

VALERY G. CHALYAN, NATELA V. MEISHVILI

THE CASES OF COOPERATION AND ALTRUISM IN FREE-RANGING HAMADRYAS BABOONS

ABSTRACT: The cases of cooperation and altruism were observed in the troop of hamadryas baboons living in freeranging conditions in Gumista Reserve from 1974. Altruism and cooperation of these animals have been studied by registration of all cases of such behaviour as well as by experimental modelling of such conditions. The observations showed that hamadryas baboons are characterized by high level of cooperative activity which is the regular component of their behaviour in extreme conditions, though it is also noted in their everyday life. Most often the cooperative behaviour has been registered in the situations of defence of the troop members waiting for the members which left behind the group, and also during the cooperative investigative activity. The investigative activity has been seen in appearance of new subjects in the field of vision, which were not so dangerous for them (not poisonous snakes for example). In such situation all juveniles were the most active in their cooperative actions, regardless of their kin relations or belonging to some clan or harem. Waiting for the troop members keeping behind has been seen many times during the troop movement. This behaviour has most been observed in males waiting for females and may be considered in this case as a fragment of herding behaviour. However, this behaviour was directed not only to females, it could also be seen towards other individuals. The cooperative actions during the defence in hamadryas baboons have been recorded in the situations of danger for all troop members and also during intragroup conflicts between the individuals. The number of animals involved in the defensive actions was variable from several individuals to all the troop members depending on the extent of danger or the severity of conflict. Among the defenders the most active reactions were seen in the animals most closely related to victim individuals - kin related ones as well as the members of the same sub-unit, first of all those of harems or clans. And, in this case, the differences in the behaviour of different rank monkeys have been noted. Young and low-ranking animals showed mainly a relatively harmless distant aggression towards the enemy and the complaint-appellation to the higher-ranking individuals. On the contrary, higher-ranking animals including adult and subadult males and some of the females demonstrated more severe forms of aggression and attacked the enemies. As a whole, the tendency and extent of cooperative actions in hamadryas baboons during the defence correlate rather strongly with the hypothesis of kin selection. It must be noted that in some cases the altruistic and cooperative actions in hamadryas baboons might be characterized using such categories as "selflessness" and "intelligence".

KEY WORDS: Hamadryas baboons - Free-ranging conditions - Cooperation - Defence

INTRODUCTION

Some characteristics of social organization of hamadryas baboons such as strict structure and regularity of social relationships have been known for a long time (Kummer 1968, Kummer et al. 1985, Sigg et al. 1982). These

characteristics are based on the arid semi-desert conditions which are typical for their habitat. High probability of altruistic and cooperative behaviour is very important for their surviving in severe conditions.

There are numerous descriptions of altruistic and cooperative behaviour in primates (Boesh, Boesh 1989,

Saayman 1971, Stolz, Saayman 1970). Most of them consider the cases in which the monkeys help the old, sick and weak individuals (Struhsaker, Gartland 1970). Though the hamadryas baboons are well enough studied and they are common in the collections of zoos, this rather curious characteristics has not been actually described. Our long-term field studies of hamadryas baboons made it possible to observe numerous cases of their altruistic and cooperative behaviour. Here we try to summarize the description of such behaviour and to present the analysis of some characteristics.

MATERIAL AND METHODS

The observations have been carried out in the Gumista Reserve located at 20 km of Sukhumi. The territory of the Reserve is an area of beech forest limited by Western Gumista river on its eastern side. Hamadryas baboons were introduced to the Reserve in 1974. Their population varied in the range of 76-500 animals in different years. All the animals have been identified and tatooed. Everyday registrations included the data of observations of their physical state, birth and mortality and social structure changes. Up to 1993 the observations in ecology, demography and behaviour had been carried out in Gumista Reserve (Chalyan et al. 1991, Chalyan et al. 1994). In 1993 the observations were interrupted due to military actions in Abkhazia. The data presented have been obtained as a result of behavioural investigations during the period 1974-1993. The data have been collected by focal animals sampling method and ad libitum observations (Altmann 1974). The cases of altruism and cooperation have been registered and subjected to analysis. Besides that, part of the material has been collected in the course of specially designed experiments directed to the establishment of behavioural characteristics of hamadryas baboons in the experimental extreme situations.

Before the discussion concerning the cases of cooperation and altruism in hamadryas baboons some preliminary stipulations should be mentioned. First of all we should specify these conceptions according to the context. We do not discuss here all the possible meanings of these concepts. In our investigation we have used the terms in more limited sense. The cooperation in hamadryas baboons is considered not in context of their everyday activity (such as the situations in which the animals help the females with bringing up the newborns) but in the frame of cooperative actions of these animals in more complex situations. Another criterion of the behavioural characteristics which have been considered by us, is the apparent communality of actions in the situations when each animal takes part in solving the problem. The aim of the investigation was to show the range of variability and the potential source of adaptive abilities of hamadryas baboons, which promoted their successful adaptation to a new habitat. Such abilities helped them to develop the adequate strategy of feeding behaviour, to adapt to new foods and to find appropriate shelter and resting places. It is suggested that the possibility to demonstrate the altruistic and cooperative behaviour in hamadryas baboons should be considered as the most important component of the adaptive resources of these animals.

The investigations of such kind are mostly descriptive without any statistical analysis of the data obtained. Each of individual observations may be considered as single and unique. Nevertheless, the accurate registration of the events along with detailed information on each of the animals studied, including their kin and social relationships, allow to consider and use the data obtained in the course of our observations as valuable scientific material.

RESULT AND DISCUSSION

It must be noted that the group of hamadryas baboons which we studied was characterized as a multilevel structure typical for these animals. It included one-male units – harems in higher organized formations – clans and bands. Though during the 20-year observational period the group which has been studied was considered as a whole troop, taking in account that it had the same sleeping places, the marked dynamics of its structure development has been noted, directed to the increase in the number of different rank sub-units.

Cooperation in the course of investigative activity

The collaborative and common activity in hamadryas baboons has been evident in numerous different situations such as in the course of their investigative activity. The common investigative activity, spontaneous and observed in the situation when the animals were presented the new subjects which attracted their attention, should be considered as the most frequently occuring expression of cooperation. The cooperative character of such activity is of great significance in a new habitat where the survival of the animals and their adaptation to a new area are mostly dependent on the extent of their cooperative activity. The activity of hamadryas baboons in the situation of new subjects appearance was stereotypic and rather typical for primates. At first the attention of all the monkeys was directed to a subject which was presented to them, and then their activity was slightly changing. The subsequent activity of the animals developed variously depending on the extent of their familiarity with the subject and its evaluation. If the subject visually identified by adults was associated with a real danger, the activity of monkeys was developing like the one in the situation of collective defence in which the investigative behaviour was not noted any more. But if the subject was not of much significance for the monkeys (it was neither food nor any dangerous item), the interest to it was progressively decreasing along with its investigation by adult animals. In such cases the young animals of both sexes continued intensive investigation of the subject. Such behaviour has been noted by us in the situation when the baboons saw the unvenomous snake (a grass-snake). Their first reaction on seeing the snake was fear. The baboons that saw the snake vocalized with alarm sounds and the other members of the group were alert and tried to visualize the dangerous subject. On examining the snake and having identified its undangerousness they were loosing their interest in it and returned to their habitual activity. After that the grass-snake was surrounded by the youngs trying to examine it, lunging, approaching, touching and pulling it. In the case when the snake did not manage to escape quickly such collective examination lasted at least 15–20 minutes.

It must be noted that there were numerous species of snakes on the reserve territory, including the venomous Kaznakov's adder. The hamadryas baboons distinguished it from the other snakes which they used to see on the territory of the reserve and it was evident by the attacking behaviour of the adder. When the baboons could not identify the snake (for instance in the case when it was presented to them by the experimentator holding the snake's head) their reaction was always the same as on seeing the adder. They uttered the alarm sounds and all the animals of the group tried to escape and did not approach the place where the snake was.

It was notable in the cooperative behaviour of hamadryas baboons that in the situation when some of the animals saw the snake all the members of the group reacted to the subject. Most of the animals were involved in the examination of the subject irrespective of their kin relation or rank. The subadults examining a grass-snake, a frog or a camera belonged to different clans or bands. Besides, during the cooperative examination the animals sometimes even joined the researchers and showed an interest in a new subject.

Waiting for the animals which were behind

Besides the joint investigative activity the cooperative behaviour of hamadryas baboons was also evident in the situation when the group members were waiting for the animals lagging behind. Such waiting was evidently seen in both spontaneous and experimental situations. To facilitate the observation of all the changes in the troop structure some food pellets have been scattered on the feeding areas of the reserve every day after giving a vocal signal. Every day the order of appearance of the monkeys at feeding places and the order of their leaving those places have been registered and the data have been used for evaluation of the troop structure. Besides, we had a possibility to observe numerous situations when the monkeys were waiting for the animals behind. The evident waiting behaviour has also been observed in the situation when the baboons started their every day marching. The sleeping places of hamadryas baboons were mostly large beech trees. On awakening they moved to the areas under the trees and then started their marching to the foraging places. It was the most appropriate time for registration of waiting behaviour. To obtain the model of the situation of waiting, individual animals were isolated for a short period of time in a cage previously used for feeding.

The observations have shown that in hamadryas baboons waiting is always social by its character, though the extent of the behaviour associated with waiting and its duration in different monkeys is highly variable according to the situation. Both the parameters - the duration of waiting and individual activity - are in close connection with many factors such as their close relation with the animals which are behind the group and their belonging to the same structural sub-unit. At first, when the weak animal is behind the group, all the baboons of the group stop moving and demonstrate waiting. Some time later (in 20-30 minutes, depending of the time of the day) some animals belonging to another band start moving. Later, after a similar interval, the monkeys of other clans also stop waiting. The longest period of waiting has been noted in the situation when the animal, which was in a visible distance behind the group, was a member of the harem or a closely related relative. In the case when the animal whom the group members had been waiting for was an old female, the most prolonged waiting (till the night nesting) has been noted only in the individuals of the same harem.

Waiting behaviour could be directed to the different animals irrespective of their sex and age. In natural conditions it was mostly directed towards the independently moving infants, juveniles as well as to the old females. Nevertheless, numerous cases have been noted in which the waiting behaviour was directed towards the adults, including the bachelor males. For the whole 20-year observational period in the reserve we did not actually witness any case when the hamadryas baboons left alone any group member and did not wait for them when they were behind the troop.

Waiting behaviour could be different in various situations. In some cases the group of monkeys just did not leave alone the animal which was behind the group, or was unable to move for some time. Sometimes waiting looked like a slow moving of the monkeys, with some animals looking back at those which were behind and uttering some sounds of calls. It was also observed that the baboons waiting for those left behind, after having moved as far as dozens of meters from them, joined the troop only on the approaching of the individuals they had been waiting for.

Waiting behaviour was a part of the normal daily activity of hamadryas baboons and occurred in the situation of danger. Nevertheless, the altruistic aspect of such behaviour was always evident. Monkeys waiting for the animals which were behind, spent part of the their daily activity time for that to the detriment of other types of activity, such as feeding. Besides, the last of waiting animals were the most probable candidates to be involved into the same dangerous situation. Sometimes waiting behaviour was not just a passive waste of time, but it was associated with some active actions connected with a real danger. It can be

illustrated by the episode which took place in September 1986: It was on the bank of the Gumista river which served as a natural barrier for the baboons. A tree washed up by the river water was bent down over the river and the animals could cross the river (from its "monkey's" bank to the left one). On September 13 we observed a group of 8 monkeys belonging to the same clan (6-7-year-old males) which crossed the river and after wondering for some time around the forest appeared on the base area, while the whole group was waiting for them across the river. On seeing them on the other side of the river the males started to cross the river jumping in bipedal position. Seven males successfully crossed the river, while one of them returned back and stayed there alone. Then one of the males which had already crossed the river again went into the river, crossed it and joined the animal which had remained on the left bank. He presented himself to that male, and then both males went to the water. The leading male easily crossed the river and again found himself on the "monkey" bank while the male following him returned again to the left side from about the middle point. The male which had repeatedly crossed the river came back again to the left bank, again presented himself to the "coward" male and quickly went to the place where the bent down tree was (at 700 meters from a ford). The "coward" male followed him and the other animals observing them were running along the river parallel to its right side with excited calls. Both males succeeded in crossing the river moving along the tree trunk (the leading male was followed by the "coward" one) and joined the troop.

Cooperation and defence

Cooperative behaviour of hamadryas baboons was the most evident in the situation of the defence of group members. Such defence has been noted in the case of intragroup conflicts or in the situation of some external danger. As it is known, the animals' mutual support during the antagonistic relationships is common for different primate species and is well enough described. Hamadryas baboons are not an exception in this respect. Moreover, the course and resolution of conflicts in the troop of hamadryas baboons is mostly collective by its nature. For instance, the major part of intra-harem conflicts between the females involves some third animal - the leading male of the harem to whom the conflicting females usually appeal. The conflicts between the females of different harems often develop to aggressive relationships between the leading males of those harems and usually the majority of monkeys of such harems are involved in them. High ranking males to whom the other males can appeal are also often involved in the conflicts. Clearing up the relations between the individuals may take place at the highest emotional level with loud vocalization but with minimum contact aggression and actually without injuries.

The signal for defensive behaviour and for the intrusion of a third animal into the conflict in hamadryas baboons is the demonstration of compliance and sneaking with

peaches of an animal presenting itself and pointing to an offender. The adolescents and females are most of all the offended animals which need defence, but sometimes there are adult males among them, which appeal to other males. The direction of appeal behaviour to a defence is linked with the rank and complex kin-related and structural relationships. Mostly, low rank animals appeal to high rank individuals for defence, though among the adult males the appealing to mutual support is frequently seen without any association with rank relationships. The above mentioned can be illustrated by the following situation observed in May 1979: An adult male (N10688) of the highest rank in the troop tried to take away a young female with a sexual skin swelling (sexually receptive female), that was already a member of a young adult male's (N13721) harem. In that situation, the young male appealed to all the other males. As a result, the male N10688 was actually attacked by all the troop members. Finally, the female which was the subject of competition remained in the N13721 male's harem.

One of the marked characteristics of the hamadryas baboons behaviour is the extremely high level of collective and well organized defence behaviour in the situation of external danger. Such situations were modelled using different forms of potential danger. The most primitive form of hamadryas baboons behaviour in a situation of danger was their reaction to all the troop members being gradually captured and examined (which was performed every year). The baboons observing the researchers reacted to their manipulations (handling, tattooing, etc.) with loud calls and attacks.

Field studies as well as the results of the experiments have shown that the expressiveness of the baboons actions, the number of individuals involved in the defence and the level of their activity are associated with the extent of the danger and its direction. The activity of monkeys during the capture and examination should be considered to be aggressive demonstrations, while a true defensive behaviour, involving first of all the adult males, was noted on their meeting with the real predators. The fauna of the reserve territory includes such animal species as wild boars, wolves, wild cats, lynxes and bears. So, meeting the predators was very probable for the hamadryas baboons living in the reserve. For the experimental modelling of the situation of meeting the dangerous predators, two variants were used - demonstration of a dog and of a wild boar to baboons. In all the cases of a sudden demonstration of a dog the sequence of defensive actions of hamadryas baboons was the following: Adult males immediately gathered around it in an offensive position in form of a ring which gradually tightened. The ring was surrounded by subadults and high ranking females (second line). All the other monkeys were behind. They supported the attacking animals with loud calls and lunges. The strategy of the behaviour of hamadryas baboons on meeting a wild boar was quite different. As soon as they saw it (a stuffed animal of medium size shown to them unexpectedly out of

the bushes), the signal of danger followed and all the monkeys disappeared from the visible area.

It must be noted that the collective defence from the external danger was demonstrated in the case when each troop's member (irrespective of sex and age) was in danger. However, the most active collective actions were undertaken in the case when a black infant (natal colour) was in danger. In this case the infant's close relatives showed the most active defence, first of all the male - leader of the harem - i.e. its biological father. The newborn's mother usually appealed to the male for getting support and kept behind him. In individual cases the newborn's grandmother - the high ranking adult female, demonstrated a very active defence. Such behaviour was noted when an infant of female N13725 was in danger (capture and handling). In that situation the infant's mother was keeping behind the male N13721 which showed a defence, and near to the male there was the newborn's grandmother (N12613) which also actively defended the infant.

Defensive behaviour of monkeys has also been observed in the situation of saving the infant which had fallen down into the water. The hamadryas baboons in the reserve were wondering along the banks with great pleasure, sometimes searching for food under the stones – the Plecoptera larvae. Sometimes they sailed and even went deep into the water – this, however, occurred only in extreme situations. In the above mentioned case the black one – a half-monthold infant, found himself on a piece of log, stuck to the river bank. Suddenly the piece of log took off and went down the river with the infant on it. A male – the newborn's father, immediately rushed into the water and caught the infant. Later the situation was repeated (by experimental modelling) and the reaction of the monkeys was the same.

The behaviour of monkeys directed to the defence of the animals of their own troop, has been characterized by variations associated with sex and rank. The activity of young low-rank animals was mainly expressed in the form of relatively harmless distant aggression towards their enemy and a complaint — when the animals appealed to the individuals of high rank. On the contrary, high-ranking animals including adult and subadult males and some of the high-rank females showed more severe forms of aggression and attacked the enemy.

During the defence of the monkeys irrespective of their age and sex, as in the case of the infant's defence, the most active were the close relatives as well as the members of the same sub-unit, first of all of the harem and clan. For instance, in the above mentioned episode of carrying the young male across the river, the male of the same clan, young male across the river, the male of the same clan, having the same father as the young animal, helped him. These data are in agreement with the results of the analysis of waiting behaviour, which also supposes high level of altruism in the actions of waiting animals, helping or altruism in the actions of waiting animals, helping or defending their group mates. In the troop of hamadryas defending their group mates. In the troop of hamadryas the baboons which was under the investigation, besides the structural traditions some effective relations along two lines of kin-relations (maternal and paternal) have been noted.

The relations between the offsprings of the same maternal line were more stable, comparing to those between the animals non-related on maternal line. Besides, the males having a common father also formed units which served as a main body for the subsequent division in clans. The analysis of the support and collective activity in the troop of hamadryas baboons taking into consideration their kinrelations shows that although all the cases of altruism in these monkeys cannot be fully explained in the frame of the hypothesis of kin-selection, most of the cases of help and defence expression were in agreement with this hypothesis. The monkeys belonging to the same troop always helped each other (waiting and defence), although the level of the expressiveness of these behavioural forms depended on such factors as kin relatedness and belonging to the same structural units. Taking into consideration that a troop of hamadryas baboons includes a high number of kin-related animals and that the kin relations are very significant in the forming of structural levels of a troop, the hypothesis of kin-selection in this species is of a great significance. Defending the members of its troop, each of the hamadryas baboons defends its relative, i.e. its own genetic contribution. It also concerns the behaviour of a male defending its harem against external enemies. Taking into account the long-term relations between the males and females, the defence in these monkeys may be considered as a chance to increase the progeny of the females.

CONCLUSIONS

Cooperative actions of baboons mostly occurred in the situations of defence of troop members, waiting for the group members lagging behind the group, and also during the cooperative investigative activity. Cooperation in baboons defence took place in the cases of intra-group conflicts or in the situation of some external danger. The extremely high level of collective and well organized defence in the situation of external danger is one of the marked characteristics of the hamadryas baboons behaviour. The expressiveness of the baboons actions, the number of individuals involved in the defence and the level of their activity are associated with the extent of the danger and its direction. The behaviour of monkeys directed to the defence is characterized by variations associated with sex and rank. The activity of young and low-rank animals was mainly expressed in the form of relatively harmless distant aggression towards their enemy and a complaint when the animals appeal to the individuals of high rank. High-ranking animals, including adult and subadult males and some of the high-ranking females, showed more severe forms of aggression and attacked the enemy. During the defence of the monkeys the most active were the close relatives as well as the members of the same sub-unit, first of all of the harem and clan. The analysis of the support and collective activity in the troop of hamadryas baboons taking into consideration their kin-relations shows that

although all the cases of altruism in these monkeys cannot be fully explained in the frame of the hypothesis of kinselection, most of the cases of help and defence expression were in agreement with this hypothesis.

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Valery G. Chalyan Natela V. Meishvili Institute of Medical Primatology Russian Academy of Medical Science Sochi, Sochi – Adler Vesseloye-I 354385 Sochi-A Russia

Tel: +7-8622-919262

Fax: +7-095-9561711 E-mail: iprim@sochi.net