their natal group must be outside the BS cluster. Three OMGs had one female immigrants, one OMG had one, and another OMG had none. The immigration does not seem to be concentrated to a particular OMG,

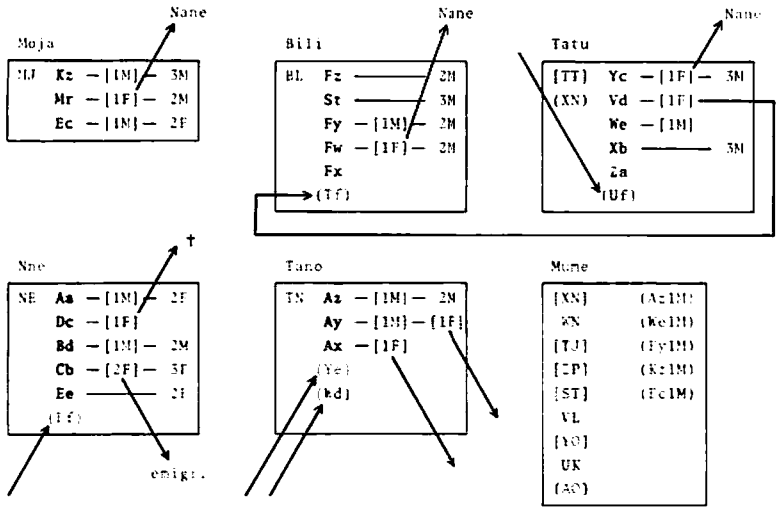

Fig. 4. Movements of adult females and female offspring into and out of OMGs.

though the number of study cases is not enough. This immigration of females corresponds to the emigration offemale offspring mentioned in the next section.

(b) Female Offspring

All the seven female offspring which were found in the first study period in 1978 and 1979 disappeared during the interval between the two study periods (Fig.4). One of them moved from the Tatu OMG to the Bili OMG as was mentioned in the previous section and made the sexual relation with the stallion of the Bili OMG. Three of them, from Moja, Bili and Tatu, were found in the Nane OMG which was discovered in June 1980. Another one (from Nne) which disappeared when it was an infant was considered to have died. The fates of the remaining two (in Tano) are not known. However, it is highly possible that they emigrated some OMG outside the BS cluster, because there were more migrants which moves out of the cluster than those which moved between OMG within the cluster. Still there is a possibility that they died, though mortality was not very high. In addition, there was one more case of emigration out of the BS cluster, which was directly observed. Thus, it is confirmed that all the female offspring leave their natal OMG at the age of around two, and also that almost all of them leave the natal cluster.

(c) Male Offspring

Of the eight male offspring which were found in OMG in the BS cluster during the first study period, five (two from Moja and one from Bili, Tatu and Tano respectively) moved to the Mume AMG in the same cluster (Fig.5). Another one (from Nane) was regarded to have died for the same reason as the female infant that disappeared at the stage of Infant. The other two disappeared during the interval between the two study periods, and nothing is known of them (Fig.5). They may have died since no young animal entered AMG from outside of the cluster; they were not found in nonresident OMGs, Wageni or Jozi.

As has been mentioned, many of the male offspring joined AMG in the natal cluster. This point makes a striking contrast to the movement of the female offspring. The age of their emigration was estimated at 1-2 or

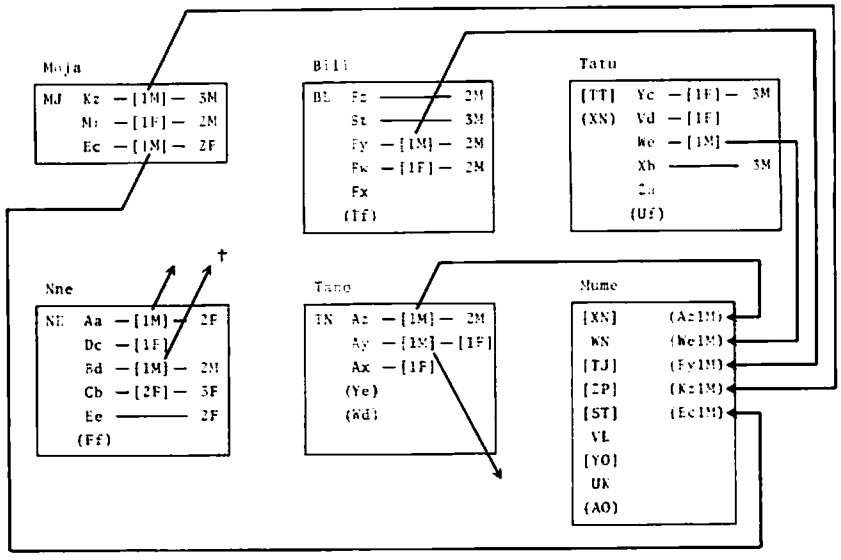

Fig. 5. Movements of male offspring out of OMGs.

3, although this study does not supply enough data on age.

It is noteworthy that there was only one case where a mother had two offspring at a time, the elder of which was a male. There was another notable case where a female offspring left her OMG on the birth of her sibling (see the section of case study).

(d) Adult Male

Males belonging to the category of Adult are stallions of OMGs and members of AMGs. Of them young immigrants to the AMG in the BS cluster were five which moved from OMGs in the same cluster as previously mentioned. They still belonged to the category of Male Offspring at the end of the first study period in 1979 and had not grown up to full size when they were found in the AMG in the second study period. Then, they belonged to the category of Young Adult in AMG. Another immigrant to the AMG was a full adult (called AO) which came from outside the BS cluster (Fig.6). AO was of the second biggest animal in body size in the AMG at the time of the second study period and became a central animal in the social relation of the AMG.

Among emigrants from AMG, XM which had been the biggest and the most dominant male until the end of the first study period, was found in the Tatu OMG as the OMG stallion instead of the former stallion, TU. TU had disappeared and could not be found again. Other emigrants from the AMG were three full adults and one young adult. They had disappeared before the beginning of the second study period and could not be found anywhere (Fig.6). In addition, the Wageni AMG and the Jozi AMG, both of which were found in the second study period, consisted of completely unknown members. Three of them had the same body size as young immigrants to the AMG of the BS cluster (e.g. Kz-1M and Fy-1M); it was confirmed that at least these three had not been born in the BS cluster.

The group transfer of adult males and male offspring is summarized as follows. First, males born and grown up in OMG leave the natal OMG before the age of two or three, and then most of them are observed to join the AMG in the natal cluster. They stay in the AMG for several years,

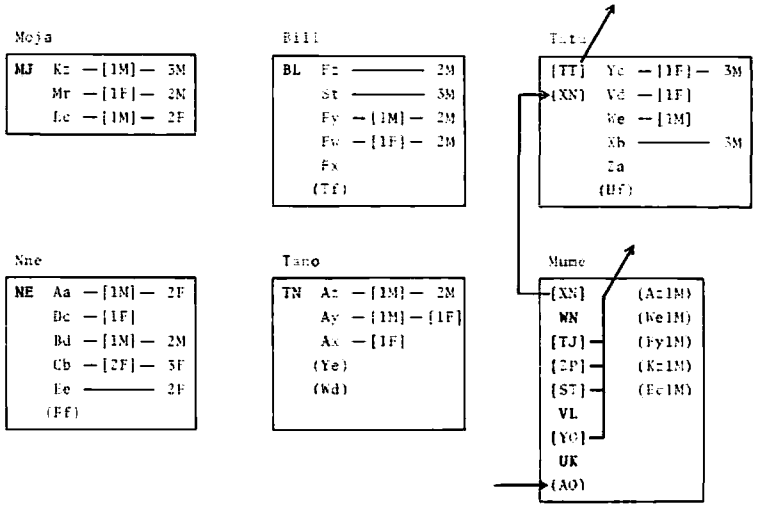

Fig. 6. Movements of adult males into and out of groups.

though many of them leave the AMG as well as the natal cluster. Since the previous social position of the full adult immigrant (AO) to the AMG was not known whether he had been a member of an AMG or a stallion of OMG somewhereelse, the fate of young emigrants from the AMG is difficult to guess. However, if AO was previously a member of an AMG somewhere, there is a possibility that emigrant males of the BS cluster joined some other AMG as well. On the other hand, it is not known whether some males from the OMG stay long in the AMG in the same cluster and can become dominant males. If it is possible, they will have a chance to taking over the position of the stallion of an OMG in the natal cluster. This point will be discussed in relation to the behavioural shift mentioned in the case study.

Figure 7 shows the balance sheet of member changes in OMG and AMG in all age-sex categories. This will be examined more closely in relations to other data from different viewpoints in the section of discussion.

Case Study: behaviour on group transfer and behavioural changes through group transfer

As we have seen in the previous section, there were many cases of group transfer found in the course of the two years' study period. Most of them, however, were not directly observed, because they took place during the interval between the two study periods. This section presents a few cases of direct observation and some cases on behavioural changes through group transfers.

Case 1. Emigration of a female offspring from OMG

This is the case where a female offspring (Cb-2F, the daughter of Cb in the Nne OMG) left her OMG on the same day when her sibling was born. Cb bore Cb-2F presumably soon after the end of the first study period and again bore Cb-3F about one year later, on 18 of May, 1980. When Cb-3F was first found, Cb-2F had already disappeared from the Nne group. Therefore her behaviour at the moment of leaving the OMG was not observed. The correlation between her emigration and the birth of her sibling, however, can be easily expected, since she had been with her mother in the Nne group until the previous day. After that she still

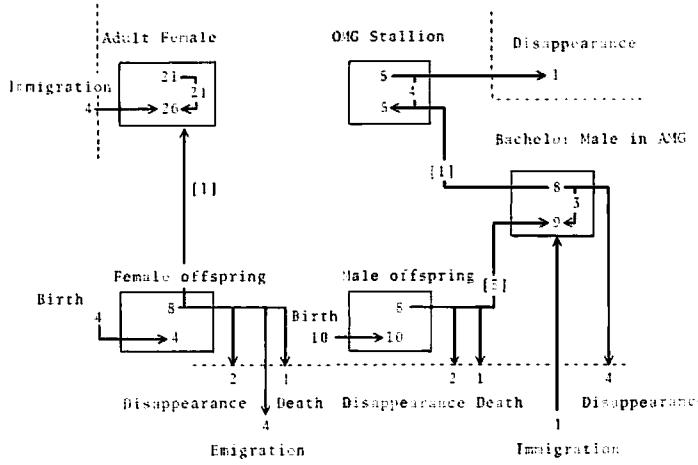

Fig. 7. Balance sheet of member changes in the Bc cluster.

stayed in the area of the BS cluster for a while, but finally left the area. The course she took after leaving the OMG finally to disappear is as follows:

> Until the evening of 19th Cb-2F could not be found anywhere, while all the other members of the BS cluster were found. Thus she had no contact with the members of the BS cluster at least. On the evening of the 19th, Cb-2F was found with the Bili OMG and the Mume AMG near the Buffalo Spring. She was chased after by the stallion of the Bili, BL, and the dominant male of the Mume, WM. In a little while BL gave up following her, while WM continued galloping to catch her. When WM caught her, she turned and began to follow WM slowly. All the while other members of the AMG were grazing in a group more than 100m apart from WM. The next morning at 7:08 Cb-2F was with the Mume AMG and the Tatu OMG in a plain 0.5km to the south west of the spring. When they were found, the stallion of Tatu (XN, the former dominant male of the Mume AMG), WM and other member of AMG were chasing Cb-2F. WM kept the shortest distance to her and interfered with the approach of others, especially of XN. When XN approached furthermore, Cb-2F ran away and all the males began to chase her. The OMG stallion frequently payed attention to his OMG, which was grazing 200m apart from him, and sometimes moved to and fro between XN and his OMG. Though fighting occurred occasionally between XN and some other males, Cb-2F's existence soon detracted XN's attention from fighting. At 7:58 all the males stopped chasing her, and at first XN returned to his OMG, and then AMG left for the south. Cb-2F began to walk to the east, after looking at both of the groups alternately. At 10:55 a.m. she went as far as the border of the Isiolo Park and further moved to the east where the BS cluster did not range. Thereafter she was never found in and around the Isiolo Park.

The males which had direct contact with Cb-2F during these two days were WN, VL and UK of the Mume AMG and BL and XN of OMGs, while other OMG stallions took no direct action to her though some may have glanced at her. As for the natal group of Cb-2F (the Nne) neither the stallion nor her mother showed any particular reaction to the disappearance of Cb-2F. On the other hand it is certain that many males were much interested in her. In this case the most dominant male in the AMG showed conspicuous behaviour, so that formation of a new OMG by a member of AMG might have been possible.

Emigration of Cb-2F from the natal cluster may have been caused partially by the absence of the male which could catch her, and consequently she left the natal cluster by herself. Such a case, however, might be typical in the emigration of females from a cluster since almost all the female offspring left the natal cluster as we have seen.

Case 2. Pair group

The pair group is noteworthy as a primitive pattern of group composition in the process of a new group-formation, though the Jozi pair did not belong to the BS cluster. The Jozi pair appeared for the first time in the Isiolo Park on May 25, 1980 in the same period when some nonresident groups (the Tisa, the Kumi and the Wageni) came to the park one by one. The pair consisted of a full adult male called PM and a young adult female called Pf. The pair came from the same south-west direction by the same route as those of the three nonresident groups. It travelled furthermore to the north and reached near the Buffalo Spring in the next morning. Its behaviour and interaction with other groups occurred thereafter are as follows:

> On June 3 the female of the pair (Pf), appeared alone without the male (PM). Pf was found near the Buffalo Spring within the Nne OMG, where the Moja OMG was grazing nearby. Though at first she was in the spread of the members of the Nne group, the response of other females to Pf was not affinitive. When one of the adult females, Cb, attacked and chased her, the stallion, NE, interfered. Thereafter Pf followed NE. Nevertheless when the OMG moved, Pf followed other females, and then NE accompanied her. This seemed to be the early stage of affiliation of Pf to the Nne group. Next day, however, Pf met PM and formed a pair again, and they did not approach other groups nearby but rather followed a territorial male of the Grevy zebra which was occupying there. This lasted for two days; then during the following three days PM was found alone. On June 16 missing Pf came alone to the Buffalo Spring, where the Wageni AMG (nonresident groups), the Mume AMG, the Moga OMG and the Tatu OMG had already arrived. The Wageni members rushed to Pf and there had some contacts with her. Soon afterward, since the stallion of the Kumi approached them, she ran away; and thereafter a chase lasted for more than 10 minutes around the spring. The Mume AMG also took part in the chase. During the chase MJ of the Moja stood watching the tag and all the females were grazing nearby. The Wageni was the first to leave the struggle, and next, the stallion of the Kumi went back to his OMG. The chase ceased when Pf was caught by WM, the most dominant male of the Mume. WM made naso-nasal contact with Pf and did not allow his group members to approach her. Afterward Pf left the Mume group and at 15:50 she was once caught by BL, the stallion of the Bili group; however, she soon separated from him again, as BL returned to his group. Then, she approached UK, the forth biggest male in the AMG, and made a nose contact with him. Suddenly UK mounted on her and succeeded in copulation. Thereafter UK and Pf left the

Mume and made a temporary consort. This relation was, however, over in a day. UK returned to the AMG and Pf disappeared next day. On the 10th and 18th of June, Pf was found once again with PM; and then my field survey was terminated.

In this way this pair was always attacked both by stallions of OMG and members of AMG, and was not stable in its social relation. As the male of the pair, PM, was a full adult, he had possibly been a member of some AMG. He tried to have stable relations with Pf by following her, as WM and UK in the Mume AMG did. It is hardly reliable that the stallion of OMG deserts his old females to make a new relation with a strange female, as was seen in the process of the tagging for the sake of Pf. As for Pf, since she was a young adult, she must have been a new emigrant from OMG somewhere. Such a scramble for a new female might have happened in Cb-2F of the Nne group after she left the BS cluster. The Jozi pair always tended to be disorganized, though it still had a possibility of growing to a new OMG. This tendency may be explained partially by antagonism of resident males to strange males, which was seen in the Wageni AMG and the Jirani AMG.

The following cases are of group transfer which I could not observe directly.

Case 3. Transfer to OMG stallion

The full adult male, XN, which moved from the Mume AMG to the Tatu was the biggest male in body size in the AMG during the first study period. He was also the most dominant animal, since he chased other AMG members away, and the others avoided him. Moreover, naso-nasal contacts and other actions of stallions were concentrated on XN. After XN left the AMG, this social position was succeeded to the male second in dominance, WM. In the Tatu OMG, XN showed the particular behaviour definite to the OMG stallion: dominant behaviour over his females, mating, leadership in procession (though this was not always shown), prevention against approach by other males to his females and so on. These behaviours were not different from those of other old OMG stallions. Furthermore, in interaction with OMG stallions and with the remaining members of AMG, he showed behaviour similar to that of other OMG stallions. On the other hand, AMG members did not show any particular behaviour to XN in comparison with that to other stallions. There were some interactions between XN and AMG members, including antagonism. Intimate interaction which was common to some extent between OMG stallions and AMG members may have been due to the individual antecedents as a member of AMG. This intimacy was in contrast with the interaction with males outside the BS cluster; fight and chasing were frequently observed between the cluster males and outsider-males.

Case 4. Transfer of male offspring to the Mume all-male group

Five of the male offspring moved to the Mume AMG. The most conspicuous change of behaviour was complete dissolution of mother-offspring relation, while this relation was strong when they were in OMG. After they left the natal group, direct contacts with their mothers was never observed. On the other hand, the stallions of the natal groups frequently visited the Mume AMG and contacted its members; however, they did not show any particular interest in the former members of the OMG, their possible sons, associating with them in the same way as with other members. Therefore, there is no positive relation between male offspring and his natal OMG, at least in actual interaction, once he leaves the group.

Case 5. Behaviour of female immigrants

The newcomers to OMG had sexual relations with the stallion of the

OMG. A distinct phenomenon which show their relation with the stallion was the order of individuals in procession. Members of a one-male group walked in a file especially when they moved for a long distance, and the order of precedence was rather stable. An instance is as follows:

> The Moja group consisted of three adult females, their offspring and one stallion. In the procession, offspring usually walked next to its mother, otherwise preceding her, therefore offspring will be excluded from data of order of procession to make it simple. The stallion walked last in 47 out of 87 procession samples. Of these 47 cases, the female order –Kz, Me, then Ec– was seen 23 times (49%, expectation=17%, $P<0.005$). Ec was slightly smaller and younger than the other two, though she also had offspring. Kz, who sometimes chased and attacked other females, was most dominant of the three females, and seemed to be older than the other two.

A similar phenomenon was seen in all other OMGs. In the Nne group, a young adult nulliparous female Ee, had been the nearest to the stallion until Ff, the newcomer, transfered to the group in 1979. Since then Ff was the nearest and Ee became the second nearest to the stallion. This order of precedence lasted at least until June 1980. The same case was found in the relation between Fx and the newcomer, Uf, in the Tatu group.

The preceding order among old females was fixed during the two years in all the four OMGs which were precisely studied. Accordingly the order of precedence or dominance rank is expected to correspond to the length of time during which females are in the OMG. Estrous females, however, became near to the stallion, which affected the order of precedence. However, the order in a long distance procession was not much affected by this, and the original order recovered when the estrous period ended. Birth of a infant did not affect the order directly, though the mother and her new infant sometimes fell behind in progress. In this case the stallion waited for them.

Four female newcomers to OMGs (three of them to the Tisa group outside the BS cluster), whose natal groups were known, did not show any response either to the natal group or to their mothers. Generally, old adult females in OMG had no relation to any other OMG; they must have dissolved the relation to the natal group when they deserted it. This is the same as that of young males which entered AMG. Only one case where an adult female contacted with a member of another OMG was observes in the Tano unit. NE, the stallion of the Nne group, mounted Ye, which was a newcomer in 1980; therefore her social relation with her stallion may not have been stable yet. This suggests the reason why the OMG stallion tends to follow the newcomer.

DISCUSSION

Group transfer of individuals and the related behaviour, which have been presented in the previous section (cf. Fig.7), are summarized in the life history of zebras as follows. All the zebras born in the one-male group (OMG) leave their natal group while they are still young. Then, almost every males joins an all-male group (AMG) in the natal cluster, whereas almost every females rather goes out of the natal cluster to join some other OMG. Once adult females move in some OMG, they seem to stay in it for the rest of their life. On the other hand a male who once joins an AMG seems to leave both the AMG and the natal cluster: this movement of males is induced from the fact that many members of the Mume AMG

disappeared and the newcomer from outside of the BS cluster joined the AMG. When the male grows up to full adult and becomes dominant of the AMG, he has chance to become a stallion in an OMG. There are two possible ways for a bachelor male to become a OMG stallion: to take over the place of an old OMG stallion or to form its own OMG by collecting young females one by one. The Jozi pair might have been an example of the latter case in the initial phase of an OMG formation.

Based on this life history of the plain zebra its social organization can be concluded as follows: the one-male group is the reproductive and also social unit where its members permanently hold both sexual and non-sexual relationship. Its diachronic maintenance is not succeeded by offspring of the group-member but by new members, both males and females, who join the OMG one by one; the lineage in OMG is positively cut off. Furthermore, the tenacity of both AMG and OMG to their moving range, social contacts among them, and their alienation with nonresident groups which appeared as migrant groups were observed in the population of Isiolo area; these facts suggest that the cluster of an AMG (or unexpectedly AMGs) and several OMGs is an entity as a higher-leveled organization than that of OMG or AMG. The females in the cluster tend to change groups once in their young stage and the males in both the AMG and the OMG come into contact with each other in the cluster, and then make the whole cluster an association unit, though they may also move out of it during their lifetime. The antagonism of the males to the male outsiders also supports the entity of the cluster. The scheme of these feature of their social organization is drawn in Fig. 8.

This scheme has some points for argument. The first point is the cause for emigration of female offspring from the natal group. It was clearly related to the birth of the sibling in my actual observation. In the BS cluster there was no case where a mother accompanied both a daughter and its younger sibling. On the other hand, Klingel (1967; 1974) states that female offspring neither get chased away nor go out by themselves, but are abducted from the natal OMG by adult males outside of the natal OMG when they are in estrus. Though estrus must be a cause for female emigration as Klingel observed, in the present study the female emigrant observed was about one year old and was not in estrus; and furthermore no female offspring was found to be with her younger sibling. Therefore the birth of the younger sibling must be an important factor in emigration of female offspring. There was one case where a mother

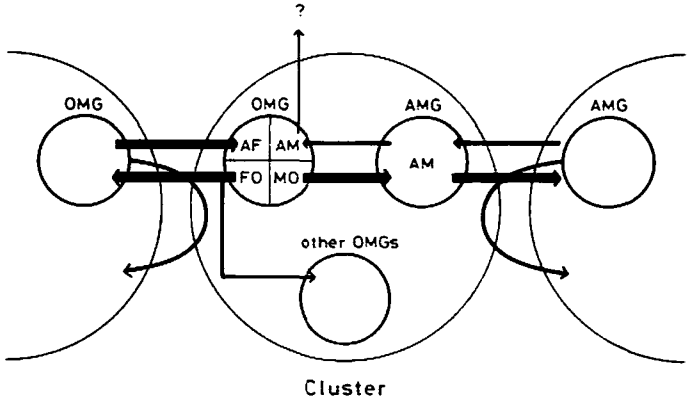

Fig. 8. Schematic Organization of the cluster in relations to group transfer of individuals.

accompanied a son (not a daughter) and its younger sibling. This results is the same as what Klingel (1967 and 1974) pointed out, where male offspring stay much longer in the natal OMG than female offspring.

The second point is that females transfer from one cluster to another once in their lifetime, though there may be some exceptions. There is no positive reason why the transfer between OMGs in the same cluster is easier than the shift between OMGs in different clusters, since no positive relationship was found between female offspring of one OMG and those of another. This is in contrast to the fact that male offspring in OMG frequently come into contact with AMG. Acquirement of a young female is not easy because of competition among adult males and also because of difficulty for a stallion of an OMG in controlling both the new and old females. While males are in struggle, the young female goes away to some other area as was previously mentioned. Even if such a female is sometimes caught by a stallion in her natal cluster, generally emigrant females tend to leave their natal area.

The third point is whether a male can became a stallion of an OMG in his natal cluster or not; in other words, whether a young male in an AMG which was born in OMG in the same cluster stay long enough in the AMG to become a stallion of an OMG in the natal cluster. If this is possible and common, the cluster can be maintained by male lineage. In the present study, however, there is no positive data to support this; on the contrary, some of the members in AMG were observed to change.

The last point is the examination of the entity of the cluster. The characteristics of the cluster which have been hitherto pointed out are as follows: 1. The association among groups in the same cluster and the local concentration of moving ranges of each OMG. 2. Antagonism between OMGs of different clusters. Cluster transfering of individuals, especially of females. On the other hand, it has been also mentioned that the cluster is such an open system as an OMG from outside a cluster can enter temporarily without interference. From these traits given above, the first one in particular can be explained as that the cluster is merely the result of concentration of their favourable environments. In fact the environment around the Isiolo National Park is rather too arid for plain zebras and their favourable habitat is limited to around the Buffalo Spring. The cluster is considered to have characteristics of 'ecological group' which is formed through the overlap of moving range of each OMG and AMG. Once a cluster is formed, neighbourhood relation, which was advocated in the study of the horse society (Imanishi, 1949; 1955), will develop among groups in the cluster and also some of antagonism will be shown to outsiders as was seen in the case of the AMG. Thus, emigration of female offspring from the natal cluster also proves to be an important phenomena in relations to the cluster organization. In conclusion, though the cluster may be formed by the environmental factors, social relation develop in the cluster, and the cluster itself becomes a social association unit.

Klingel (1967) enphasized that each OMG and AMG can move independently even in a big aggregation of 3,000 zebras and concluded that only OMG and AMG are the clearly organized social unit as "Ein über die Familien und Hengstgruppen hinausgehende Organisation war nicht festzustellen". Ecological aggregation such as a cluster may not be formed in the uniform environment, and may show a different feature in a huge migrant group such as in Serengeti. A completely uniform environment, however, does not exist; and accordingly, such a cluster is considered to be easily formed and to be common, though more precise study in the uniform environment is required.

Other species which have non-territorial one-male groups and form an aggregation of OMGs are found in Equidae; their social organization is almost same as that of plain zebras (Klingel, 1968; 1974a). Almost all

terrestrial mammals with OMG other than Equide are territorial species. A few species with non-territorial OMG, which has been studied in detail are Gelada Baboons and Hamadryas Baboons in Primates.

Gelada baboons (Theropithcus gelada) have the non-territorial one-male groups, and all the OMGs aggregate in a 'band' joined by AMG. The band is more constantly organized than the cluster of plain zebras, which can be easily visualized in the field. Each OMG and AMG in a band, however, can move independently and sometimes enter neighbouring bands, and moreover bands can joint each other; therefore, in point of independence OMG and AMG of gelada baboons are similar to those of plain zebras. Such nature of OMG and AMG leads to the idea that each OMG of gelada baboons has its own home range and the band is organized in the concentrated area of home ranges of OMGs (Ohsawa, 1979b). This is superficially similar to the zebra cluster. Nevertheless, the social organizations of both species are completely different in the point of mechanism of formation and maintenance of OMG. In OMG of gelada baboons, while leader males can be altered and all the male offspring eventually emigrate from the natal OMG as seen in plain zebras, none of the females can transfer the OMG (Ohsawa, 1979a). Accordingly the OMG of gelada baboons is regarded as a matrilocal social unit. In contrast, the OMG of plain zebras are clearly not matrilocal and probably not patrilocal, but its lineage is rather succeeded by newcomers, both male and female, positively being cut off.

On the other hand, the social organization of hamadryas baboons (Papio hamadryas) is also different from those of either plain zebras or gelada baboons, though it has OMG and the band as in gelada baboons. Bands of hamadryas baboons are clearly antagonistic and more closed than that of gelada baboons, so they are regarded as homologous rather to multi-male groups of anubis baboons and OMGs are their subunit (Kummer, 1968; Itani, 1972). Furthermore, transfer of female between OMG in a band was reported (Kummer, 1968; Sugawara, 1981: the latter report concerns hybrids with anubis baboons); then the band is regarded as the basic social unit as multi-male groups of anubis baboons and OMGs of gelada baboons (Itani, 1972). The OMG of hamadryas baboons is not homologous to that of plain zebras at least.

As has been seen above, though a few cases of superficially similar society besides Equidae are found in Primates, their social organization are much different from that of plain zebras in their mechanism of social integration especially in relation to their life history and their origin must be different from that of plain zebras. As for the origin of OMGs of plain zebras, territorial OMGs maintained throughout a year, such as the Vicuna (Koford, 1957), may offer some available data for further discussion, considering that territorial species, such as Grevy zebras, are found in Equidae, though they do not have the OMG type (Klingel, 1974b). In the case of Equidae, if the territorial type is the original type of the OMG type of plain zebras, the problem to be solved is how the territoriality was disoluted in Equides social evolution. Intensive study of the development of neighbourhood relation between two territorial groups may offer a key to the solution.

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