

THE DEVELOPMENT OF BEHAVIOUR IN FREE-LIVING BABOONS
(PAPI • ANUBIS)

Chapter I: The Nucleus

Introduction

2. The questions asked

3. The experimental design

4. The results

5. The conclusions



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by

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PREFACE

The work was carried out in the Gombe Stream National Park, Tanzania between January 1970 and September 1971.

I am indebted to Dr. Jane van Lawick for allowing me to use the facilities of the Gombe Stream Research Centre as a base for my fieldwork and to my supervisor Professor R. A. Hinde for his constant help and advice. I would also like to thank Appolynaire Sindimwu for assistance in the field. I am grateful to Dr. Leanne Nash and other people at the research centre for much fruitful discussion, and I express my gratitude to Miss Frankie Edmunds for her encouragement during the writing of the thesis.

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I declare that the contents of the thesis are based entirely on my own work and that the manuscript does not exceed 80,000 words.

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INTRODUCTION

1. The aims of the study

The major part of this study is concerned with an attempt to understand some aspects of the development of movement patterns and social behaviour in free-living baboons, and the ways in which infant baboons eventually become integrated into the adult social structure of the troop.

The first chapter of the study deals with the mother-infant relationship, and an analysis is made of the relative contribution of mother and infant in maintaining the mother-infant bond and the roles of each in bringing about the age changes in the relationship which lead to the infant's independence.

The second chapter is concerned with play behaviour and sets out to determine the importance of social play in the development of movement patterns and social relationships. Agonistic, sexual, maternal and paternal play patterns are considered.

In a subsidiary section data are presented on non-social play including manipulatory and locomotor play in order to assess to what extent movement patterns might also develop outside the context of social play.

2. Why a field study?

Few quantitative studies of the development of social behaviour in individual free-living primates have so far been carried out. This is largely due to the practical

difficulties involved in recognising and following a particular animal in the wild and recording behaviour at the same time. Field studies have the added disadvantage that it is difficult to control or allow for the many variables that exist in the physical and social environment of a wild group. Not least of these is the presence of the observer.

However, the social and physical environment of a wild monkey is much richer than that of any captive monkey and, as Jay Dolhinow and Bishop (1971) have stated, 'the complexity of social relationships which structure the life of the individual ... can be appreciated only in the field'. It is known that the interactions between a mother and infant baboon may be influenced by the nature of their social companions (Rowell, 1968). Furthermore, there is much evidence that the social structure of baboon (and other primate) groups may be affected by ecological factors (Kummer, 1968, b; Rowell, 1967, a and b). Thus the social environment in which a young primate develops may be altered by placing animals in captivity.

It has also been claimed that animals in captivity play because there is 'nothing else to do', their primary needs being provided for (see Thorpe, 1966). Thus if one is to assess the importance of play in behavioural development it is essential to know to what extent animals play in the wild. Moreover, laboratory studies tend to underestimate the complexity of play patterns that may occur in nature (Hinde, 1971).

Clearly it is not possible to gain a complete

understanding of primate behavioural development from either field studies or laboratory studies alone; the two approaches should complement each other (see Mason, 1968). At the present state of knowledge however, primate social development, and particularly play behaviour, is little understood, and many basic problems can be approached through quantitative observational studies in the field (see Hall, 1968). Such studies are needed in order to formulate testable hypotheses which can form the basis for future experimental work in both the field and laboratory.

3. The study area

The study was carried out in the Gombe Stream National Park, Tanzania between January - November 1970 and April - September 1971. The geography and ecology of the park have been described in some detail by van Lawick-Goodall (1968) so I will give only a brief description here. The park consists of a strip of land about 10 miles long and 3 miles wide along the eastern shores of Lake Tanganyika. From the lake at 2,500 feet above sea level the land rises steeply to the rift escarpment of 5,000 feet, 3 miles inland. Between the escarpment and the lake run a series of steep-sided parallel valleys. The bottoms of the valleys contain gallery forest or dense thickets of scrub and lianas, whereas the ridges between the valleys consist largely of open grassland and savannah woodland.

Most tree species lose their leaves in the dry season, which lasts from May to September, and visibility during this time is good. In the wet season, tall grass and dense

foliage limits visibility to a few yards in some areas, though the wide shingle beach is a good observational area at all seasons.

My work was largely confined to one baboon troop ('Camp Troop') which occupied an area of about two square kilometres. Their range included the lower part of a forested valley, a grassy ridge, a strip of savannah woodland behind the beach and the beach itself (Plates I, II and III). A small stream also runs through the area. A chimpanzee research station, consisting of several prefabricated huts was within the troop's range, and here the chimpanzees were periodically fed bananas. Although feeding baboons was discouraged, they did occasionally succeed in obtaining bananas or banana skins. However, the troop did not generally linger at the feeding station.

4. The baboon troop

The baboons had the physical characteristics of the olive baboon, Papio anubis (Napier and Napier, 1967). At the beginning of the study in January 1970, Camp Troop, originally consisting of about 65 animals, had recently divided into two smaller groups of about 40 and 25 animals. Between January and April the two halves of the troop continued to sleep in the same sleeping trees, though they always remained separate during the day. After this time, the two groups gradually spent less and less time sleeping together, and the larger group began to occupy sleeping trees at the opposite end of their range. Several males, including four adults, one adolescent and one



Plate I. Part of the forested valley within Camp Troop's range.

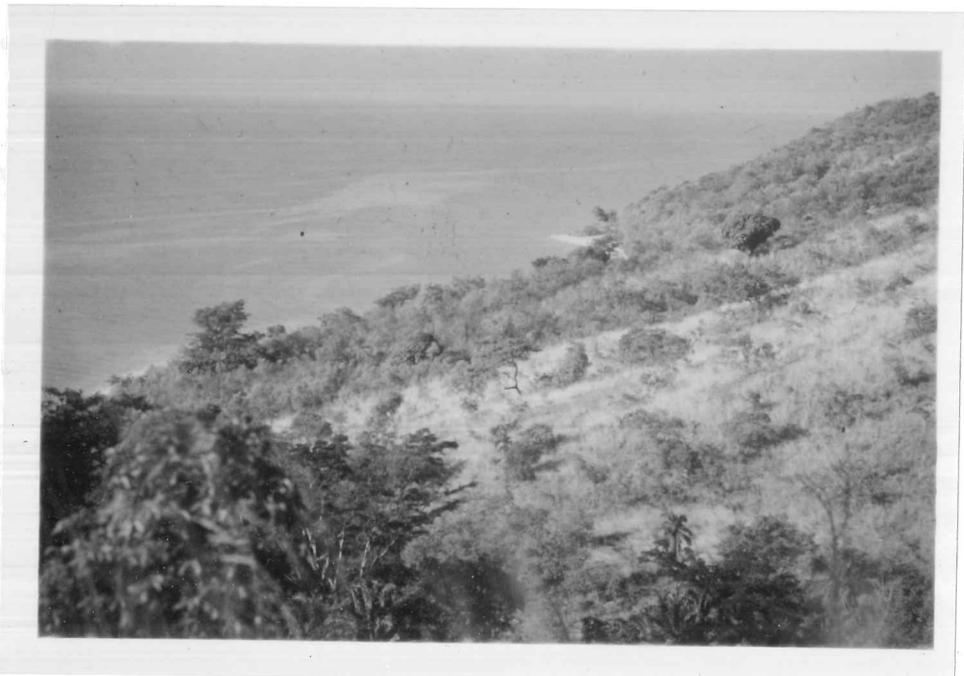


Plate II. An open savannah ridge within Camp Troop's range.

juvenile alternated between the two halves of Camp Troop during the time when they slept together. After this time adult males occasionally changed troop membership between all the three adjacent troops, though no further troop changes by immature males were observed. Females were never seen to change troops.

My studies were confined to the larger part of Camp Troop whose membership fluctuated between 40 and 45 animals during the study period. There were about equal numbers of males and females in the troop, though there were somewhat more adult females than adult males and fewer young females than young males owing largely to the difference in maturation rates of the sexes. Females reached maturity at 5 years, but although males reached sexual maturity at about the same time, they did not acquire their full stature and long mane until 7 or 8 years of age. There were 9 births and 5 deaths between January 1970 and September 1971. The main predator of the baboons were chimpanzees, and one infant was taken by chimps during the study.

After the transitional period following the splitting of the troop, the baboons settled down to a fairly regular daily routine, leaving the sleeping trees at 7 a.m., following a circuitous route through their range and returning at about 5 p.m. Thus it was quite easy to find the troop once I had achieved familiarity with their habits and regular daily routes. The bulk of the troop always remained as a close-knit group, most animals being within a circle of 50 m. radius even when they had spread out to feed. When the troop was travelling fairly fast (for

example as they left the sleeping trees), the animals kept even closer together. Usually the speed of movement did not exceed a fast human walking pace and was generally much slower. Because of the small range and dense food supply the troop only travelled about a mile during the day (Savannah baboons by contrast occupy an area of 2 - 15 square miles and travel about 3 miles a day (DeVore and Hall, 1965)).

The troop had been previously watched by Bonnie Ransom during 1968 and were used to seeing people round the chimp research station. When I arrived therefore, they were partially habituated to human observers. However, they became gradually more tame during the study, and after a few months I was able to mingle with the troop and follow particular individuals on foot at a distance of 15 - 20 feet. Although animals often threatened me at first, they gradually became less interested and usually ignored me. I came to acquire little more significance than another forest animal, and although I doubtless influenced their behaviour in subtle ways, I felt it safe to assume that my influence was not large enough to invalidate my findings.

5. Field methods

I was able to use the facilities of the Gombe Stream Research Centre as a base from which to work. The first few weeks were spent in practice at following the troop and trying to get them used to my presence. Once I had become familiar with the most regular routes used by the baboons, I cleared paths through the undergrowth in order to make following easier. Having achieved this, I began

to make more detailed observations on the animals, becoming acquainted with their behavioural repertoire and learning to recognise individuals. I then made qualitative descriptions of the behaviour patterns I wished to record as a preparation for the quantitative studies (see later).

In order to assess the age changes in the frequency of the different behaviour patterns I watched animals representing different age stages. The ages at which the different animals were watched in the mother-infant and the social play studies are shown in Fig.i. It should be noted that I did not perfect my play recording methods until August 1970 and play data recorded before this time were not used. Thus mother-infant records covered a larger time span than play records in 1970. The youngest animals were first seen a few days after birth and so their ages are known fairly accurately. The approximate birth dates of the animals born during 1968 (K, E, M and D) were recorded by Bonnie Ransom, but the births of G, L, H, Gd, J, Sn and Gb were not observed and the ages given here are all estimates based on size and coat colour. The estimates for the youngest animals (G and L) are probably accurate to within one month, and those for the oldest animals (J, Sn and Gb) to within six months.

6. Statistics

All the statistical tests used in the thesis are based on non-parametric techniques and are drawn from those presented in the book by Siegel (1956). Non-parametric tests are particularly suitable for my data for two reasons.

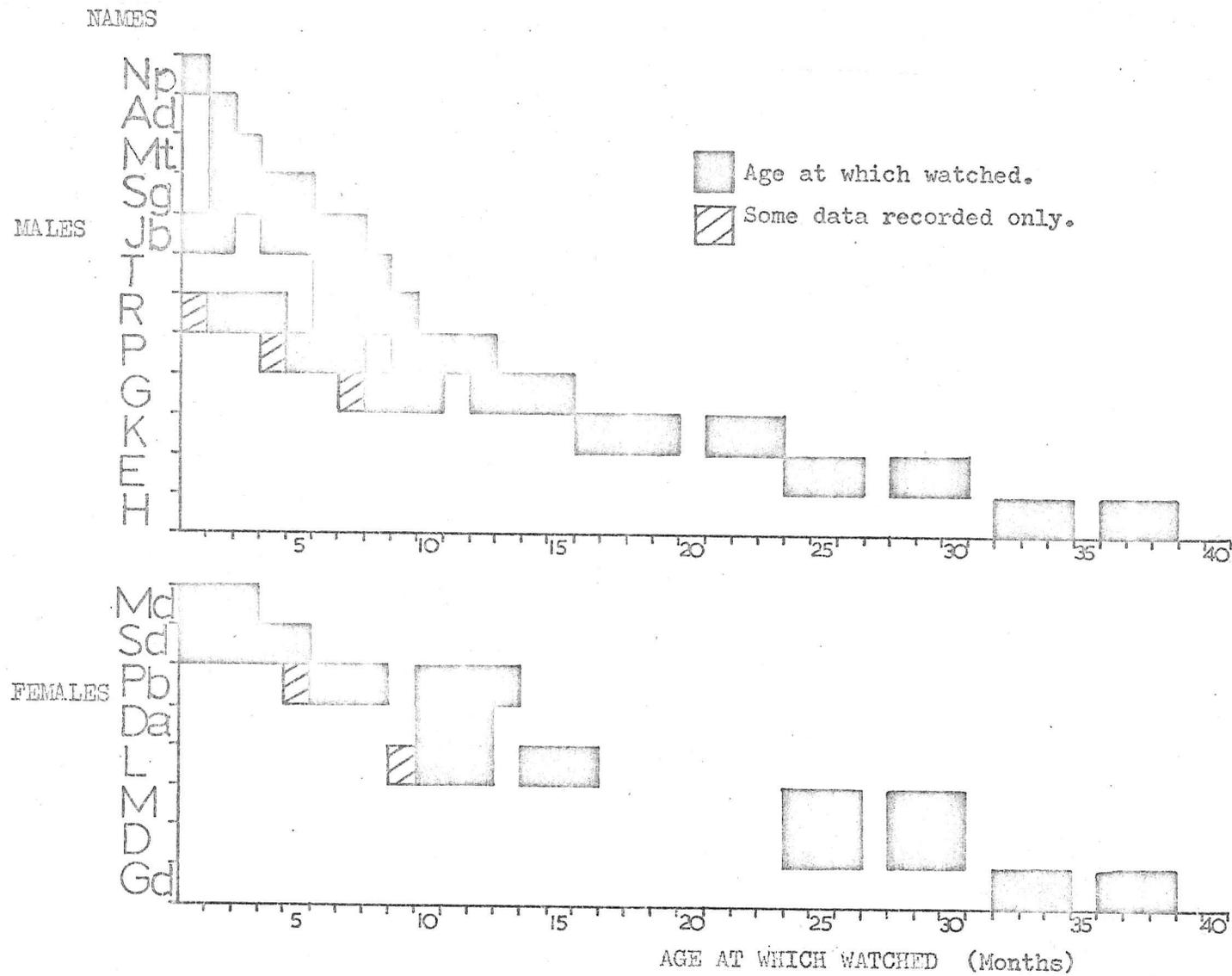


Fig. 1 a. The ages at which each animal was watched for the mother-infant study.

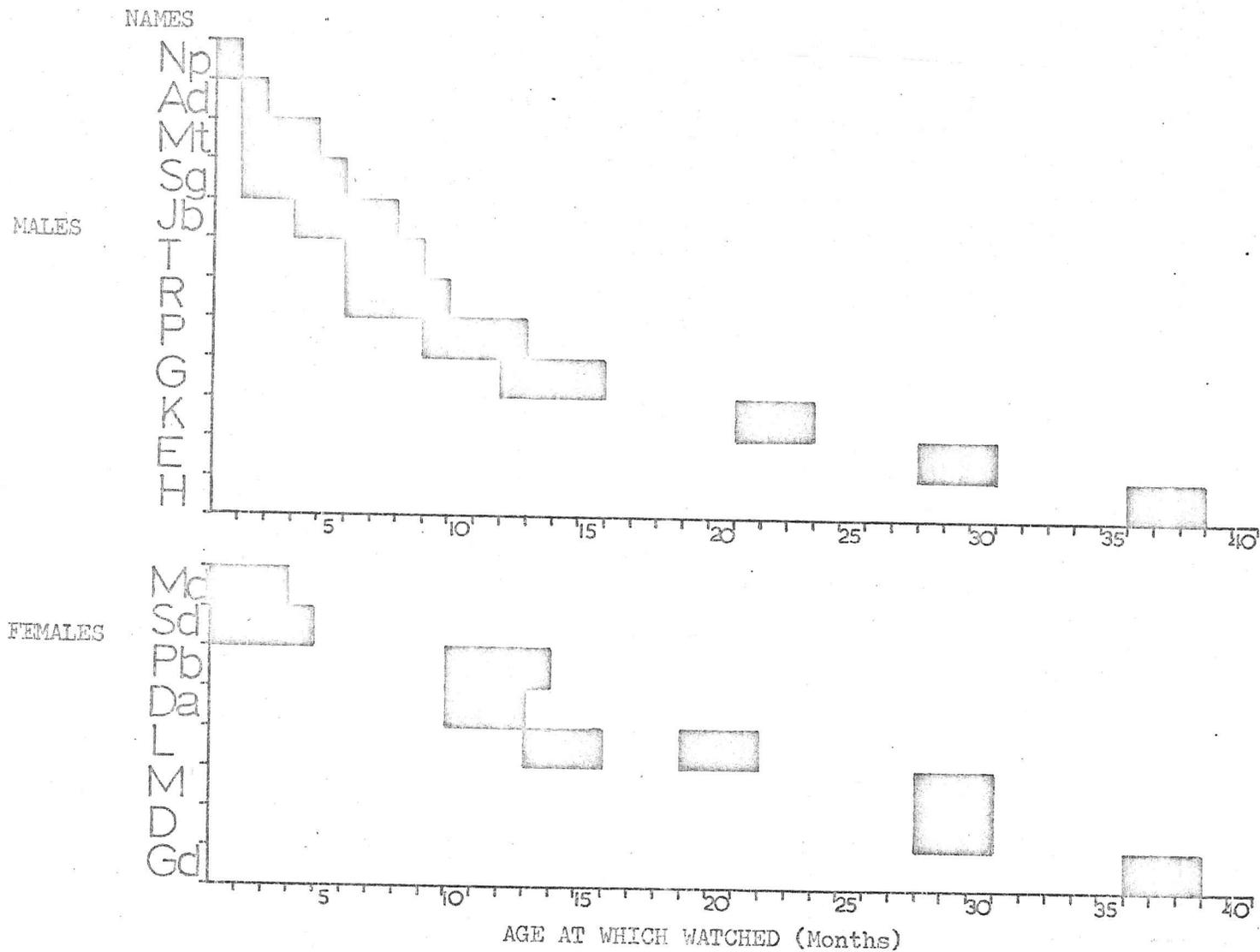


Fig. i b. The ages at which each animal was watched for the play study.

Firstly they do not carry the assumption that the data are drawn from a normally distributed population. Secondly, many of the tests are 'ranking tests' requiring measurement only to the ordinal level.

My data are largely concerned with age changes and sex differences in the frequency of behaviour patterns. In order to assess the probability that the age changes observed occurred by chance I used Spearman rank correlation coefficients (sometimes referred to as 'rs' in the text) comparing the rank order of the different points (representing different individuals of different ages) with the rank order of the ages of the individuals concerned. To test the statistical significance of sex differences in the frequency of measures I used three different tests depending on the nature of the data, namely: the Wilcoxon matched-pairs signed-ranks test (six independent pairs of animals, one of each sex matched for age were available for comparison); the Mann-Whitney U test and the Chi square test.

CHAPTER ONE

THE MOTHER-INFANT RELATIONSHIP

CHAPTER ONE

THE MOTHER-INFANT RELATIONSHIP1. Introduction

'The learning that brings the individual baboon into full identity and participation in the baboon social system begins with the mother-child relationship.' (Washburn and DeVore, 1961)

Although an infant monkey is born at a level of motor development roughly equivalent to that of a six month old human infant, it is at birth unable to walk and is dependent on its mother for transport, food and protection. Thus a baboon's earliest social interactions are with its mother, who shields it from excessive interference from other troop members during the first few weeks of life. Only gradually does the infant begin to interact with other baboons and become independent of its mother (see DeVore, 1963). Thus a logical starting point in a study of baboon social development is the mother-infant relationship.

Some aspects of mother-infant relations in captive baboons for the first three months of life have been studied quantitatively by Rowell, Din and Omar (1968) and a descriptive account for free-living animals is given by DeVore (1963). Mother-infant behaviour has been studied to a varying degree in a number of other primate species. The most detailed studies have concerned rhesus monkeys (e.g. Hansen, 1966; Harlow and Harlow, 1962 and 1969; Harlow, 1963; Hinde et al., 1964, 1967, b and 1968; Kaufmann 1966) and these are of particular interest here since rhesus monkeys are closely

related and have a similar social structure to the baboon (DeVore and Hall, 1965).

The Harlows' studies have involved social deprivation experiments in which infants experienced profound changes in their social environment, including maternal or peer deprivation, or both, for periods up to the whole of the first year of life. Their work has amply proved the importance of social experience for normal social development, deprived animals being socially maladjusted and inadequate in play, sexual and maternal behaviour. By providing a mother surrogate of various sorts they have also been able to demonstrate some of the physical characteristics of the mother which are most important to the infant. However, their experimental regimes have generally been too drastic to point to exactly which aspects of social experience are important for social development, and how individual differences in social development might come about in a wild primate group.

Hinde's studies, by contrast, have concentrated first on the normative aspects of behaviour and have made a detailed analysis of the changing patterns of interactions between mother and infant which lead to the infant's independence. Infants are brought up in a relatively complex social environment, and Hinde seeks to achieve a deeper understanding of the relationship by observing the effects of short periods of maternal deprivation and subtle manipulations of the social group. He has been able to demonstrate that the mother plays a large part in promoting the infant's independence and that aspects of the individual

differences between mother-infant pairs are due to differences in both the mother's and the infant's behaviour. The presence of other adult females may affect the relationship by making mothers more restrictive of their infant's attempts to leave them (Hinde and Spencer-Booth, 1967, a). Brief periods of maternal deprivation at 8 months of age cause great distress to the infant, and influence the relationship it has with its mother when they are reunited (Spencer-Booth and Hinde, 1967). Separated infants are more disturbed by slightly strange situations than are controls up to 22 months later though there are marked individual differences between mother-infant pairs in the recovery rate after separation (Hinde, 1971).

Rowell's methods for baboons have been similar to those used by Hinde, and she has also carried out experiments in which the other animals in the group are removed or reduced in number. Her conclusions are very similar to those for rhesus monkeys (Rowell, 1968).

Mother-infant relations have also been studied in some detail in pigtailed macaques (Jensen and Bobbitt, 1967), in pigtailed and bonnet macaques (Rosenblum and Kaufmann, 1967), langurs (Jay, 1963) chimpanzees (Van Lawick-Goodall, 1968) and some non-primate mammalian species (see Rheingold, 1963). Present knowledge concerning mother-infant relations in primates has been reviewed by Hinde (1971).

The purpose of this chapter of the study is to give a quantitative account of mother-infant relations in free-living baboons up to the age of 18 months which extends and is comparable with existing knowledge on baboon mother-

infant behaviour. It also provides a background knowledge of the early social development of some of the animals I observed in the play study. The social development of an infant through relations with its mother and through play behaviour with peers cannot be looked upon entirely as two separate aspects of social development, one must be aware of the interactions between them. For example, social experience with peers may largely compensate for a lack of social experience with a mother, particularly if a mother surrogate is provided (Harlow and Harlow, 1969). There is also evidence that the relationship an infant has with its mother may affect the extent of play with peers. When rhesus monkey infants are deprived of their mothers for 6 days but left with the monkey group, the amount of social play decreases (Spencer-Booth and Hinde, 1971). Infants brought up with peers only from birth exhibit little play, and that which does occur is in 'slow motion' (Harlow and Harlow, 1965). Individual differences in the restrictiveness of mothers may also affect the amount they are able to interact with other group members (Hinde and Spencer-Booth, 1968). In chimpanzees the effects may be more direct since mother chimps play a great deal with their infants (Van Lawick-Goodall, 1968).

2. The questions asked

The mother-infant study is intended to throw light on some aspects of the following questions:

- a. In what ways do mother and infant baboon interact and how does their relationship change with age?

- b. What are the relative roles of mother and infant in determining the relationship and in bringing about the observed age changes?
- c. Does the nature or stage of development of the infant's relationship with its mother influence the amount of play in which the infant takes part?

The study is primarily concerned with the normal stages of development of the relationship rather than with individual differences between mother-infant pairs. However, up to five infants were watched at each age stage so that some conclusions concerning individual and sex differences are possible.

3. Field methods and check-sheet design

I used similar methods and check-sheet design to those used by Hinde et al., (e.g. 1964) on rhesus monkeys and later used by Rowell (1968) on baboons. This should facilitate comparison between the different studies.

Each infant was watched at two weeks of age, and subsequently at monthly intervals for at least four hours each month. Records for different animals were made over the same time of day so far as possible, most watches being in the morning. Nearly all records were made in the dry season, but during the wet season records were suspended during rain in order that data from different times of the year should be compatible (rain is known to affect mother-infant behaviour in baboons (Rowell, 1968)). I recorded mother-infant behaviour on check-sheets divided into minute intervals. For some behaviour patterns I

recorded whether or not that pattern occurred in each minute. Other categories were recorded each time they occurred, regardless of whether or not they had previously been recorded in that minute. The mother-infant record was usually suspended when play took place in order to record details of play behaviour (see also under methods in play chapter), and during this time the infant was largely off the mother. Thus the data are biased towards giving a somewhat low estimate of the degree of independence of the infant. The mean length of time for which a mother-infant record was suspended for a play record was about half an hour. Thus the figures for time off mother calculated from a 4 hour mother-infant record are up to about 11 per cent too low.

In addition to the quantitative records I made supplementary descriptive notes on the behaviour of all the infants in the study.

From the check-sheet data I calculated the age differences in the relative frequencies of various categories of mother-infant interaction. These are now considered in turn.

4. Time spent on the mother's nipple

Fig. 1.1 shows the age changes in the percent of minutes watched in which the infant was seen to be on the mother's nipple. Two week old infants were on the nipple in about 80 percent of minutes watched and during a large part of this time they were asleep (Plate IV). Time on the nipple steadily decreased with age, becoming very

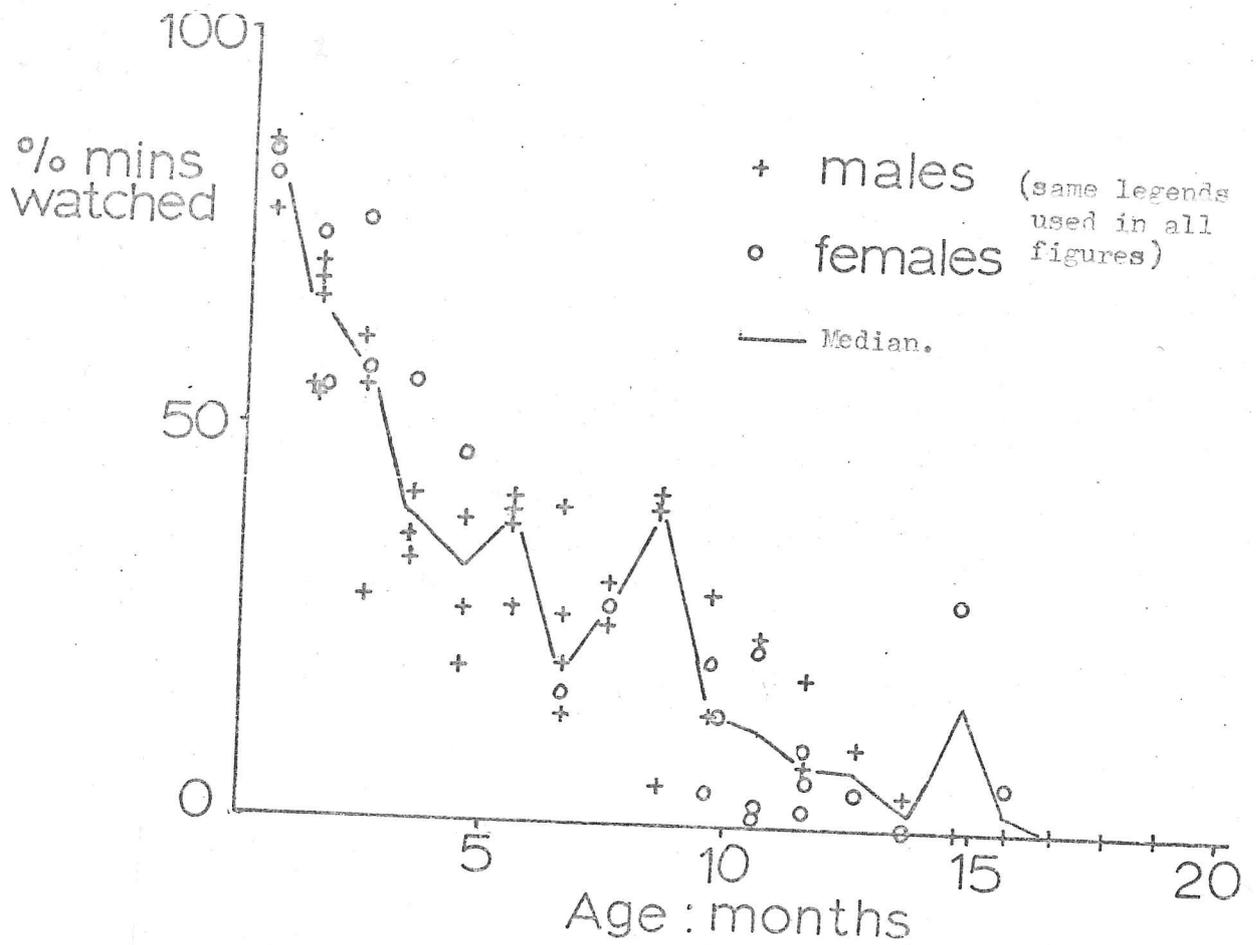


Fig.1.1. The percent of minutes watched in which the infant was on the nipple.

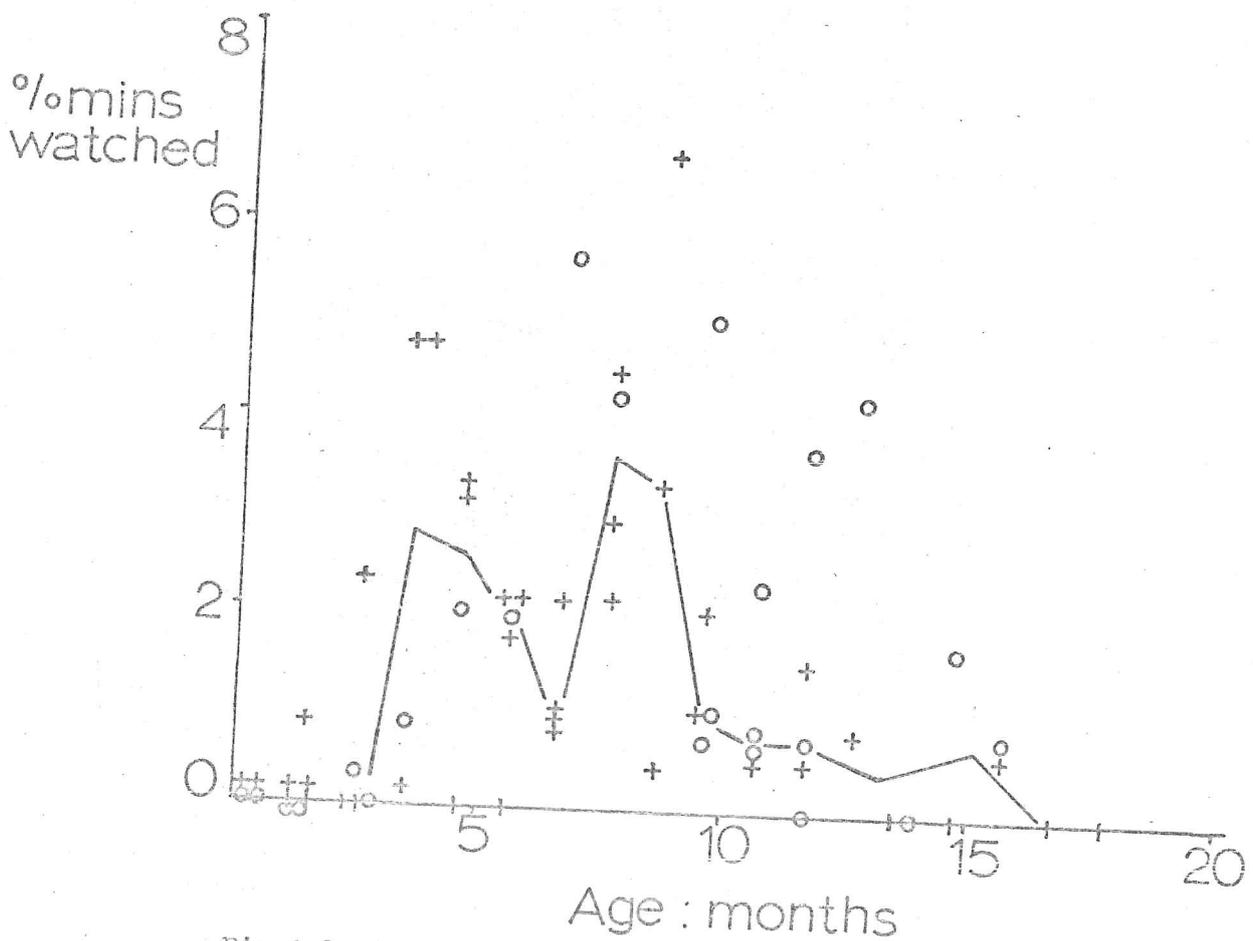


Fig.1.2. The percent of minutes watched in which the infant was rejected by the mother.



Plate III. Some of Camp Troop on the beach.



Plate IV. A six month old infant asleep on the nipple.

infrequent by 16 months. This meant that infants were independent of their mother's milk by the time the next infant was born, the minimum interval between births observed being 19 months.

Whilst the infant was on the nipple it was not always possible to see whether or not it was suckling. However, infants did sometimes appear to be on the nipple but not suckling, so this measure is probably not an exact reflection of the relative amount of milk obtained at different ages. When riding ventral on the mother the infant often held the nipple in its mouth though appearing not to suckle, the nipple being used as an extra means of support. Thus it is possible that, as the infant becomes older and spends less time riding ventral, the proportion of time when it is on the nipple but not suckling may decrease. Thus the slope of the graph may imply a faster rate of weaning than in fact occurred.

5. Rejections by the mother

The term 'rejection' is used to mean an intervention by the mother which prevents the infant's attempt to gain the nipple. She may simply move her arm between her breast and the infant, preventing its advance, or if the infant is persistent she may push it away from her, sometimes quite roughly, or even bite the infant's arm. The infant often becomes very distressed, even from a gentle rejection, and may rush away from the mother in a tantrum and vocalise for several minutes.

Mothers were first seen to reject their infants at

the age of 6 - 10 weeks in males and 10 - 14 weeks in females. Rejections became most frequent (in terms of the percent of minutes watched in which they occurred) for both sexes between six and nine months of age (Fig. 1.2). Rejections continued until the infant ceased to attempt to gain the nipple at about 16 months old.

I also assessed rejections (R) as a percentage of the number of successful attempts (A) and unsuccessful attempts (R) by the infant to take the nipple. The expression calculated was thus $\frac{R}{A+R}$. This measure gives an estimate of the number of rejections relative to the number of attempts, successful or otherwise, by the infant to take the nipple, and so allows for the age changes in the extent to which the infant sought the nipple. The relative frequency of rejections tended to increase with age ($r_s = 0.84$; $p < 0.01$, Fig. 1.3). Thus mothers became steadily less tolerant of their infant's attempts to gain the nipple as infants became older.

6. Vocalisations

The age changes in the frequencies of three types of vocalisation were estimated by calculating the percent of minutes watched in which they occurred.

Gecking: is a staccato one-phase noise made by the infant when in pain or discomfort. Gecks may occur one after the other in a series, and frequently occur following a rejection, but they also occur in other contexts such as rough play.

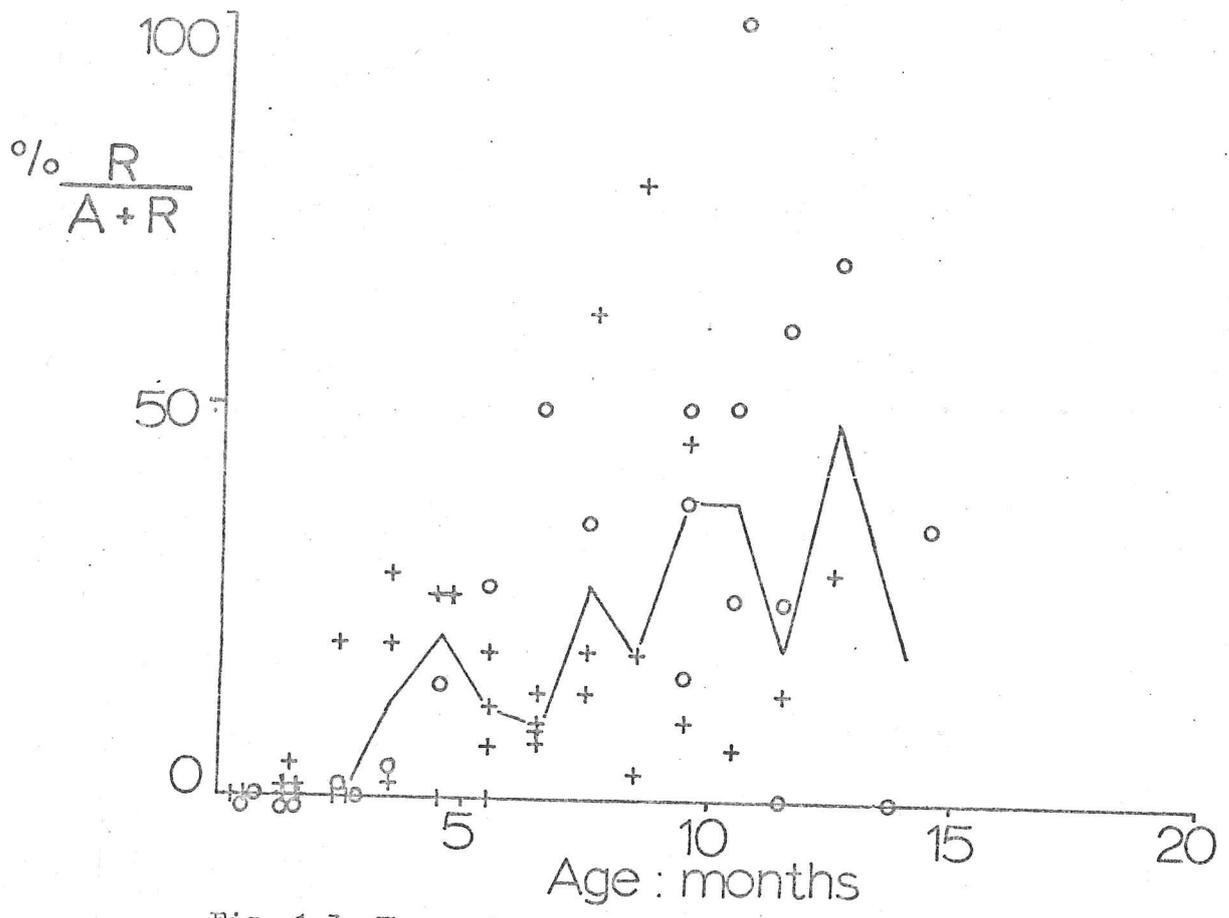


Fig. 1.3. The number of rejections as a percentage of the number of attempts, successful or otherwise, by the infant to gain the nipple.

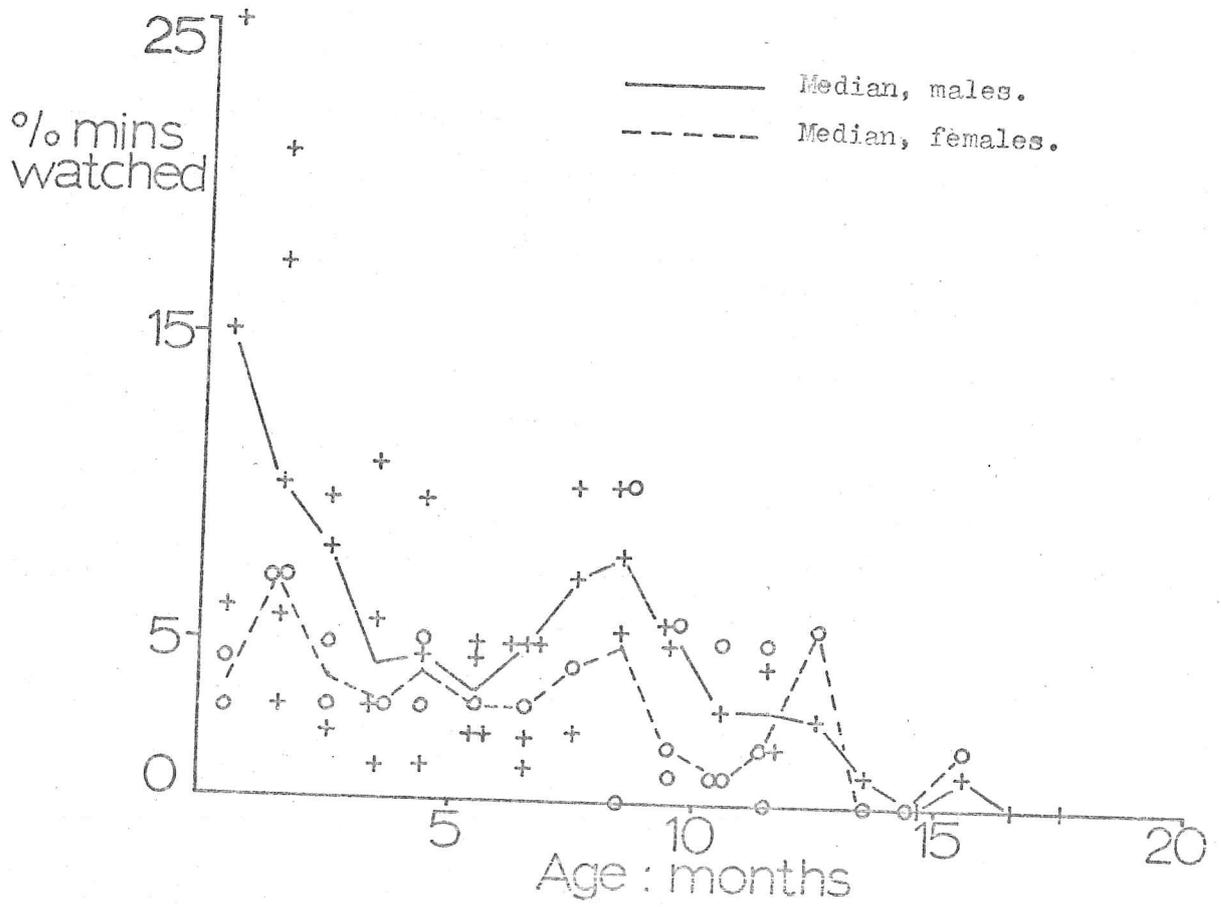


Fig. 1.4. The percent of minutes watched in which geeking occurred.

Screaming: also occurs when the infant is in pain, but usually in more intense situations, and may also be heard in contexts other than rejections, such as rough play and aggression.

Moaning: is not usually the immediate response of a rejection, but frequently occurs a short time afterwards. Moans may be interspersed with both gecks and screams following a rejection, and may continue for several minutes after other vocalisations have ended. Moans seem to express a state of frustration and discontent rather than physical discomfort. Unlike gecks and screams, moans are rarely heard in contexts other than mother-infant interactions, and are seldom heard in animals over sixteen months of age, at which time they are weaned. Thus the relative frequency of moaning is probably a better indication of the state of the infant's relationship with its mother than are the frequencies of the other types of noise.

In male infants, peaks in frequency of vocalisations occurred between 7 - 10 months (gecks), 7 - 10 months (screams) and 6 - 9 months (moans) (Figs. 1.4, 1.5 and 1.6). These peaks correspond roughly to the peak in the frequency of rejections which came at 6 - 9 months. There was an additional higher peak in gecking during the first four months.

In female infants gecking and screaming showed no particular age trends. Gecking was generally less frequent in females than in males ($p < 0.01$; Wilcoxon matched-pairs test). There was also a peak in moaning between 8 and 13 months old.

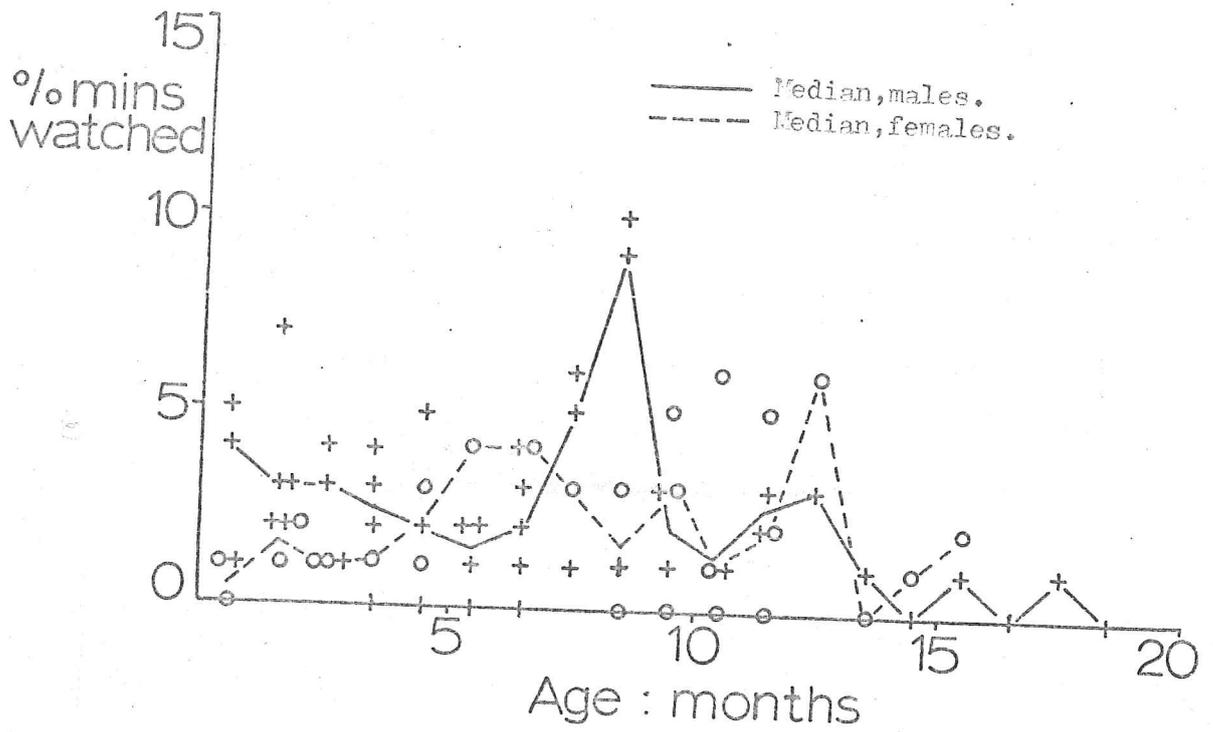


Fig. 1.5. The percent of minutes watched in which screaming occurred.

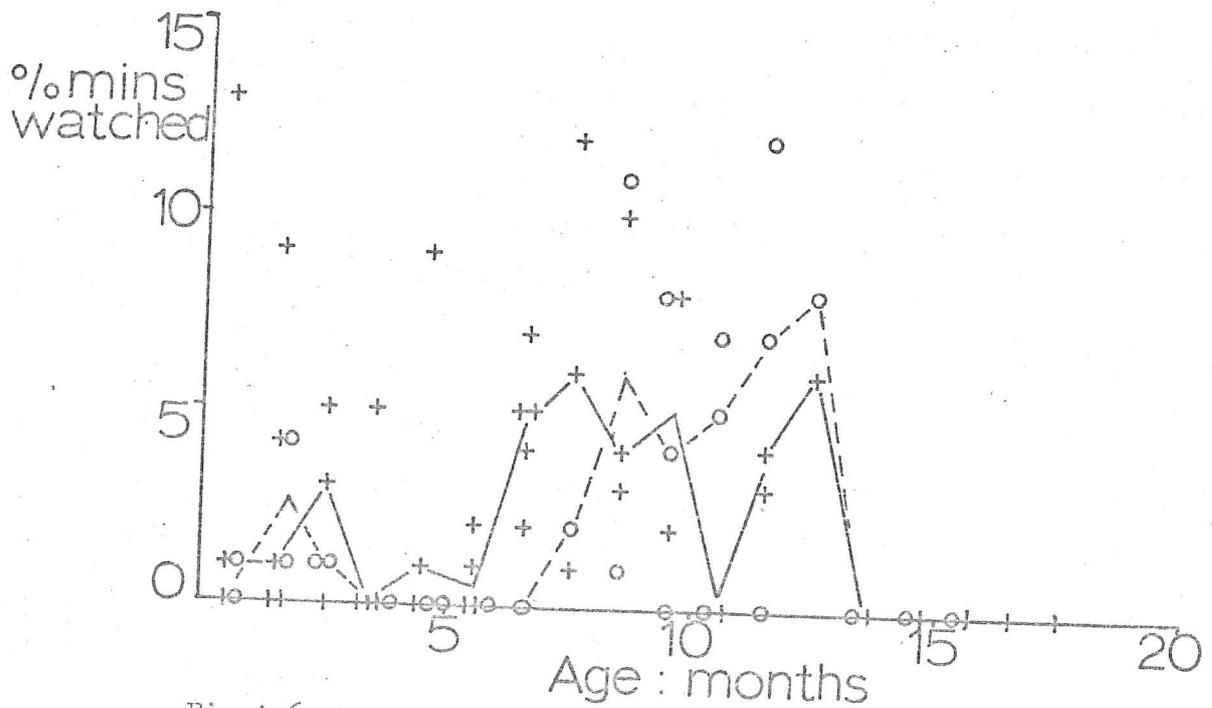


Fig. 1.6. The percent of minutes watched in which moaning occurred.

7. The relative role of mother and infant in maintaining nipple contact

Each time the infant lost or gained the nipple I recorded whether the mother or the infant was chiefly responsible. From these data an assessment can be made of the relative role of mother and infant in maintaining nipple contact and in the process of weaning.

When the infant is newborn the mother frequently assists it to gain the nipple by lifting it and pressing it towards her breast. This most often happens when the infant gecks or screams, or when the mother is about to move away after a period of rest. The infant usually responds by taking the nipple in its mouth, and when it does so in this context I considered that the mother had initiated the nipple contact. During the first two months of the infant's life, no mother was seen to push her infant off the nipple, but some started to do so from two months onwards, though different mothers varied considerably in the time when they started to do this. This was termed a breaking of nipple contact by the mother.

Infants were able to take the nipple without the mother's help from the age of one day or less, but could not manage to do so if they slipped down far away from the nipple. If this happened, a geck usually caused the mother to hoist them up to the breast. As infants became older they tended to initiate nipple contacts relatively more frequently and to break them relatively less. Likewise mothers broke nipple contacts relatively more and initiated contacts relatively less, many mothers not initiating at all when

the infant was more than nine months old.

For each age group I calculated the value of the percentage of initiations of nipple contact which were due to the infant minus the percentage of breaks which were due to the infant, i.e. $\% \frac{I_i}{I_i + I_m} - \% \frac{B_i}{B_i + B_m}$ where I = the number of initiations and B = the number of breaks of nipple contact, i, by the infant and m, by the mother. The magnitude of this expression is a measure of the relative role of mother and infant in maintaining nipple contact. It can be seen that if the overall value of the expression is negative then the mother has a larger role than the infant in maintaining nipple contact, but if the expression is positive the infant has the larger role. In Fig. 1.7 the value of the expression is plotted against age. The data indicate that the role of the infant steadily increased relative to that of the mother with age. For the first six months of life mothers had a greater role than the infant in maintaining nipple contact, but after six months the reverse was true.

The value of this expression is representative of the behaviour of both partners in the relationship in that it is affected by a change in the frequency of initiations or breaks by either partner, and the value of the expression for the mother can be calculated from that for the infant, and vice versa. The expression is not wholly independent of the total number of *initiations* and *breaks*, which could be affected by a change in the level of locomotor activity. However, a change in the frequency of initiations and breaks could not account for a change in the sign of the

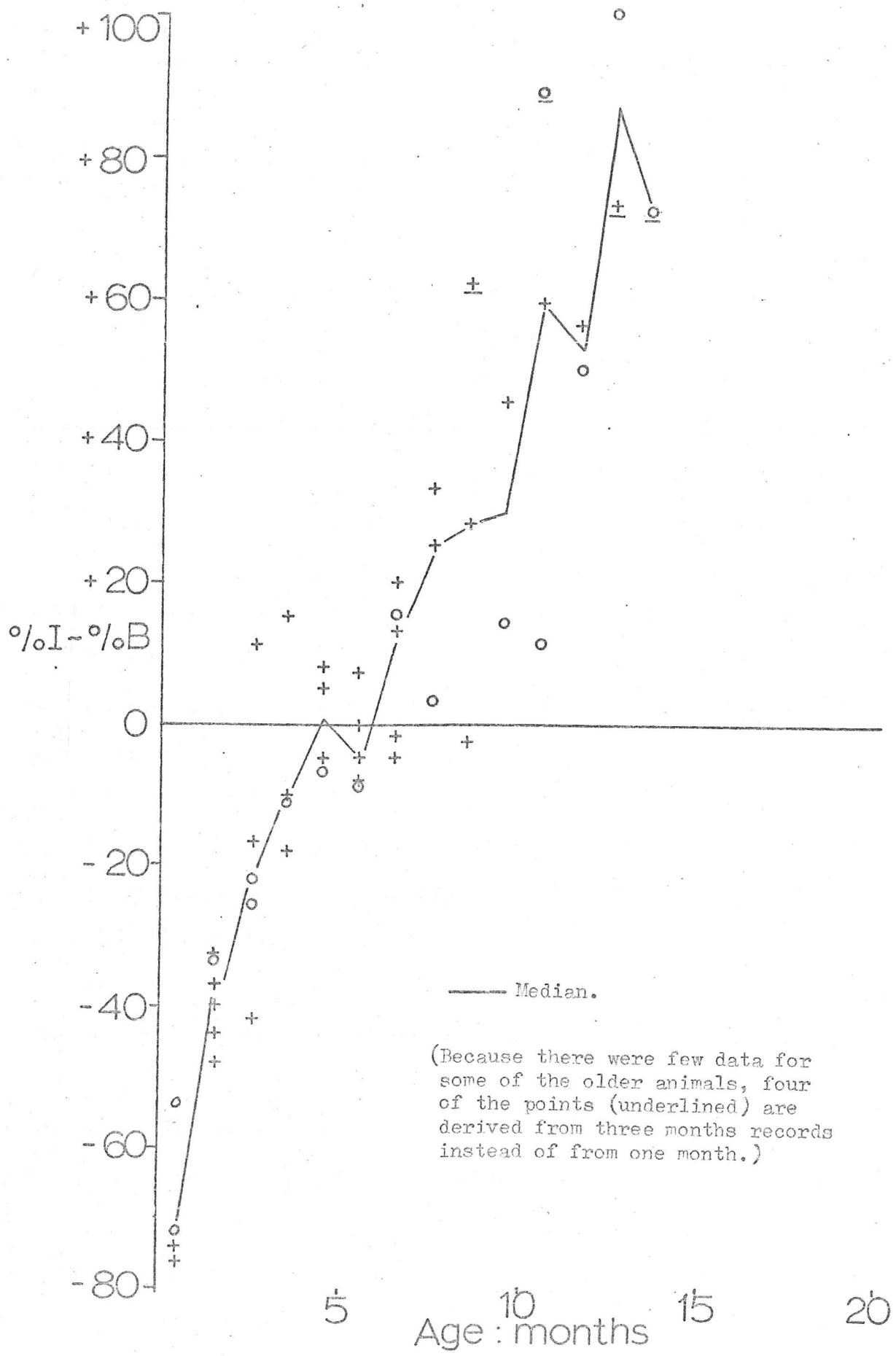


Fig.1.7. The relative role of mother and infant in maintaining nipple contact, ie.the percent of initiations minus the percent of breaks of nipple contact which were due to the infant.

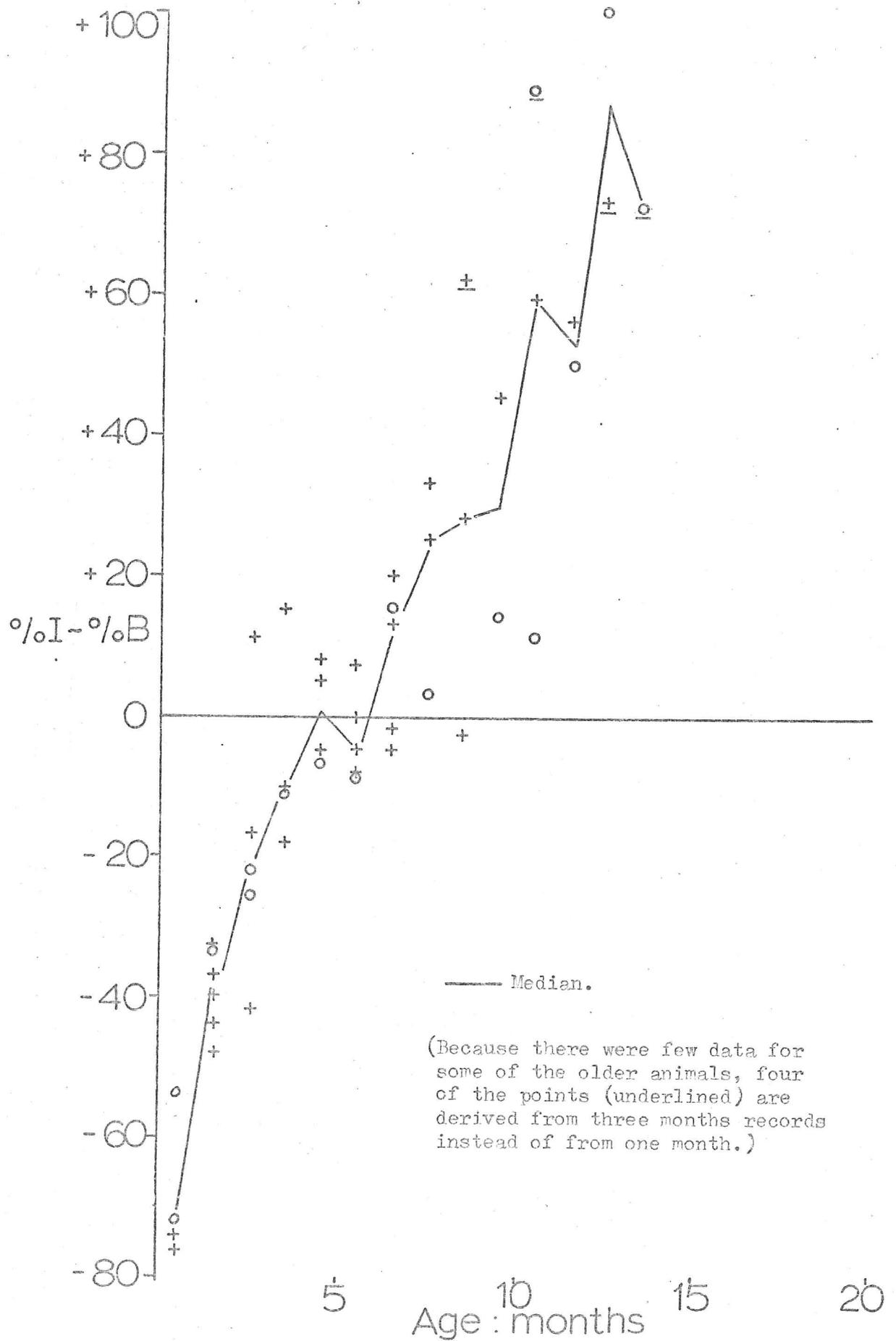


Fig.1.7. The relative role of mother and infant in maintaining nipple contact, ie.the percent of initiations minus the percent of breaks of nipple contact which were due to the infant.

expression and is unlikely to account for the large changes observed in its value (Hinde and Atkinson, 1970).

8. Time out of contact with mother (Total time off)

The infant was considered to be out of contact with its mother when no part of their bodies were touching. However the infant was also counted as being out of contact if only its tail was touching the tail of the mother.

Some infants were seen to go out of contact at two weeks of age, and all were doing so at six weeks old (Fig. 1.8). Time off increased to about 80 percent of minutes watched at six months old. Between six and eleven months there was no increase in time off but after this age it increased again to almost 100 percent.

9. Time out of arm's reach

The distance of 60 centimetres is approximately the distance a mother can reach and retrieve her infant. The percent of minutes watched in which the infant was seen more than sixty cm. from its mother increased steadily with age, reaching about 95% at thirteen months (Fig. 1.9). The number of minutes out of arm's reach was also estimated as a percentage of the number of minutes in which the infant was out of contact with the mother (Fig. 1.10). This gives a measure of the amount of time spent at a distance from the mother which is independent of the amount of time spent out of contact. This measure also showed a steady increase with age until at 13 months old, infants going out of contact with their mothers nearly always went out

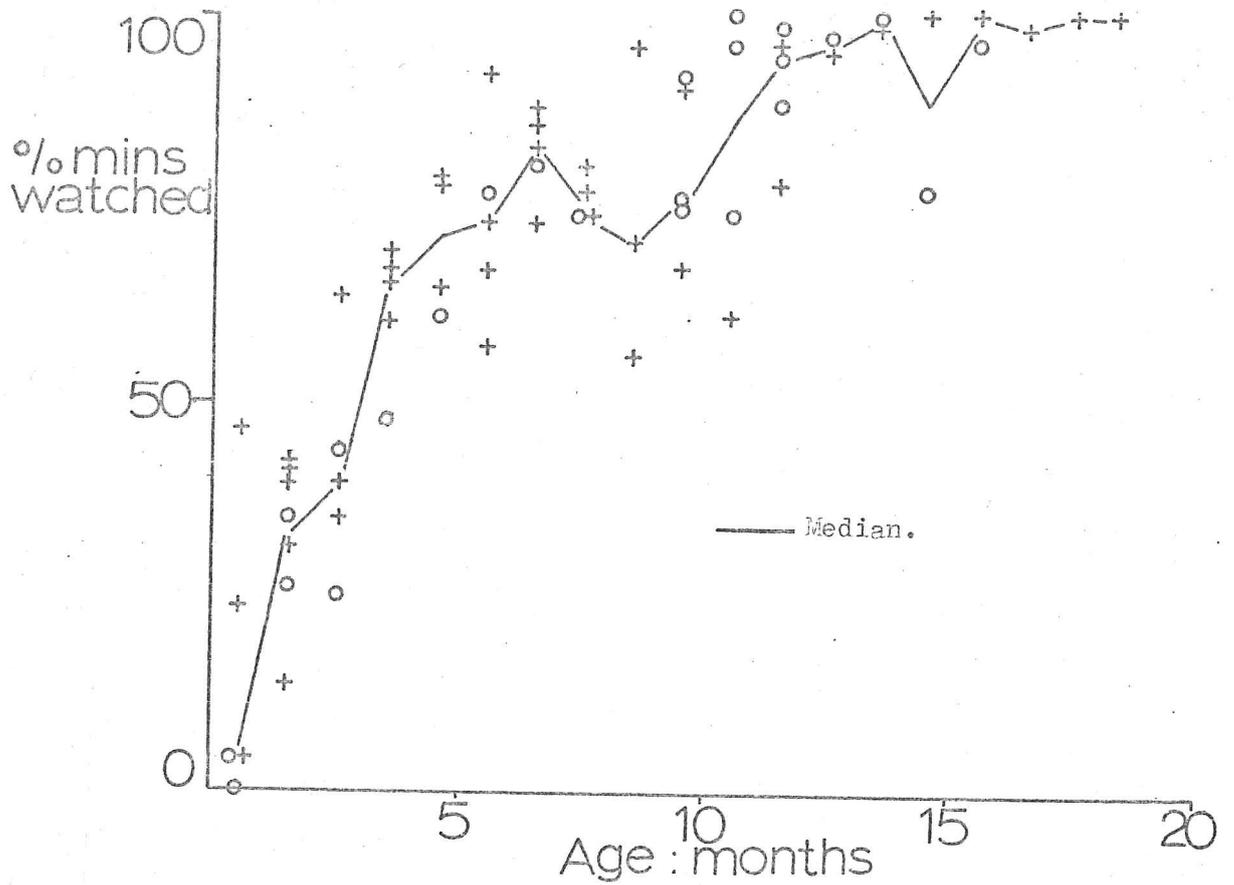


Fig.1.8. The percent of minutes watched in which the infant went out of contact with its mother ('Total time off').

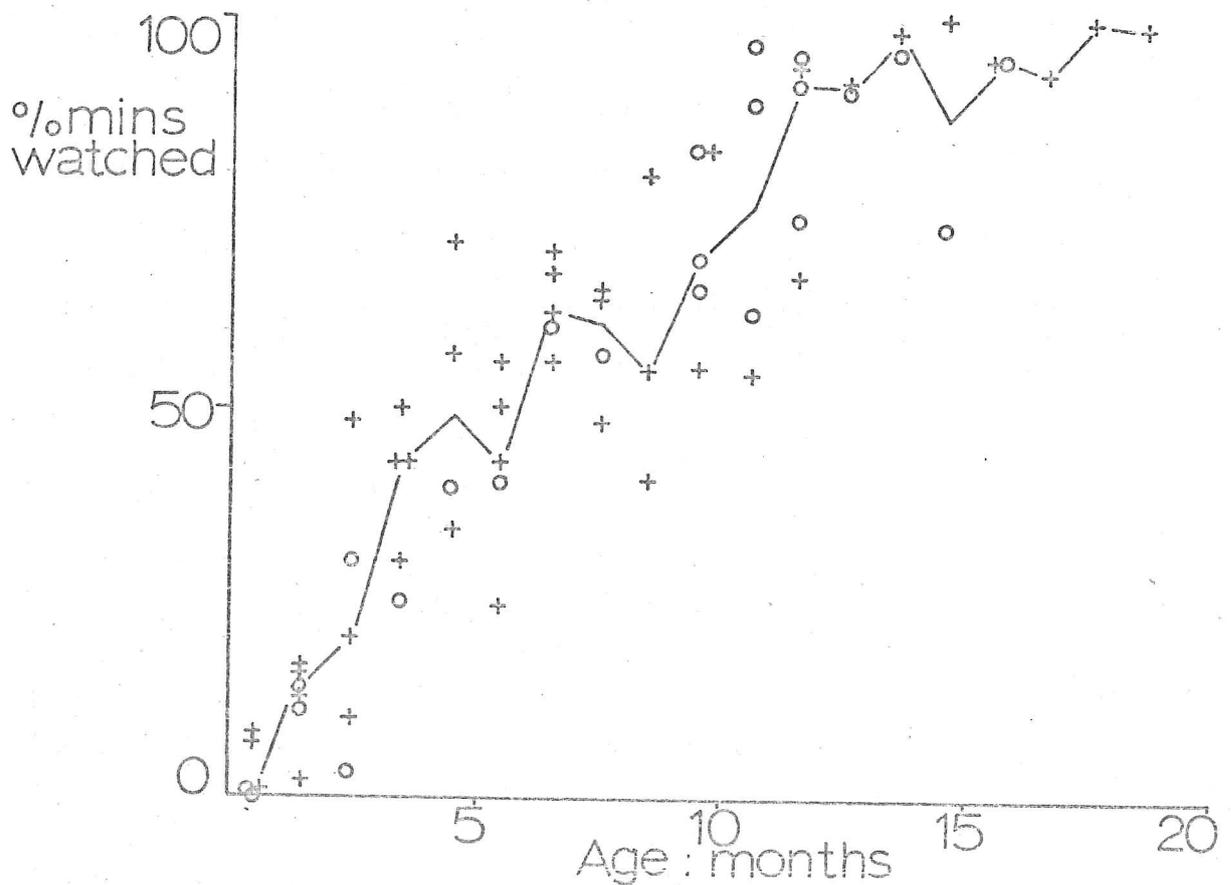


Fig.1.9. The percent of minutes watched in which the infant went out of arm's reach (>60cm.) of its mother.

of arm's reach within that minute.

10. Time wholly out of arm's reach

This is a measure of the proportion of minutes watched throughout which the infant was more than arm's reach (60 cm) from the mother. It is thus a measure of the amount of time the infant was out of contact with mother and could not quickly make contact with her, or she with it.

Some two week old infants spent whole minutes out of arm's reach, and from $3\frac{1}{2}$ months onwards all animals watched did so (Fig. 1.11). From $3\frac{1}{2}$ months there was a steady increase in this measure until it reached about 95 percent at 16 months old.

At 16 months, a large proportion of the time the infant was less than arm's reach was occupied in grooming with the mother. These data may not reflect the true situation at all times of day, particularly in the evening when animals tended to associate more in family groups, and infants stayed close to their mothers prior to going up into the sleeping trees. Infants up to two years or more in age may sleep in their mother's arms, especially if there is no younger sibling.

11. Riding on mother

The newest infant observed was no more than 12 hours old, and seven were seen within 48 hours of birth. From the earliest time at which they were observed each infant was able to cling to its mother's belly without her support (Plate V). But mothers sometimes did give additional

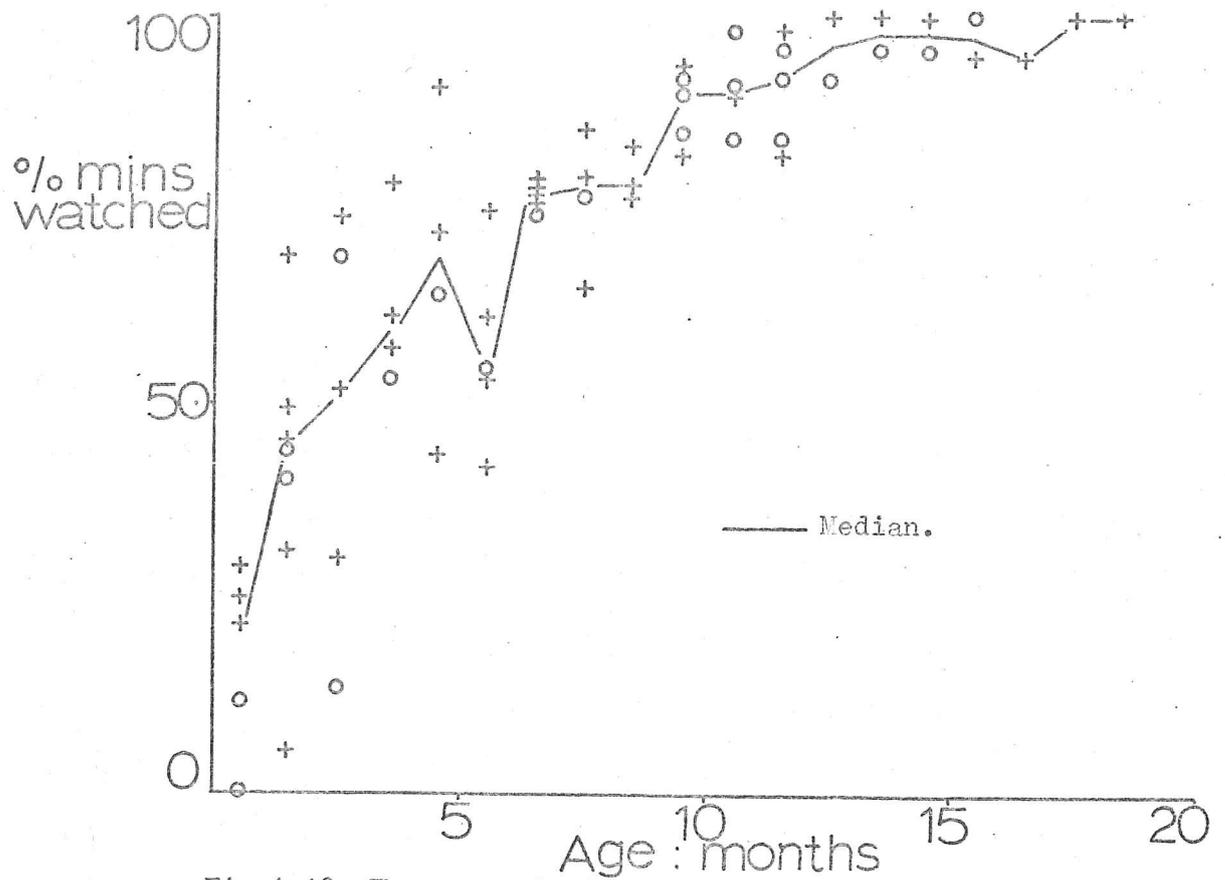


Fig.1.10. The percent of minutes in which the infant went out of contact with its mother in which it also went out of arm's reach, ie. Mins > 60 cm.
Total time off.

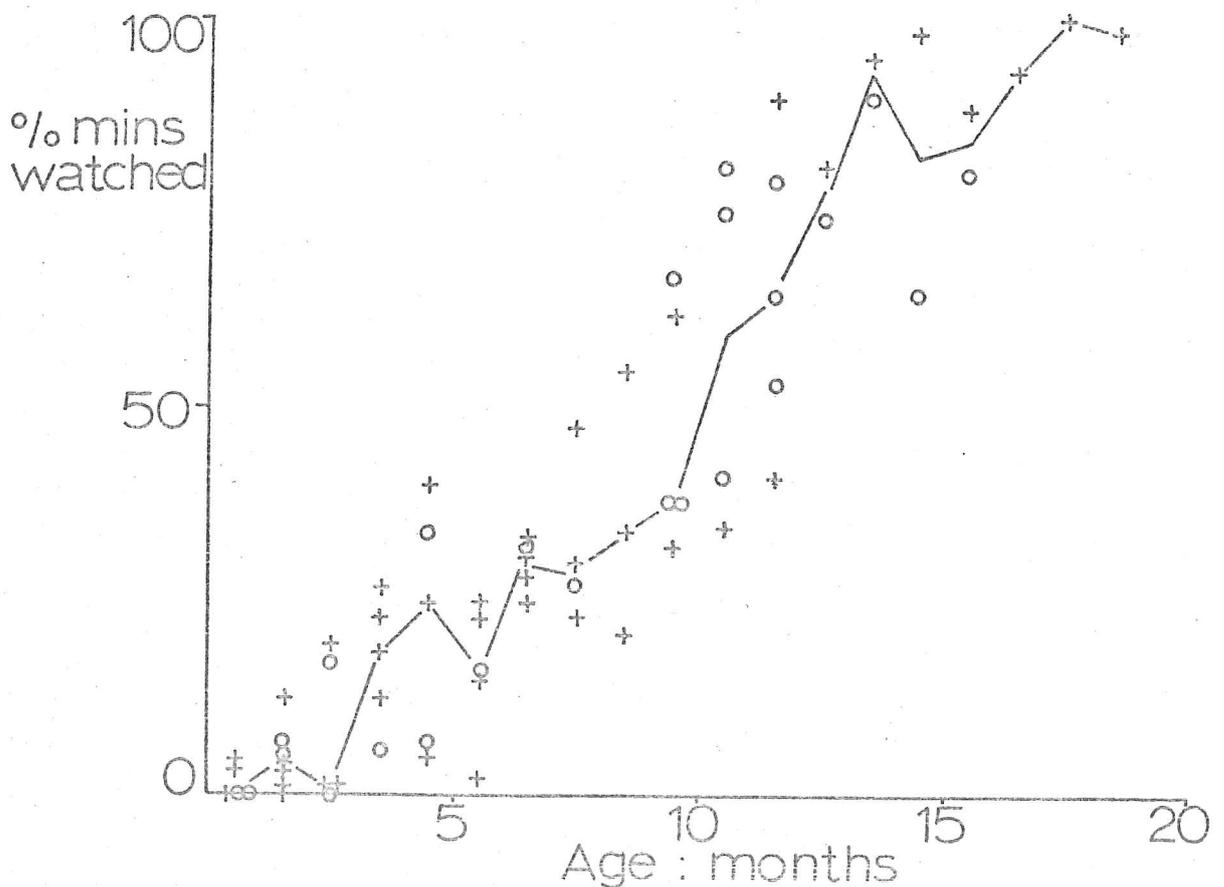


Fig.1.11. The percent of minutes watched in which the infant was out of arm's reach of its mother throughout the minute.

support, particularly during the first week, when jumping or making other sudden movements which might have dislodged the infant. The infant gained additional support by holding the nipple in the mouth, and the youngest infant observed was already doing this.

From about 6 weeks old infants started to ride dorsally on their mothers (Fig. 1.12 and Plates VI and VIII). Dorsal riding was never seen to be started by any initiative of the mother. Instead the infant usually reached the back by climbing up one of its mother's legs, and dorsal riding began as soon as the infant had the strength to climb up.

Ventral riding became less frequent with age, and occurred in less than 4 percent of minutes watched after 6 months. Dorsal riding reached a peak at $2\frac{1}{2}$ months and from 4 months onwards was more frequent than ventral riding. Little riding of any sort occurred after 11 months of age in any of the infants watched. However, dorsal riding continued up to 18 months in some infants not included in the study.

The increasing locomotory independence of the infant is partly a reflection of its own increasing mobility, but it is to some extent affected by the mother's behaviour. She may prevent the infant from starting to ride, for instance by not standing still, or may terminate a period of riding by sitting down, or by pushing the infant off her.

Pushing the infant off the back was especially frequent at times when much rejection from the nipple was taking place ^{and} caused similar 'temper tantrums'. A common sequence

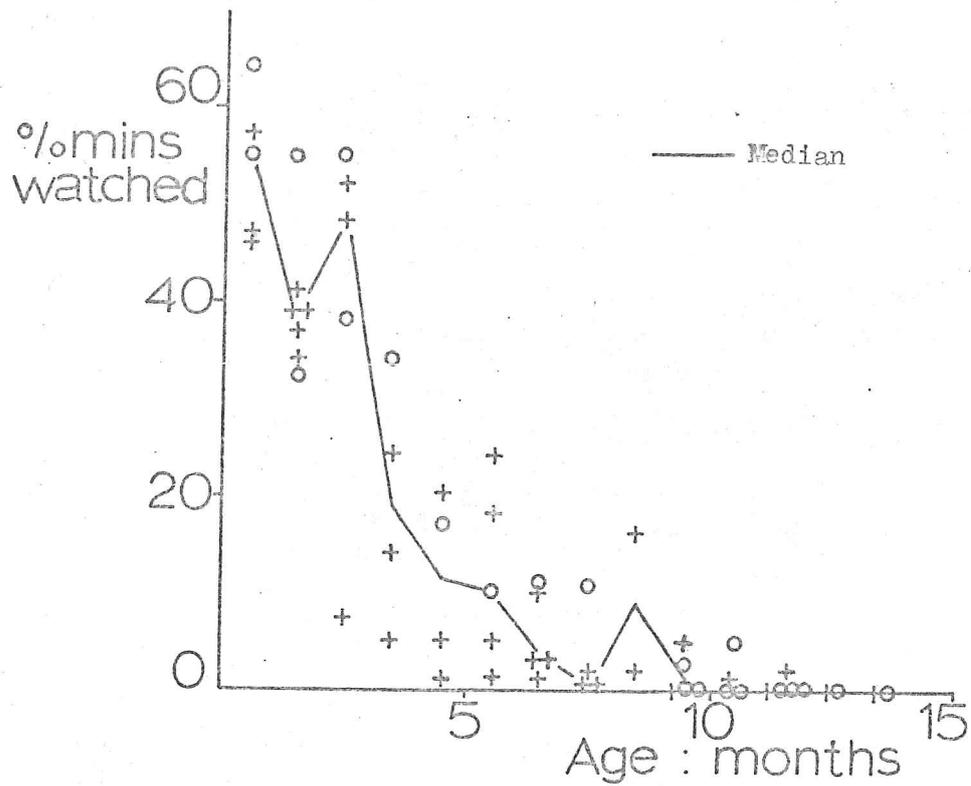


Fig.1.12. Riding on mother : the percent of minutes watched in which infants rode ventral (above) or dorsal (below).

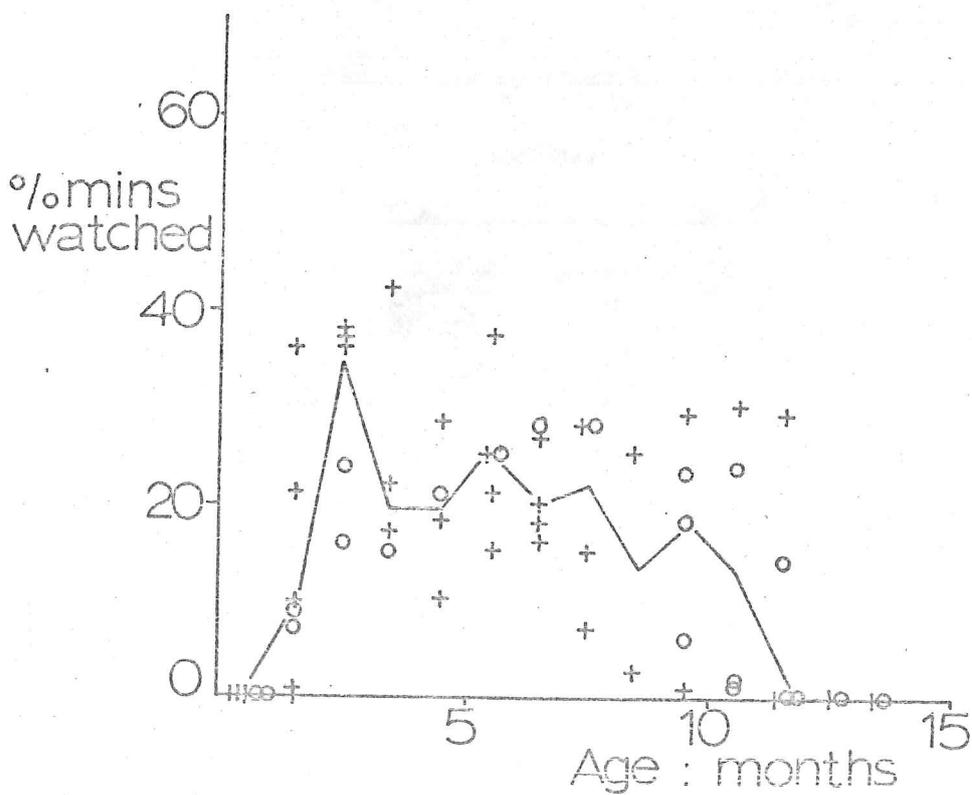




Plate V. Five week old infant riding ventrally on mother.



Plate VI. Disoriented attempt by five week old infant to ride dorsally on mother.



18. Fig. 18. Plate VII. Four month old infant riding dorsally on mother, correctly oriented.

1. It is about the limit of visibility in the distance.



Plate VIII. Wrestling play between an eighteen month old and a six month old male. Both animals are showing the 'play face'.

of behaviour might be: infant attempts to take nipple in mouth as mother is walking along, and mother brushes it aside (a rejection); infant immediately goes dorsal, and mother turns round and brushes it off. Such sequences may go on for several minutes, and are accompanied by much gecking, screaming and moaning.

In times of danger, either from other baboons or from outside threats infants up to 18 months old may rush to their mothers (or vice versa) and be carried by them either dorsal or ventral. Older siblings also frequently perform the function of the mother in this context.

12. Time more than five metres from mother.

This distance was chosen for three reasons:

1. It is about the limit of visibility in the densest parts of the range.
2. It was hoped that it would give some information about mother-infant distance changes for age groups beyond the limit for which such data could be obtained for the 60 cm. category.
3. To provide data on the relative roles of mother and infant in maintaining this degree of proximity (see next section).

I estimated the distance between mother and infant by eye.

One infant was seen at more than 5 metres from its mother at two weeks old, and from this age, the percentage of minutes watched in which infants were seen at this distance steadily increased, reaching about 95 percent at

14 months of age (Fig. 1.13).

By comparing Figs. 1.9 and 1.13 it can be seen that, during the first 14 months, the proportion of minutes watched in which the infant was seen at more than 60 cm. from the mother, and in which it was also seen at more than 5 m. from her increased. Thus infants spent an increasing proportion of time out of arm's reach at more than 5 m. from their mothers as they grew older. After 14 months, infants going out of arm's reach nearly always went more than 5 metres away during that minute.

From 14 months of age Fig. 1.13 shows no increase. Thus the data do not show whether the distance an infant keeps from its mother continues to increase after 14 months or whether by this stage it has reached a maximum. Data using a larger distance category would be necessary to determine this.

13. Approaching and leaving

When the distance between mother and infant changed from more than 60 cm. to less than 60 cm. (approaches) or vice versa (leaves), or from more than 5 metres to less than 5 metres or vice versa, I recorded whether the change in distance was due primarily to a movement by the infant or to a movement by the mother.

From these data it is possible to make an assessment of the relative role of mother and infant in maintaining mutual proximity at these two distances, using a method equivalent to that used for the data on maintenance of nipple contact, and first used by Hinde et al (1964).

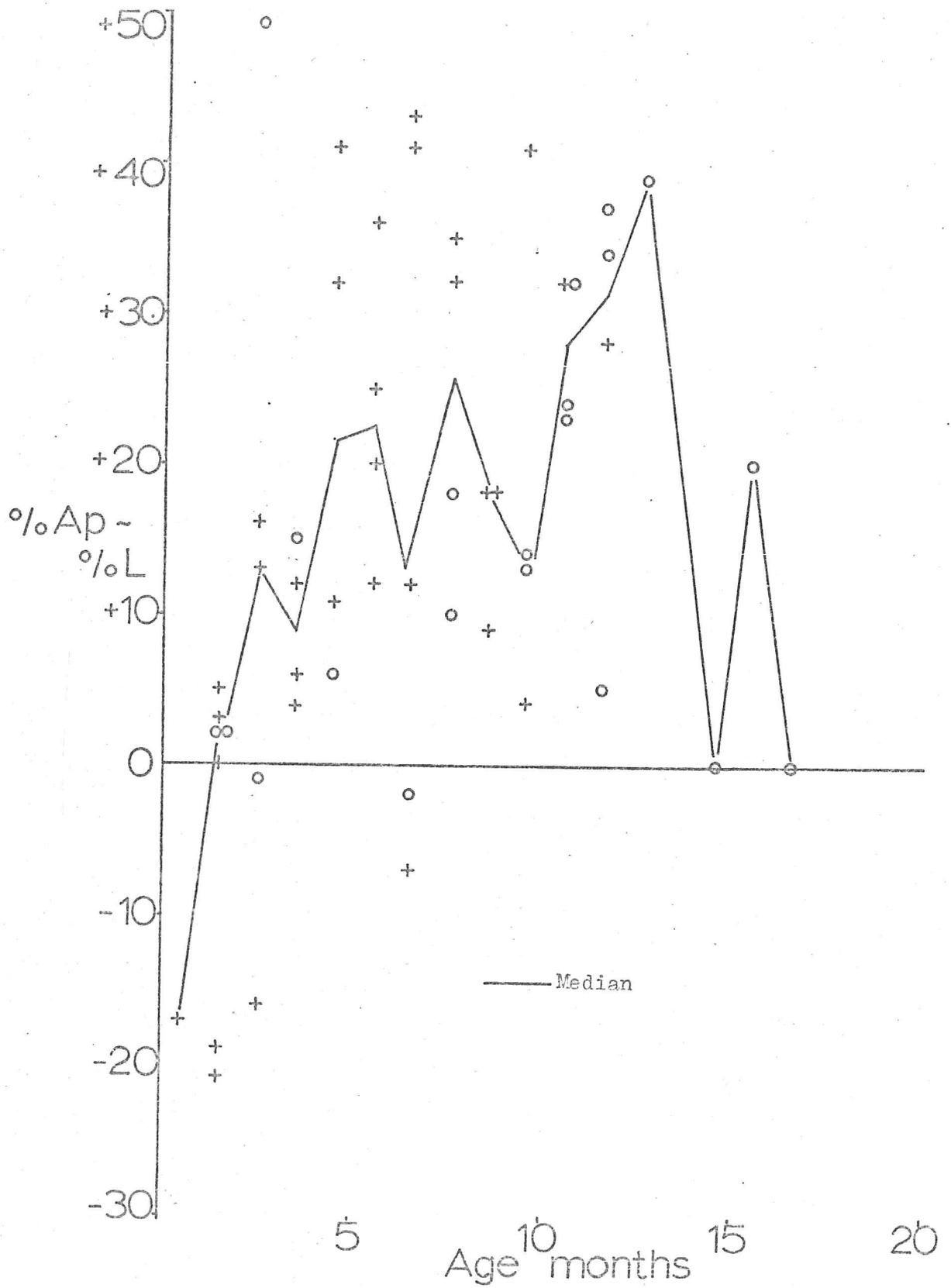


Fig. 1.14. The relative role of mother and infant in maintaining mutual proximity, ie. the percent of approaches minus the percent of leaves over the 60 cm. 'boundary' which were due to the infant.

For each animal at each age stage and for the two distance categories I calculated the value of the function: percentage of approaches which are due to the infant minus percentage of leaves which are due to the infant ($\%A_p - \%L$). The value of this function gives an indication of the relative role of mother and infant in maintaining mutual proximity and how this changes with age (Hinde and Atkinson, 1970).

a. Approaches and leaves over the 60 cm. 'boundary'.

Fig. 1.14.

The value for $\%A_p - \%L$ by the infant was usually positive. Of the seven negative values, five fell within the first three months of life although there were also seven positive values during this time. This suggests that during the first three months, some mothers had a greater role than the infant in maintaining proximity at this distance, but from three months onwards the infant usually had the greater role.

b. Approaches and leaves over the 5 metre 'boundary'.

Fig. 1.15.

If one month's data were not sufficient to calculate a figure for $\%A_p - \%L$ then data for two or more months were lumped (see Fig. 1.15). The criterion used was that $A_p + L$ must equal 10 or more for both the mother's and for the infant's data. (In Fig. 1.15 I have also replotted the approaches and leaves data for the 60 cm. distance lumped in the same way for comparison).

In 18 cases the value of the function was positive, in 11 cases negative and in 3 zero. Its value showed no apparent age changes, but there were few data for animals

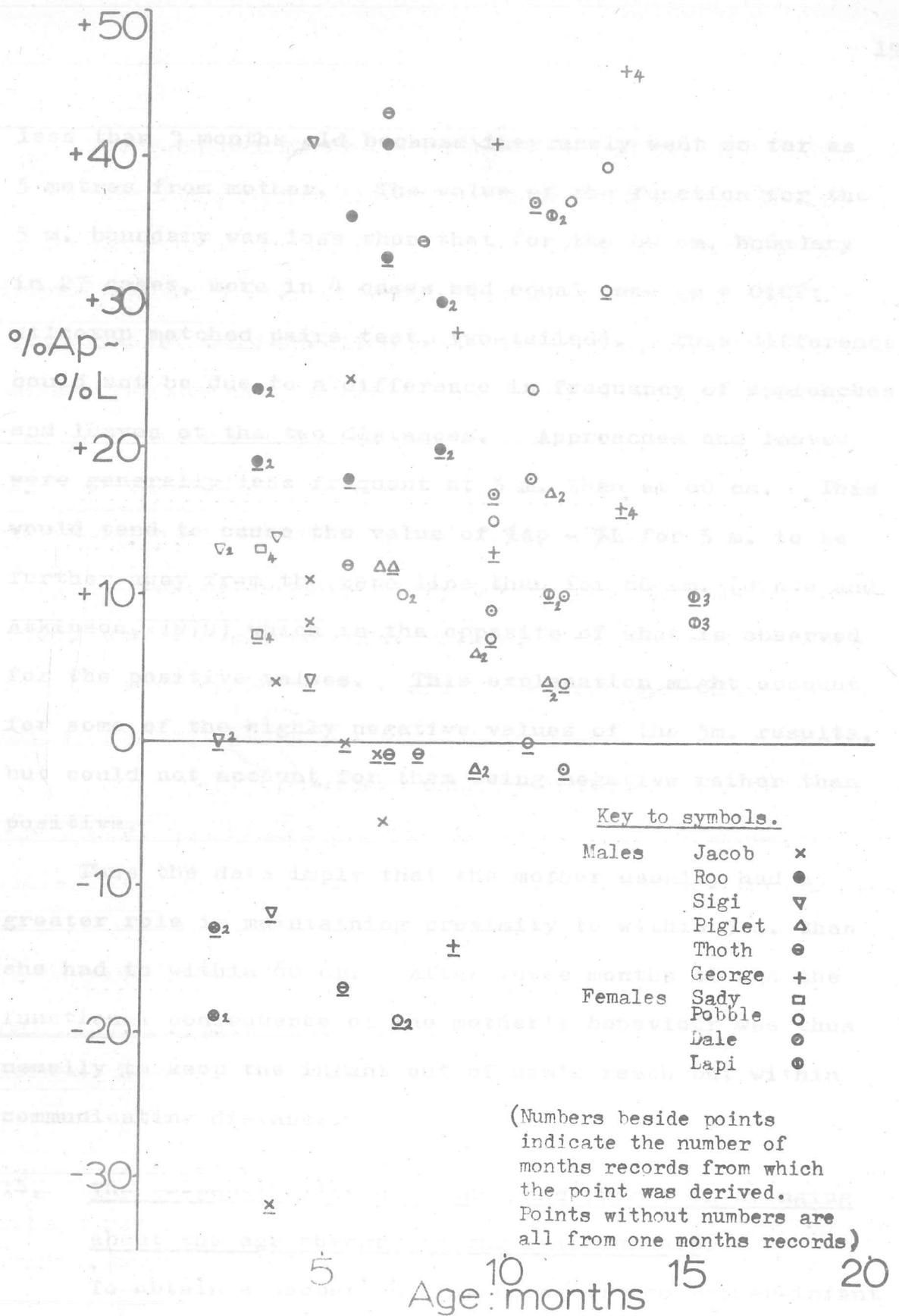


Fig. 1.15. The relative role of mother and infant in maintaining mutual proximity to within 5 metres (symbols underlined) and to within 60 cm. (symbols not underlined). When $Ap + L$ equalled less than ten for either mother or infant, data were pooled from upto four months records and the mean age plotted. Data for the 60 cm. distance were pooled in the same way in order to facilitate comparison, but are otherwise the same as those in Fig. 1.14.

less than 3 months old because they rarely went so far as 5 metres from mother. The value of the function for the 5 m. boundary was less than that for the 60 cm. boundary in 27 cases, more in 4 cases and equal once ($p = 0.02$; Wilcoxon matched pairs test, two-tailed). This difference could not be due to a difference in frequency of approaches and leaves at the two distances. Approaches and leaves were generally less frequent at 5 m. than at 60 cm. This would tend to cause the value of $\%Ap - \%L$ for 5 m. to be further away from the zero line than for 60 cm. (Hinde and Atkinson, 1970) which is the opposite of what is observed for the positive values. This explanation might account for some of the highly negative values of the 5m. results, but could not account for them being negative rather than positive.

Thus the data imply that the mother usually had a greater role in maintaining proximity to within 5 m. than she had to within 60 cm. After three months of age the functional consequence of the mother's behaviour was thus usually to keep the infant out of arm's reach but within communicating distance.

14. The responsibility of mother and infant in bringing about the age changes in the relationship.

To obtain a deeper understanding of the mother-infant relationship it is essential to know whether the observed age changes in the measures are due primarily to changes in the mother's or the infant's behaviour. Examination of correlations between measures can help to answer this question (Hinde and Spencer-Booth, 1968).

Hinde suggests that a convenient starting point for understanding the age changes in mother-infant relations is to consider four hypothetical types of basic changes in the behaviour of mother and infant: namely an increase or decrease in the tendency of mother and infant to respond positively (i.e. other than by avoidance or aggression) to the other. Table 1.1 shows the predicted directions of the effects of the four types of basic changes in behaviour on some measures of mother-infant relations.

Table 1.1

The predicted directions of the effects of four types of basic changes in the behaviour of mother or infant on some measures of mother-infant relations

	Time off	R	R/A+R	%I-%B	>60cm. only	%Ap-%L
Infant leaves mother more	+	-	-	-	+	-
Infant approaches mother more	-	+	+	+	-	+
Mother leaves infant more	+	+	+	+	+	+
Mother approaches infant more	-	-	-	-	-	-

For example, if the infant tends to leave the mother more, it is likely to be rejected by her less often. Hinde states that 'It is apparent from the table that, if the changes in mother-infant interaction could in fact be accounted for in terms of one or more of these simple changes, then certain

measures would always be correlated with each other' (Time off and Time more than 60 cm. only; R , $R/A+R$, $\%A_p - \%L$ and $\%I - \%B$) 'Relations between measures provide a means of assigning to mother or infant immediate responsibility for changes in the measures'. For example, an increase in Time off is likely to be due more immediately to the infant if associated with a decrease in absolute or relative frequency of rejections, but to the mother if associated with an increase.

The nature of the age changes in the mother-infant relationship.

By examining the data (looking at medians) I have made an assessment of the extent to which this method helps in understanding the observed ^{age} changes in mother-infant relations in baboons.

Up to the age of 8 months (see Table 1.2) there were significant positive correlations between the two sets of measures predicted as being highly correlated above (Time off with Time more than 60 cm. only, and R with $R/A+R$, $\%I - \%B$ and $\%A_p - \%L$). The correlation between Time off and Time more than 60 cm. only, remained high up to 16 months of age when both measures reached an asymptote.

As Time off and Time at a distance increased over the first 8 months, so also did R , $R/A+R$, $\%A_p - \%L$ and $\%I - \%B$ (the measures being significantly correlated with each other). This indicates that it was largely changes in the mother's behaviour which were immediately responsible for the increase in Time off and Time at a distance during the first 8 months.

Table 1.2

Spearman rank correlation coefficients between group medians of measures of mother-infant relations

	R	R/A+R	T > 60cm.only	%I-%B	%Ap-%L
Time off	0.78* -0.55	0.83** -0.24	0.92** 0.86**	0.93** 0.83*	0.84** -0.19
R		0.96** 0.40	0.79* -0.62	0.90** 0.39	0.81* 0.40
R/A+R			0.76* -0.1	0.90** 0.39	0.90** 0.65
T > 60cm.only				0.95** 0.95**	0.71* -0.45
%I-%B					0.81* 0.68

Upper figures are for the period 0 - 8 months.

Lower figures are for the period 8 - 16 months except those for R/A+R which are for the period 8 - 15 months and those for %I-%B which are for 8 - 14 months.

* = $p < 0.05$

** = $p < 0.01$

After 8 months R and R/A+R were not significantly correlated owing to a decrease in the absolute frequency of rejections (associated with a decrease in time on the nipple) the relative frequency of rejections remaining high. From about this age also, the infant had a greater role than the mother in maintaining nipple contact. It is difficult to assess the relative contribution of mother and infant in bringing about the changes in behaviour which led to a change in the correlation between these two measures after 8 months, but they probably depended on the behaviour of both. For instance the failing of the mother's milk, her maintenance of a high

relative frequency of rejections and her decreasing role in maintaining nipple contact perhaps discouraged the infant from seeking the nipple. Physical and mental changes in the infant such as increased discriminatory and manipulatory ability (see Chapter 2, B), increased energy demands and physiological changes perhaps led to an increasing preference for and dependence on solid food which also caused it to seek the nipple less, and led to a decrease in the absolute frequency of rejections.

15. Individual differences in the mother-infant relationship

So far I have considered only the median points on the figures. There was, however, considerable variation between individuals in the measures. Some of these were sex differences (for example gecking, Fig.1.4), but most differences did not seem to be correlated with sex. It is not possible to make an assessment of the extent to which these differences were due to differences in the mother's or the infant's behaviour (cf. Hinde and Spencer-Booth, 1968) because not enough infants were watched at each age stage. However, some of the differences between individual infants were consistent between months and between measures, indicating that the differences were not simply due to sampling errors. Thus in free-living baboons, individual differences in social development may come about through individual differences in mother-infant relations.

16 DiscussionComparison with other baboons studiesRowell

Rowell et al. (1968) give quantitative data for mother-infant relations in captive baboons for the first three months of life. The groups consisted of nine animals including four adult females with infants, one adult and one sub-adult male and some additional adult and juvenile females.

Rowell recorded her data on check-sheets divided into half-minutes whereas my check-sheets are in minute intervals. This would tend to make Rowell's figures lower than mine, the effect increasing the shorter the bout length of the particular behaviour pattern. Another discrepancy is that my data are biased towards being too low for Time off mother by about 11 percent (see methods section).

Some of Rowell's data are not directly comparable with mine because the measures she used are not the same (for instance she recorded whether the infant was on the nipple with eyes open ('sucking') whereas I lumped all situations in which the infant was on the nipple). Two of her measures are directly comparable. These are Time out of arm's reach and Time wholly out of arm's reach (see Figs. A and B). For both these measures Rowell's figures are higher than mine throughout the three months. The differences are too large to be accounted for solely by the bias in my recording methods.

Differences in social environment are known to affect mother-infant relations in both baboons and rhesus monkeys (Rowell, 1968; Hinde and Spencer-Booth, 1967, a). Rhesus

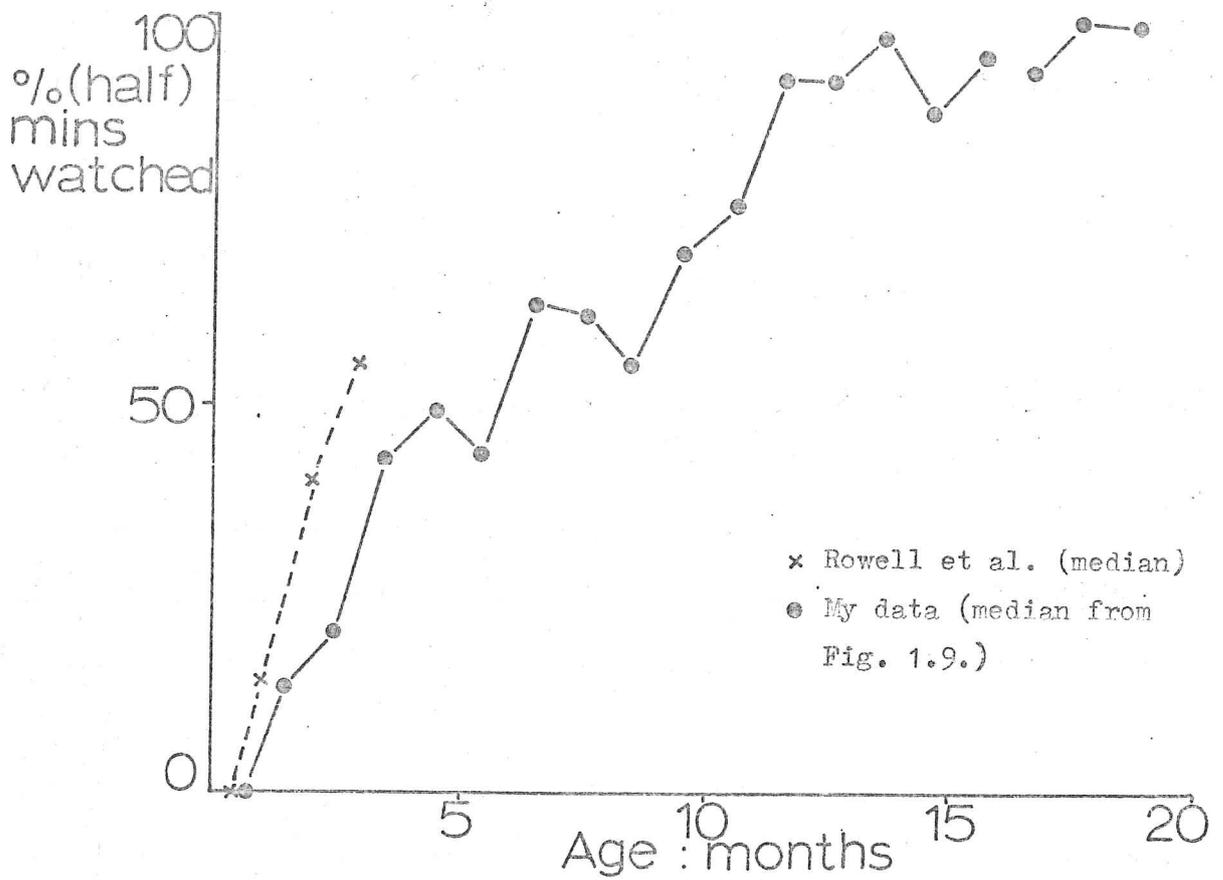


Fig. A. Time spent out of arm's reach by captive baboon infants (Rowell et al.) and free-living infants (my data).

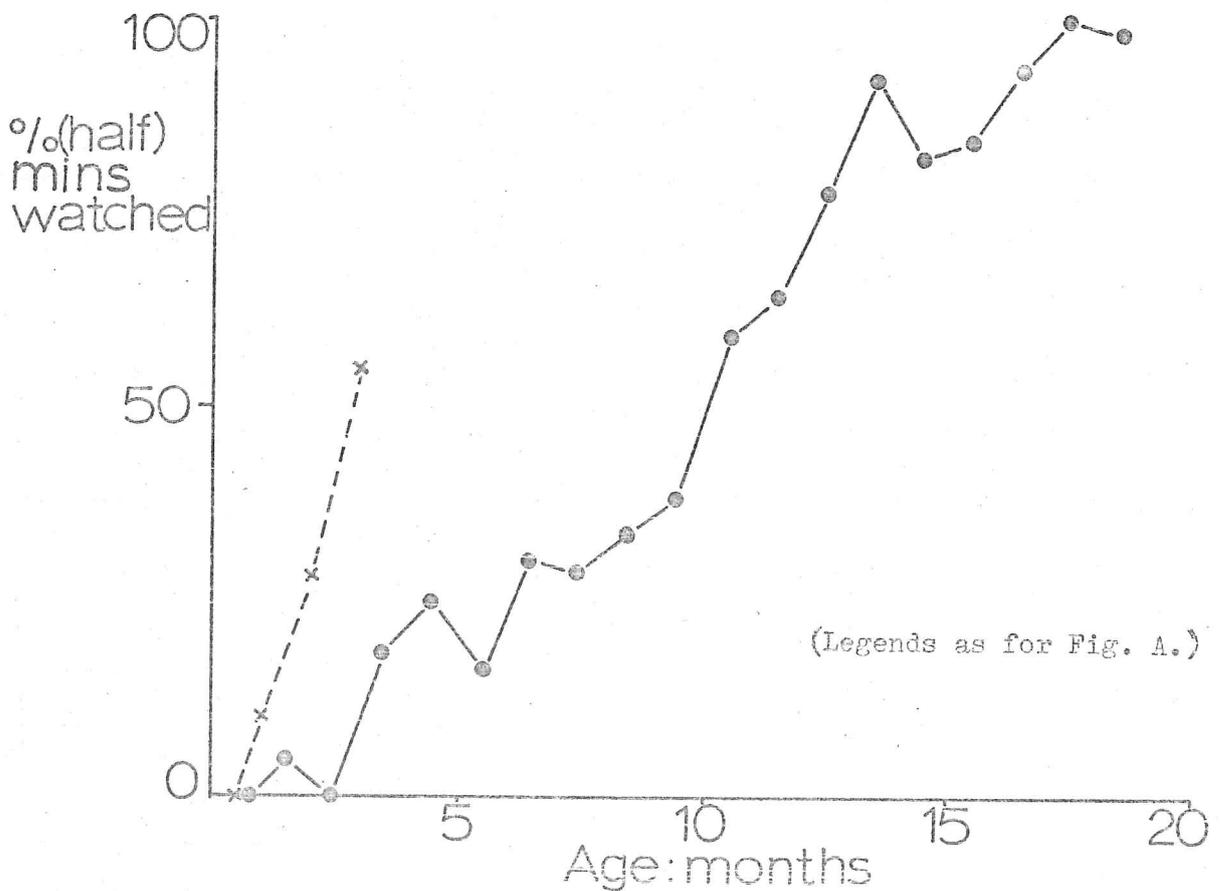


Fig. B. Time wholly out of arm's reach by captive baboon infants (Rowell et al.) and free-living infants.

infants reared in isolation with their mothers spent more time at a distance and more whole minutes at a distance from mother during the first three months than did group-living infants, and Rowell reaches similar conclusions for baboons. In rhesus the difference was shown to be due largely to differences in the mother's behaviour. There was a considerable difference between the group composition of Rowell's captive animals and the Gombe troop. Most notably, Rowell's groups contained only 9 animals with one adult male and no juvenile males. (The Gombe troop consisted of over 40 animals with 11 adult males, 15 adult females and many juveniles of both sexes.) It was noticeable that the approach of other adult females (which often attempted to pull small infants away from their mothers and handle them) frequently caused the mothers to go to and pick up their infants, or the infants to rush back to their mothers. Small infants also avoided juvenile animals (especially juvenile males, which tended to play roughly) in the same way. Thus the larger number of potentially frightening animals in the wild group may account at least in part for the wild mothers and infants keeping closer together than the captive ones. The close-knit nature of the troop in the Gombe habitat may have enhanced this effect. Other dangers such as those from predators and humans may have had a similar influence in the wild group.

If the difference in time spent at a distance by the two groups of baboons is due largely to differences in the mother's behaviour (as might be expected from the rhesus monkey data) then one might predict that wild mothers rejected their

infants less and approached them and restricted them more than captive mothers. However, wild baboon mothers were never seen to restrict their infant's attempts to leave them (neither did Rowell see this in wild baboons in Uganda) whereas captive mothers did so. This would tend to create an effect opposite to that which was observed. Unfortunately Rowell presents no data concerning rejections and approachings and leavings, but she does give data for making and breaking physical contact between mother and infant. If the model represented in Table 1.1 can predict some of the characteristics of the mother-infant relationship, then one would expect that the relative roles of mother and infant in maintaining physical contact would be positively correlated with their relative roles in maintaining mutual proximity. This is clearly the case; Rowell's data indicate that the mother has a greater role than the infant in maintaining contact until 2 months of age, and my data indicate that relative roles in maintaining proximity show very similar age changes. Thus so far as a comparison can be made there appears to be little difference between the relative roles of mother and infant in maintaining their spacial relationship in the two groups. Thus the difference in time spent at a distance is perhaps due to differences in the behaviour of both the mother and the infant.

DeVore

DeVore (1963) gives a qualitative description of mother-infant relations in free-ranging baboons from observations of Papio anubis in the Nairobi National Park and Papio

cynocephalus in the Amboseli Reserve. His descriptions are a composite of observations on the two races.

Some of DeVore's descriptions of the age changes in the mother-infant relationship agree fairly closely with mine, but in others there is some disparity. I will now list some of DeVore's conclusions and describe how they differ from mine, starting with those concerning the youngest animals.

DeVore states that:

1. "Throughout the first month of life the infant rarely leaves its mother's arms" and "The infant will not leave its mother for even two minutes until it is 9 weeks old."

My data for "Time off" show that 4 out of six infants watched spent some of their time out of contact with their mothers at 2 weeks of age, two of them for more than 20% of minutes watched. It was not uncommon for infants to be out of arm's reach at 6 weeks old for more than two whole minutes. One female infant (which was somewhat exceptional) was out of arm's reach for periods of up to 12 minutes at this age.

2. "Vocalisations between mother and infant are very few" (referring to the first month of life).

Three types of vocalisation (gecking, screaming and moaning) occurred in the first month in the Gombe animals. Gecking occurred in 11% of minutes watched in males and 3% of minutes watched in females at 2 weeks old (percentages given are group medians) and was quite important in causing the mother to hoist the infant up to the breast when it had lost its hold on the nipple.

3. From the time the infant is able to walk a little and follow its mother when she is moving slowly (about 2 months of age) "the infant takes almost all the initiative in grasping the mother's belly and riding".

My data on initiation of nipple contact are contrary to this. Initiation of nipple contact by the mother involves clasping the infant to her belly, very often prior to walking away. The figures for initiation of nipple contact are therefore almost equivalent to those which would be obtained for initiation of ventral riding. The mother had a greater role than the infant in initiating nipple contact up to the age of six months.

4. The infant rides ventrally more than dorsally "up to the age of two months".

The figure from my data would be 4 months.

5. Between 4 and 6 months of age "the mother allows the infant to ride or not as it wishes".

In the Gombe troop the mother was not always passive. Sometimes mothers would prevent the infant from starting to ride by not standing still or terminate a period of riding by sitting down. One mother was seen to push her male infant off her back when it was 5 months old.

6. "Shortly after the 9th or 10th month, on the average," the baboon infant undergoes rejection from taking the mother's nipple and from riding dorsally.

My data show that rejections from the nipple may start as early as six weeks, reaching a high frequency by 4 months, and declining again at 10 months. Rejections from riding dorsal may start at 5 months.

7. "It is the resumption of the mother's sexual activity which terminates the close mother-infant bond."

A male infant at Gombe whose mother came into full oestrous when he was 12 months old followed her during much of her consortship with adult males. This mother resumed sexual activity earlier than the three others for which I have figures. The infants of the other three became largely independent of their mothers before the mothers started cycling again, and did not accompany them on their first consorts. Thus there was no evidence that the resumption of sexual behaviour terminated the close mother-infant bond in the Gombe troop.

Kummer

Kummer (1968, a) gives some information about mother-infant relations in Hamadryas baboons (Papio hamadryas) and his conclusions are similar to mine so far as they go.

For instance, Kummer claims that after about the age of 4 to 6 months the initiative in the mother-infant relationship passes to the child. This is in agreement with my data on the relative roles of mother and infant in maintaining nipple contact; before 4 months the mother had the greater initiative and after 6 months the infant had, their roles being about equal between 4 and 6 months. He also notes that mothers do little to control the excursions of their black infants; the Gombe mothers also showed no restrictive behaviour. One point of difference is that in Hamadryas baboons, black infant males leave their mothers more than do black infant females. My data for Time off

and Time out of arm's reach show no such sex differences.

Comparison with Rhesus monkeys

Hinde et al. (e.g. Hind, Rowell and Spencer-Booth, 1964 and Hinde and Spencer-Booth 1967, b and 1968) have made a detailed quantitative study of mother-infant relations in captive rhesus monkeys. The methods used by Hinde are those which were adopted for my own study so that direct cross-species comparisons are possible. One important difference in our methods is that Hinde's check-sheets, like Rowell's were divided into half-minute intervals, whereas mine were in one-minute intervals. As explained previously, this would tend to cause a bias towards Hinde's figures being lower than mine.

I will now compare some of the measures of mother-infant relations in the two species, looking at group medians.

Time on the nipple

My data are not directly comparable with Hinde's because I lumped all situations in which the infant was on the nipple, whereas he separates being asleep and being awake on the nipple.

Rhesus infants continued to go to the nipple up to 100 weeks of age (23 months) whereas baboon infants went on the nipple very little after 16 months.

Rejections

In rhesus monkeys there is a peak in the frequency of rejections at 5 - 6 months and another peak at 11 - 12

months. My data show peaks at $4\frac{1}{2}$ and 8 months, rejections declining to a low level at 10 months (Fig. C). The apparently higher frequency of rejections in baboons between 3 and 9 months can be explained by my recording in whole minutes and Hinde in half minutes which would double my figures for an almost instantaneous category of behaviour such as this.

Rejections were first observed at one week old in rhesus compared with six weeks in baboons.

Total time off

The data are very similar in the two species (Fig. D). Both show an initial increase in Total time off followed by a stable period between 5 and 11 months, prior to a further increase at the end of the first year. The somewhat larger values obtained for baboons may be due to the difference in recording methods.

Time out of arm's reach as a percentage of Total time off

Using this expression the methodological difference is negated and the data for baboon and rhesus are directly comparable (see Fig. E).

Between 0 and 6 months the medians cross over twice, those for baboons being lower between 3 and 6 months. After 6 months the figures for baboons show a consistently higher value than those for rhesus, the latter showing no increase between 10 and 18 months.

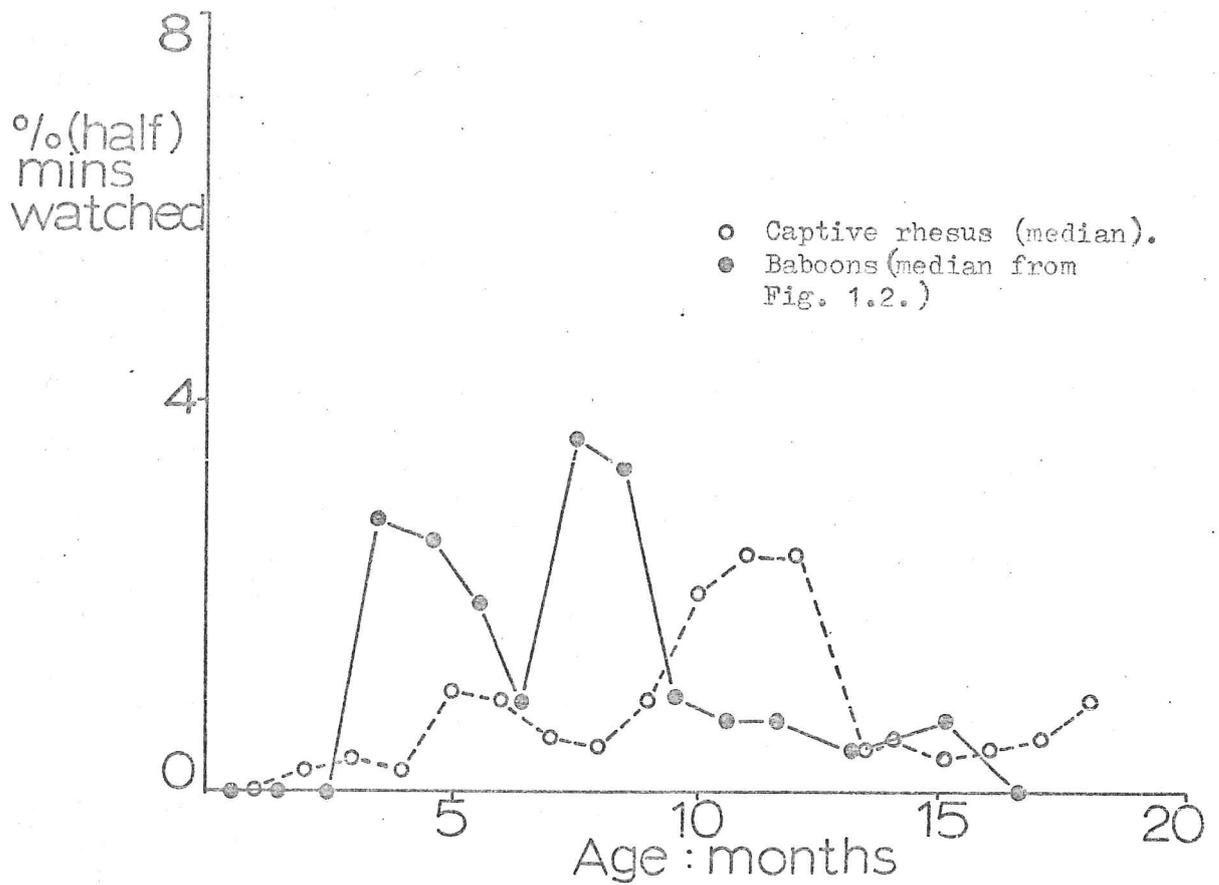


Fig. C. Rejections by the mother in captive rhesus monkeys (Hinde and Spencer-Booth) and in free-living baboons (my data)

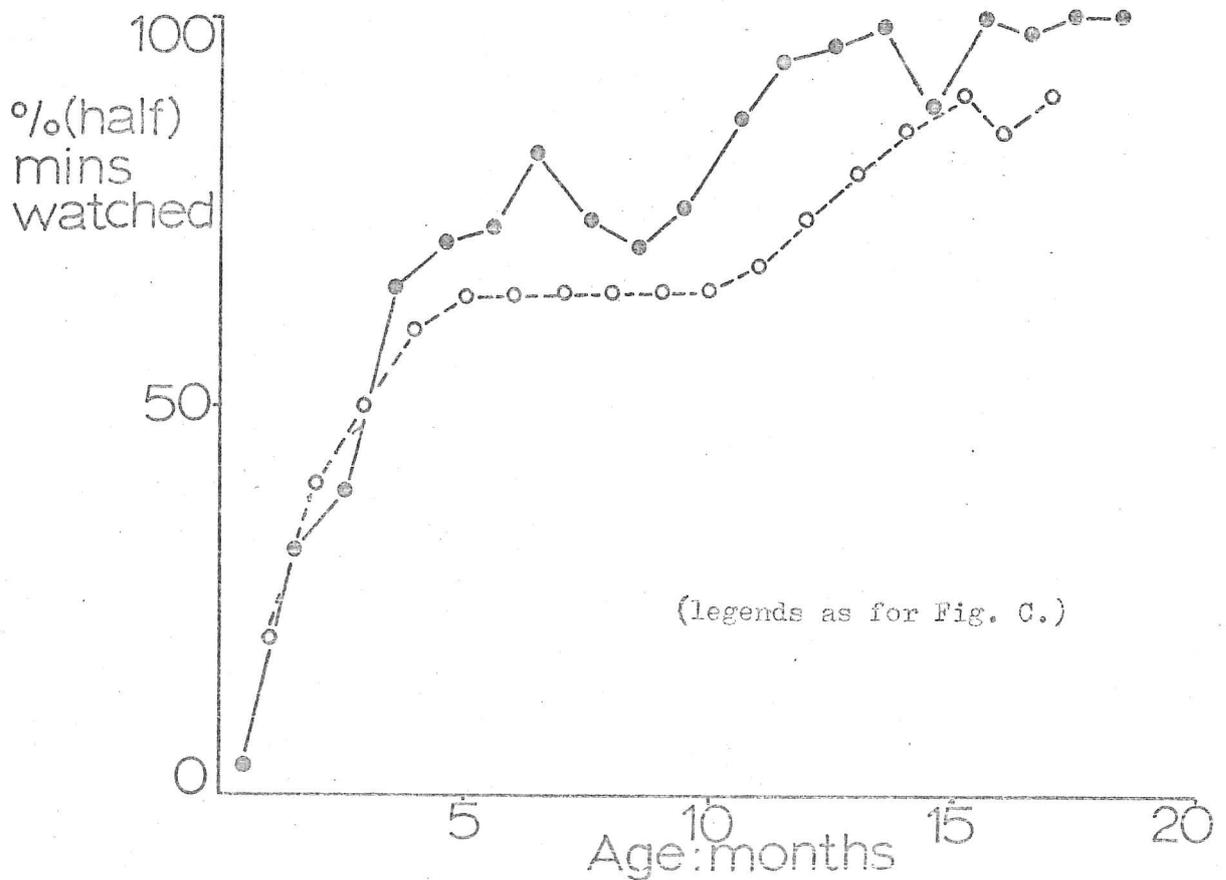


Fig. D. Total time off mother in captive rhesus monkeys (Hinde and Spencer-Booth) and in free-living baboons (my data).

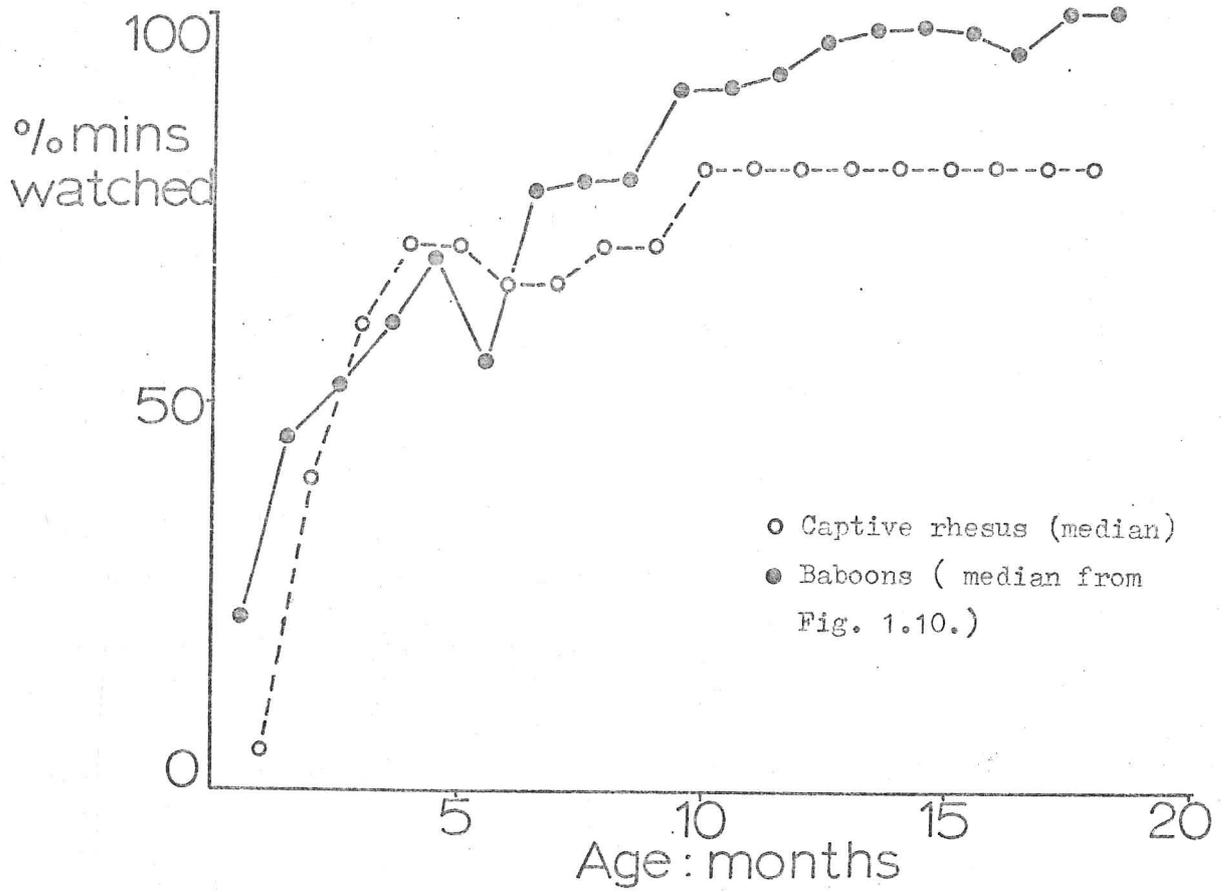


Fig. E. The percent of minutes in which the infant went out of contact with its mother in which it also went out of arm's reach in captive rhesus monkeys (Hinde and Spencer-Booth) and in free-living baboons (my data).

Approaching and Leaving

The data for baboons are very similar to those for rhesus, showing a change from a negative to a positive value in the early months.

Restrictive behaviour

Captive rhesus mothers restrict their infants' attempts to leave them in the early weeks, and in this they differ from wild baboons (but not from captive baboons as mentioned above). Free ranging rhesus monkeys do restrict their infants (Kaufmann, 1966). Thus it seems that rhesus mothers restrict their infants in most situations, but baboons do so only in the captive setting.

It is clear that the age changes in the frequency of measures of mother-infant relations are very similar in the two species, though there is a tendency for baboon infants to reach a given stage of independence at an earlier age. Rowell (1968, b) comes to the same conclusion comparing the two species for the first three months of life. The relative roles of mother and infant in maintaining the relationship are also similar in rhesus and baboon, and in both species changes in the mother's behaviour play a large part in promoting the infant's independence.

CHAPTER TWO

PLAY BEHAVIOUR

CHAPTER TWO

PLAY BEHAVIOURIntroduction1. Definition of Play

The purpose of this chapter of the thesis is to try to assess the function of play in the development of behaviour in baboons. An essential prerequisite to such a study is to arrive at a definition of play. No satisfactory definition has yet been proposed, and the term 'play' has been used loosely to include very diverse types of behaviour in many different species. Behaviour called 'play' is generally comprised of behaviour patterns seen in other functional contexts (Loizos, 1966). Some examples are: the aerobatics of birds (c.f. Beach, 1945): exploratory and manipulatory behaviour in ravens (Lorenz, 1956), cattle (Brownlee, 1957), non-human primates (Loizos, 1967) and humans (Hutt, 1966): locomotory activities in kittens (Beach, 1945), cattle (Brownlee, 1954), deer (Darling, 1937; Muller-Schwartz, 1968) and primates (Bertrand, 1969; Loizos, 1967): predatory behaviour in carnivores e.g. kestrels (Tinbergen, cited Thorpe, 1963), kittens (Egan, 1972; Leyhausen, 1965) and lions (Shenkel, 1966): aggressive behaviour in polecats (Poole, 1966), dogs (Ludwig, 1965), buffalo (Lumia, 1972) and primates (Loizos, 1967): sexual behaviour in mongooses (Rensch and Ducker, 1959), ungulates (Brownlee, 1954; Lumia, 1972) and primates (Harlow, 1962) and the 'ludic' behaviour such as art, philosophy and pure science in humans (Berlyne, 1960).

The diversity of these examples renders it unlikely that all the behavioural sequences called 'play' form a natural category of behaviour; that is, they are unlikely all to be related by either causal factors or function. Beach (1945) has said that "no single hypothesis can be formulated to explain all forms of play in every animal species". It seems that the nearest one can come to a definition of play at the present time is through a description of the characteristics of the movement patterns involved, for although play encompasses patterns of behaviour seen in many functional categories, even untrained observers may agree whether or not an animal is playing, since play often gives an impression of a lack of 'seriousness' (Hinde, 1970; Loizos, 1967).

Several authors (e.g. Bertrand, 1969; Ewer, 1968; Hinde, 1970; Loizos 1966; Lorenz, 1956; Marler and Hamilton, 1966) have described some of the differences between the motor patterns in play and the same patterns occurring in their 'originally motivating context' (i.e. in 'non-playful' exploratory, locomotory, predatory, aggressive and sexual behaviour etc.) which give rise to the impression of the lack of seriousness of play. For example:

1. Behavioural sequences in play may be reordered.
2. Elements of a number of functionally unrelated actions may intermingle in a single play sequence.
3. Components of a functional sequence may be omitted.
4. The intensity of components may not be in keeping with that of the sequence as a whole; movements may be exaggerated or inhibited during play.

5. The movement patterns in play often involve objects which would be inadequate to elicit those patterns in the normal functional context.

Owing to these characteristics, play tends to be 'uneconomical' and 'inefficient' in terms of the original motivating context (Loizos, 1967), and rarely leads to the normal functional consequence of the behavioural systems concerned. Berlyne (1960) has defined play as 'any behaviour that does not have a biological function we can clearly recognise'. At the present state of knowledge a precise definition of play is not possible, and a definition in terms of the lack of an immediate biological function of play (as a consequence of the characteristics of the movement patterns in play, listed above) seems to be the best one can achieve. Such a definition applies better to some aspects of play than to others (see below).

There are, however, some types of behaviour which are not normally considered as play but which might be included in play using the criteria outlined above. Ritualised behaviour, for example, is characterised by exaggeration and omission of components, but sequences are generally more rigid in ritualised behaviour than in play (Loizos, 1967). Incomplete chains of behaviour are also known, for example, from the hunting behaviour of satiated animals (Hinde, 1970).

Behaviour may also be recognised as play by the presence of specific gestures, facial expressions and vocalisations which may occur exclusively in the context of play. For example, a half-crouch with the forelegs stiffly extended is used as a play invitation gesture in dogs and

cats (Loizos, 1967), a sudden vertical jump often precedes play in mongooses (Rensch and Duker, 1959) and jackal/s may invite play with head-shaking movements (H. and J. van Lawick-Goodall, 1970); a special facial expression (the 'play face') occurs in primate play (Altmann, 1962; Van Hoof, 1967) and a special vocalisation ('laughing') also occurs in some primates, for instance in chimpanzees (van Lawick-Goodall, 1968). There may be "intra-specific 'understanding' of the play-mood and the signals or gestures which go with it", both between two animal species and between an animal and a man (Thorpe, 1966). However, such signals are not universal amongst all the behaviour which shares the other characteristics of play described above, and so their presence or absence cannot be used as a criterion by which play may always be recognized.

Thus, instead of starting with an elaborate definition of play and then studying those aspects of behaviour which conform to the definition, I selected for study behavioural sequences which appeared to lack the normal functional consequence of the behavioural system concerned. Precisely what I mean by the 'normal functional consequence' of a behavioural sequence will be described separately for each category of play in the two sections of the study. The two sections are called social play and non-social play. I shall define the former as play which is oriented towards another individual, and the latter as play which is oriented towards inanimate objects.

2. The Function of Play

Many hypotheses have been proposed as to the function of play behaviour, but there has been very little experimental investigation of the problem. Groos (1898) included all incomplete reactions as play, and envisaged their function as being practice at the behaviour patterns involved. This theory is the most generally accepted (c.f. Beach, 1945; Berlyne, 1960), though the evidence for it is somewhat conflicting. For example, Shenkel (1966) considers that play behaviour in lion cubs is important in the development of predatory and aggressive behaviour patterns, and Eibl-Eibesfeldt (1963) found that the orientation of the neck bite in the predatory and sexual behaviour of polecats was better in animals which had had the opportunity to play with litter mates than in animals which had been raised in isolation. In contrast, the movement patterns involved in the aggressive behaviour of polecats are known to appear one by one in their completed form and do not require practice for their development (Poole, 1966). In domestic cattle, locomotory, aggressive and social play continue long after these patterns have become fully developed, and Brownlee (1954) claims that the function of such play is the maintenance of tone and adequate vascularisation of the play muscles rather than in the development of motor patterns. Nor does this theory account for the persistence of play into adulthood in some species, for example cats (Loizos, 1967), bonnet macaques (Simonds, 1965) and chimpanzees (Van Lawick-Goodall, 1968). Thus all that one can say from the available evidence is that one of the possible functions of play is in the development of

some behaviour patterns, and that play is perhaps not important in the development of others.

Another hypothesis concerning the function of play is that it establishes familiarity with the environment and with conspecifics. Lorenz (1956) describes the exploratory play of a young raven and suggests that, through such play, ravens discover the biological relevance of objects in the habitat. Further evidence in harmony with the theory comes from experiments with chimpanzees, which have demonstrated that a certain degree of novelty of surroundings or play objects is important in inducing social play (Mason, 1965) and object manipulation (Welker, 1956). The curiosity of primates is well known (e.g. Butler, 1966); monkeys may learn to solve mechanical problems during object manipulation without any conventional reward (Harlow et al., 1958), and chimpanzees allowed to play with sticks are subsequently more capable of using them as a functional extension of the arm (Birch, 1945). However, Loizos (1967) has pointed out that it is not necessary to play (i.e. exaggerate and reorder components of behavioural sequences etc.) in order to learn about the environment; simple exploration would be adequate. This may be the case in human children: new objects are not incorporated in play until they have been thoroughly investigated (Hutt, 1966).

The social behaviour of monkeys and apes is far more complex than that of any other species of animal. Social play is known to occur in a large number of primate species (e.g. Bertrand, 1969; Hinde, 1971), and it has been suggested that social behaviour as well as motor skills may

develop during primate play (Loizos, 1967). Jay Dolhinow and Bishop (1970) state that, to a large extent through play, 'each individual (primate) from an early age gradually acquires a knowledge of all the other animals in the troop, their tolerances and personalities'.

Most observations of primate play have been of a qualitative nature, but Harlow and Harlow (1962) have experimentally demonstrated the importance of early social experience for the normal social development of rhesus monkeys. Infants deprived of all social interactions with other monkeys during their first year of life were subsequently inadequate in their social responses, notably in sexual, maternal and play behaviour, but infants allowed daily contact with peers developed almost normally. Although these experiments do not demonstrate that the social experience of play is specifically important for the development of adequate social responses, the fact that infants brought up with just their mothers were more socially retarded than infants brought up with only peers is suggestive.

No experimental investigation has yet been made of baboon play behaviour, though field studies have shown that baboon play patterns are very similar to those that have been described for rhesus monkeys (e.g. Harlow, 1963), and include play-fighting, play-climbing, tail-pulling, chasing, somersaulting and jumping etc. (Bolwig, 1959; Hall, 1962, b). Washburn and DeVore (1961) have implied that social play in baboons has an important function in development stating that 'in play groups, the skills and behaviour patterns of adult life are learned and practiced'. The importance of

play in baboons may not be confined to the development of behaviour since Hall (1962, b) found that some play-fighting and locomotory play occurred in adults.

From the preceding discussion it will be clear that comparatively little investigation into the problem of the function of play behaviour has been carried out in any species, but that previous studies involving both primate and non-primate species have pointed towards questions which it may be profitable to ask in an attempt to understand the function of play in baboons. Thus: is play behaviour in baboons important in the practice of movement patterns, in learning about the environment and conspecifics and in the development of social behaviour? The remainder of this thesis is concerned with an attempt to answer these questions, firstly for social and secondly for non-social play.

CHAPTER TWO

A. SOCIAL PLAY

A. SOCIAL PLAY

1. The Behaviour Patterns Studied

The behaviour patterns which were studied, and are here called social play are patterns seen also in aggressive, sexual, maternal and paternal behaviour, but which for various reasons (see below) did not achieve the normal functional consequence of the behavioural systems concerned. In using such a broad definition I have inevitably included as play the imperfect execution of some behaviour patterns by young animals which sometimes appeared in a 'non-playful' manner (i.e. without reordering and exaggerating components of behavioural sequences etc.), for example some incipient sexual behaviour patterns. Some writers (e.g. Loizos, 1966; Thorpe, 1963; 1966; Jay Dolhinow and Bishop, 1970) hold that such incomplete behaviour patterns, characteristic of the initial maturation of some behavioural sequences, should be excluded from play. Insofar as the broad purpose of this study is to attain a further understanding of the development of baboon behaviour in general, and is not specifically confined to play behaviour, I have included such behaviour in the study. Whether or not the behaviour I shall include as play conforms exactly to what previous authors have called play seems unimportant so long as I define precisely the behaviour patterns I am considering.

(i) Aggressive play

Aggressive behaviour patterns which were classed as play were those in which certain intense gestures and facial expressions of threat were absent (see Table 2.1).

Threatening signals in baboons included:

- (a) Slapping the ground or vegetation whilst making jerky lunging movements towards the opponent. Similar bobbing movements but without slapping also occurred in play, but were usually made much closer to the partner than during aggression proper.
- (b) Staring at the opponent and showing the whites of the eyelids, usually with the mouth closed. Staring at the opponent did also occur in play, very often preceding making physical contact. However, it was normally accompanied by the 'play face' (see below) and the white eyelids were not shown. (Staring also occurred in other 'friendly' contexts in baboons, but when it did so it was always accompanied by appeasement gestures; for instance staring is accompanied by lipsmacking when an adult female approaches a black infant (DeVore, 1963)).
- (c) Tooth grinding and yawning (canine display).
- (d) Raising the hair on the mane and uttering 'pant grunts' (adult males only).

These communicatory signals could be regarded as an external manifestation of the animal's motivation to attack, and some of the signals were probably ritualised intention movements of attack (for example, slapping the ground and lunging at the opponent). When aggressive behaviour occurred without intense threat (i.e. in aggressive play) some of the other patterns seen in aggression proper were also omitted. Most notably there was no hard biting in play, and the animals involved showed relatively little fear. Thus it is argued that the functional consequence

of aggressive behaviour (gaining access to a desired object or place by inflicting a painful bite or threatening to do so) did not occur in play as defined by the absence of intense threat, and this is the justification for separating aggression from aggressive play on this basis.

When talking about the functional consequence and absence of threat gestures, it is essential to define the length of the behavioural sequences under consideration. Here the functional consequence means that of aggressive behaviour as a whole. In smaller units of aggressive behaviour (such as the movements involved in bringing about physical contact) the functional consequence may occur in play as well as aggression. Furthermore, during short periods of aggressive behaviour all threatening signals may be absent, and separating such behaviour from play is difficult. For instance, an animal may be fighting, but showing extreme fear with no element of threat. Because in short sequences of aggression one partner may not show threat, the criterion used to distinguish play was that neither partner should be showing threat. Such a situation hardly ever occurred in aggressive sequences. This definition has the disadvantage that it sometimes happened that one animal played whilst its partner was aggressive to it. Such interactions usually involved animals differing in size, the smaller animal threatening the larger (usually whilst eliciting support from a third animal) whilst the larger animal played. Such sequences were usually rather short-lived, changing to exclusively play or exclusively aggression when the third animal arrived.

Table 2.1Occurrence of communicative gestures in aggression and aggressive play

	<u>Aggression</u>	<u>Play</u>
Slapping ground or vegetation	+	0
Jerky lunging movements	+	+ close to opponent
Staring at opponent	+	+
Showing whites of eyelids	+	0
Tooth grinding	+ males	0
Yawning	+ males	0
Hair raised on mane	+ adult males	0
Pant grunt	+ adult males	0
Play face	0	+
Laughing	0	+
Hard biting	+	0
Fear face	+	+ slight
Tail vertically upright	+	0
Defaecation	+	0

In practise there was little difficulty in making a distinction between play and aggression, even in short sequences, because threatening behaviour nearly always preceded an aggressive interaction, whereas play was often preceded by specific play signals.

Although the distinction between aggression and aggressive play is to some extent arbitrary, it does separate two aspects of aggressive behaviour which did not appear to be

simply extremes of a continuum. When intense threat was absent, movements were much less intense (in terms of the speed of movements made), and play behaviour was often preceded by a special face called the 'play face'. The play face occurred exclusively during or preceding play and was characterised by a wide open mouth with the lips slack and not drawn back in the corners (Plate VIII). It has been claimed that the play face indicates to the animal being approached something about the nature of the movements which are to follow ('metacommunication' Altmann, 1967). A staccato vocalisation ('laughing') also occurred exclusively in play, and play was often preceded by a special bouncy gait or by rolling on the ground and looking at the partner. If during play an animal was hurt, play often changed abruptly into aggression. Threatening behaviour appeared and there was a sudden change in the intensity of the movements. The facial expressions of fear which were present to only a small extent in play became very marked. Holding the tail vertically upright and defaecating, which indicated more intense fear, occurred in aggression but not in play. Wounding was frequent in aggression involving adult males, but never occurred in play.

Thus aggressive behaviour seems to be divisible into two sorts, each characterised by the presence or absence of particular behaviour patterns and communicatory signals.

(ii) Sexual play

Sexual behaviour was much less easily divisible into sexual play and sexual behaviour proper by the criterion

of functional consequence.

Sexual behaviour did not reach its functional consequence of copulation with insemination for several reasons. For example, considering the male's behaviour, the object to which sexual behaviour was directed was not always appropriate (it may have been an inanimate object, an animal of the wrong species or of the wrong sex, an immature animal or a female in the wrong stage of the sexual cycle.) Alternatively, the functional consequence was sometimes not reached because the subject was immature or the mounting disoriented or incomplete. In sexual behaviour there was no common factor which could be used to make a distinction between those patterns which usually led to the functional consequence and those which did not.

However, at the beginning of the study I did make a preliminary classification of sexual behaviour into sexual play and sex proper. Sexual behaviour involving young animals, or involving a young animal and an adult male was arbitrarily included in play (= sexual play). Sexual behaviour involving an adult female or two adult males was excluded from play. The classification divides those sexual patterns which were often interspersed with aggressive play patterns from those which were not. Although I now feel that this classification was not useful, it affected the way I recorded behaviour and hence the assessment of the amount of play (Fig. 2.1). Since adult males hardly ever mounted juvenile females, one can say that all sexual patterns involving young animals were included in play except those between young males and adult females. All sexual behaviour

was recorded however (sexual behaviour other than play being recorded on the mother-infant check sheet), and the data for sexual play and sexual behaviour proper are pooled in the section on the development of sexual behaviour (Section 10) in which the classification outlined above is not used.

(iii) Maternal and paternal play

When an animal other than the mother or an adult male carried an infant it was classed as play. When an infant was carried by a female it was considered to be maternal behaviour which did not reach its functional consequence of protecting and feeding the infant. The animal which did the carrying usually carried the infant clumsily and for short periods only, and could not provide it with milk. When males carried an infant it was probably not related to maternal behaviour. Adult male baboons are known to carry infants in several social contexts, and may enhance their effectiveness in aggressive interactions by so doing (Ransom and Ransom 1971). Young males did not 'use' infants in this way in aggression, but their behaviour in play may have been homologous to the behaviour of the adults, differing from it by the absence of threat.

It can be seen that the behaviour chosen for study, and called play by the criterion of not having a functional consequence did not have a functional consequence for several different reasons, and lumping them together as 'social play' is somewhat artificial. The reasons for not reaching a functional consequence included incompleteness and

disorganisation of patterns, immaturity of one or both of the partners, wrong hormonal state of partner and motivational differences. However, the play patterns all lacked an obvious adaptive function and conformed to a large extent to what has been called play in other primate studies (e.g. baboons; Bolwig, 1959; Hall, 1962, b; Washburn and DeVore, 1961; rhesus monkeys; Harlow, 1962, a; Hinde and Spencer-Booth, 1968).

2. The questions asked

It has been suggested that social play is important for the development of motor coordination, and there is evidence that it may also be important in the development of social behaviour (see Introduction). This section of the study sets out to test these hypotheses and asks the question:

'How is social play in baboons important for the development of behaviour patterns and for an animal's integration into the social structure of the troop?'

It is not possible to answer this question directly by experimentally depriving animals of peers with which to play. By doing this one inevitably also deprives them of all other types of social interaction and other influences that peers may have. Thus the problem must be tackled indirectly by asking related questions which should throw light on the primary question:

1. How does the amount of play in which the infant takes part vary with age and sex?
2. What types of movement patterns are seen in play and how does their nature and frequency change with age and sex? How do these movement patterns compare with those seen outside play and with those that occur in adults?
3. What kinds of social relationships appear in play and how do these relationships compare with those seen outside play and with those that occur in adults?

If parallels can be seen between the movement patterns and social relationships which appear in play and those seen in adult animals, and especially if the movement patterns

and social relationships become more like those of adult animals with age, this would be good evidence for the importance of play in the development of behaviour.

3. Field methods and check-sheet design

In order to compensate for any tendency for daily peaks in play activity watching was carried out at the same time of day for all individuals, so far as possible.

Individuals representing the two sexes and different age classes were selected for study. For most of the study period all infants and juveniles were watched.

Play records were made simultaneously with mother-infant records when possible. Usually this was too difficult, and so mother-infant records were suspended during the time the individual was playing, and resumed afterwards. Thus the length of each monthly watch was four hours (the length of a mother-infant record) plus the time the mother-infant record was stopped for exclusive play recording (0 - 1½ hrs. i.e. up to about 5½ hours altogether). For each bout (see below) of social play I recorded the following details, speaking into a portable tape recorder and later transcribing to a check-sheet. These data should help to answer the questions posed above.

1. The length of each play bout and the time between each bout. This was measured using a stop watch and estimated to be accurate to within one second either way.

A play bout was defined as 'a sequence of play uninterrupted by a break of one second or more'. In rough-and-tumble play (see below for definition) a bout was considered to have finished if both partners ceased movement for more than one second (regardless of whether they were still in contact). In chasing play (see below) the bout was considered finished if one of the partners stopped running

for more than one second.

On the check-sheet, each line represented one bout of play.

2. The names of the playing animals. (Play usually occurred in dyads.)
3. The initiator and terminator of each bout. The initiator was the individual which started to play first or approached the other partner, and the terminator was the one that stopped playing first or left the other partner. This definition overlooks the fact that an animal was sometimes 'invited' to approach and play (for instance by the partner rolling on the ground and looking at the other one) but this was relatively infrequent. A decision could not be made for all bouts as to which partner was the initiator and which the terminator, and so this was recorded only for those bouts where one partner clearly had such a role.
4. The movement patterns seen in each play bout. Details of the movement patterns recorded are given in the next section.
5. Vocalisations in play.
6. The names of the other animals which came within a radius of five metres of the playing animals during the bout.

4. Classification of play movement patterns

The categories of 1. Aggressive, 2. Sexual and 3. Maternal and paternal play, often occurred in sequences in which components of the three categories were mixed up with each other, but they will be described under these headings for convenience.

1. Aggressive play

Aggressive play is the largest component of social play. It can be divided into rough-and-tumble and approach-withdrawal play.

(a) Rough-and-tumble

This category is very similar to what has been called rough-and-tumble play in other primate studies (e.g. Harlow, 1963; Hinde and Spencer-Booth, 1968) and involves wrestling, hitting, sparring, pulling and mock biting movements.

Wrestling

Wrestling is rough-and-tumble play in which both partners are active. It involves rolling on the ground with pulling, pushing and hitting movements (Plates IX and X), and also includes play in which both partners are standing upright (see under 'sparring').

Mauling

If one partner is totally inactive throughout a bout of wrestling play it is considered to be mauled by the active one. Active and passive roles are indicated on the check sheet.

Sparring

Sparring is rough-and-tumble play in which both partners are standing facing each other. It usually involves

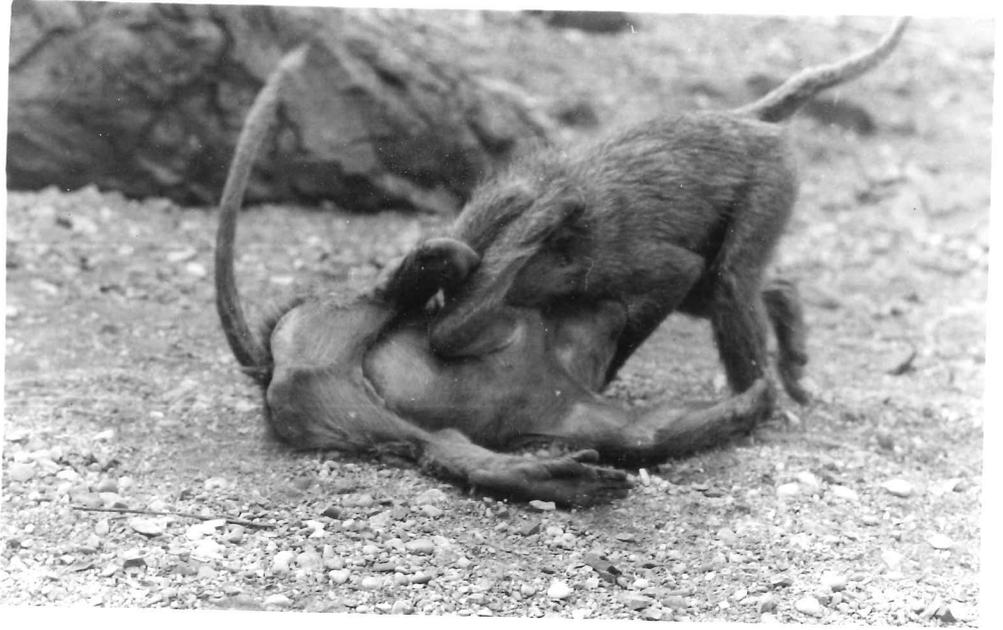


Plate IX. Postures during wrestling play with mock biting between two eighteen month old males.



Plate X. Postures during wrestling play with mock biting between two eighteen month old males.

grappling with the arms around the neck, and hitting towards the head, and is generally more vigorous than wrestling play (Plates XI and XII).

Mock biting

Mock biting occurs during wrestling and mauling play. The jaws are not usually closed hard. A study of the parts bitten in play was carried out separately, but this was not recorded on the main check sheet.

In summary, rough-and-tumble play is divided of wrestling and mauling according to whether or not both partners are active during the play bout. Sparring is a type of wrestling, and mock biting may occur during any type of rough-and-tumble play.

(b) Approach-withdrawal play

This category is divided into chasing and being chased. A chase is defined as behaviour in which one animal runs in pursuit of the other for a distance of two feet or more.

2. Sexual play

It was sometimes difficult to decide whether a play pattern should be classed as sexual or rough-and-tumble. Thus I used the arbitrary distinction that, if an animal stood with its feet on the ground or clasped ^{the} legs of its partner and its hands on the back or haunches of its partner, it was considered to be sexual behaviour.

The following details of all sexual behaviour were recorded:

Males:

The orientation of the mount and whether the feet were used



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Plate XI. Sparring play with mock biting between a two year old and an eighteen month old male.

Maternal and paternal play

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 carrying



Plate XII. Sparring play between a five year old and a three year old male. Animals are about to mock bite one another.

to clasp the legs of the partner.

The number of pelvic thrusts.

Whether intromission occurred.

Whether there was ejaculation.

Females:

The role of the female in sexual behaviour is much less variable than that of the male, and appears in adult form at an early age. Sexual behaviour was simply recorded as a mount (i.e. each instance of sexual behaviour was recorded) but no subdivisions were made. However, females did sometimes adopt the role of the male in sexual behaviour and vice versa.

3. Maternal and paternal play

Maternal and paternal play is divided into four categories; carrying and being carried dorsally, and carrying and being carried ventrally.

5. Age changes and sex differences in the amount of play
 1. Methods of analysis

To obtain an estimate of the changes in the amount of play with age, the lengths of all the play bouts which occurred during the relevant watch of each individual were summed, and then divided by the number of hours for which the animal was watched. This gave a figure in units of seconds per hour spent playing.

Each point of Fig.2.1 represents a figure derived from at least 8 hours record. It is a combination of the figure for the four hour record of the individual concerned, plus the figures for the amount each of the other individuals played with it during their records.

For example, considering four animals A, B, C and D: if A was watched for 4 hours and played with B for 400 seconds, and B was watched for 4 hours and played with A for 600 seconds, then the amount of time A played with B was $\frac{400 + 600}{4 \text{ hrs.} + 4 \text{ hrs.}} = 125$ seconds per hour.

The total amount of time A spent playing was thus the sum of A with B, + A with C, + A with D, seconds per hour.

The total for B would be B with A, + B with C, + B with D, seconds per hour. Thus the same data were used for several different points on the graph (in the above example, the amount of time A played with B was used for the totals of both A and B).

It sometimes happened that the animal being watched played with two or more animals simultaneously. When this occurred I counted it as if it had played with each of the animals separately. This makes the calculations of the

amount of time spent playing with each other individual more accurate, but was not a common enough event to significantly affect the calculations of total time spent playing. Bouts in which more than two animals were involved comprised about 3.5 percent of all bouts. Most of these involved three animals and the third animal usually took part only briefly during the bout.

There were two adolescent males which were not themselves watched during the main part of the study owing to lack of observation time. Hence the figures for the amount the other animals played with them are based on 4 hours observation only. The three year old male was the only animal that played a large amount with these two adolescents.

Some separate 8 hour watches of individuals (including the two adolescents) were made during a later phase of the study to obtain data for age groups where data were lacking. The figures for the total seconds per hour spent playing by these animals was derived from the 8 hour watch alone.

It should also be remembered that some but not all sexual behaviour patterns were included in play. However, this does not affect the following discussion about the age changes and sex differences in the amount of play, because sexual patterns comprised only up to about 5 percent of total play (see also Section 10).

Results

Play occurred in one male infant at two weeks of age, and occurred in all infants watched by 6 weeks. Infants up to this age seemed to approach other, often larger animals,

fearlessly and started to play with them, and play was often terminated by the mother picking up the infant and walking away. Mothers also sometimes threatened animals which approached their infants to play in the first few weeks. The play face was first seen at 17 days of age in a male infant as it approached another animal before playing with it. After six weeks of age, mothers had a much smaller role in preventing their infants from playing. By this time motor coordination was quite good; infants could run short distances and climb into low bushes, and play increased rapidly.

In males play reached an initial peak at $4\frac{1}{2}$ months of over 200 seconds per hour (Fig.2.1). After this age play decreased, reaching a significant trough at $8\frac{1}{2}$ months ($p < 0.001$; Mann-Whitney U test) before increasing again towards another higher peak at about 14 months of age of over 300 seconds per hour. From 14 months, play decreased steadily until at 5 years old males played for about 30 seconds per hour.

For females fewer data were obtained, and there is a gap in the record between 5 and 9 months of age. The amount of play often fluctuated widely from one month to the next, even for one individual, and it is not possible to identify any peaks. Play apparently remained at a fairly uniform level between the ages of one to three years, but never reached such high levels as it did for males.

Considering all age groups, there was a tendency for males to play more than females. In five of six independent pairs matched for age, the male played more than the female. In the sixth pair the reverse was true, and so this was not

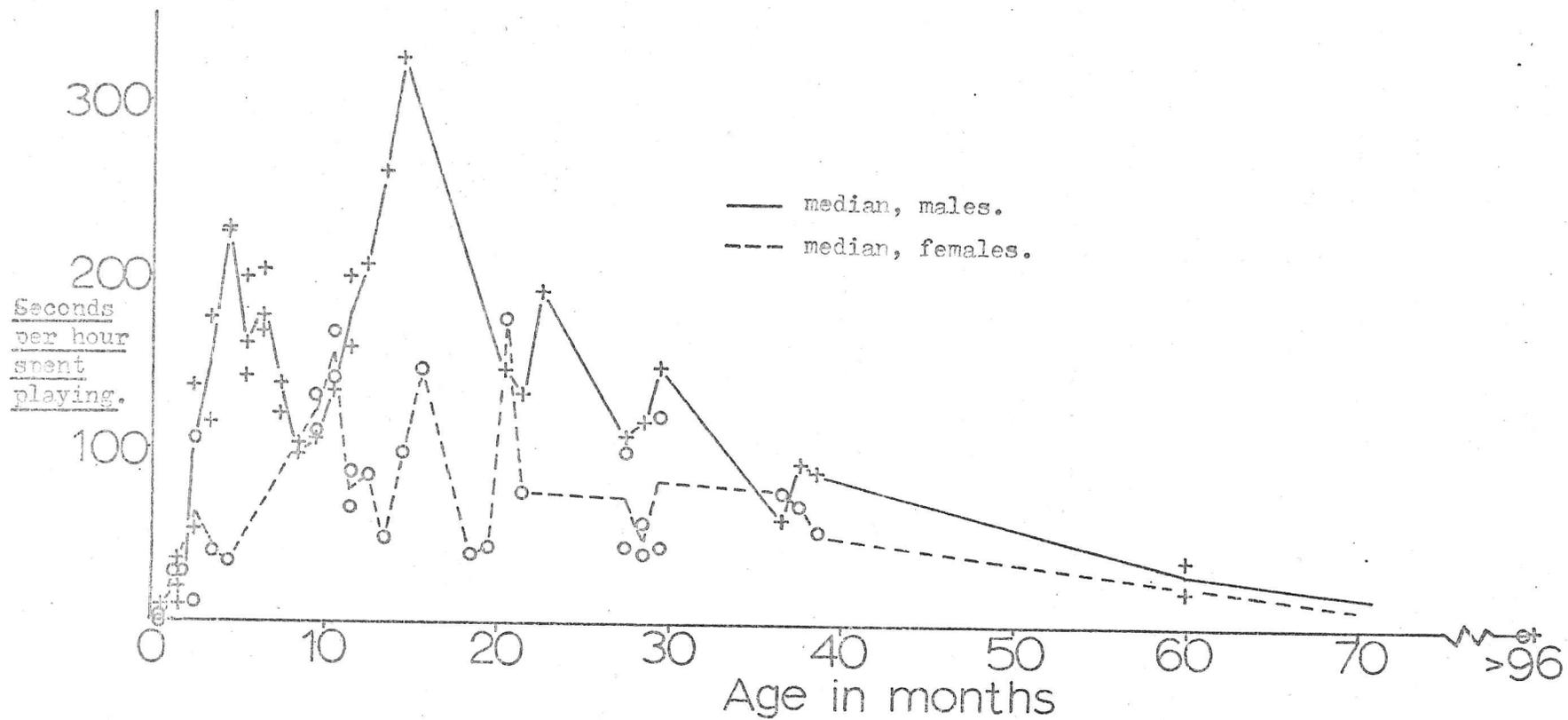


Fig. 2.1. The age changes in the amount of play.

a significant difference by the Wilcoxon matched-pairs test.

Play amongst adults was fairly infrequent, and when it did occur always involved a juvenile and an adult, and never two adults together. Eight hour watches were carried out on adult males and adult females. The 8 hours on adult males included watches on 6 different adult males representing different ages and the 8 hours on adult females included 4 individuals representing different ages and different stages in the sexual cycle. A rate of 1 second per hour spent playing was obtained for males, and 0 seconds per hour for females (though adult females did in fact play occasionally). From other casual observations it appeared that older adult males tended to play more than younger ones, but the reverse was probably true for adult females.

Discussion

There is very little previous information concerning the amount of play at different ages in baboons. A qualitative account of social play in free-living baboons in East and South Africa is given by DeVore (1963) and Hall and DeVore (1965). Social play is described as beginning in the 1st - 4th month, increasing in the second half of the first year and continuing into 2nd, 3rd and 4th years (juvenile females dropping out of play groups in the 3rd and 4th years). Rowell (1968) states that social play was an important behaviour pattern by the fourth week in captive baboons, and that play with other infants increased steadily throughout the first three months of life. The only data concerning sex differences in the amount of baboon play relate to *Hamadryas* baboons (Kummer,

1968, a). Males from the black infant stage onwards were much more common in play groups than were females. Thus, so far as they go, previous data on baboons are consistent with my own.

In general, the age changes and sex differences in the amount of play in baboons followed fairly closely those which have been described for rhesus monkeys. Hinde and Spencer-Booth (1968) give data showing that rough-and-tumble play in rhesus began in the second or third month of life, and reached an initial peak at 4 to 5 months of age, followed by a slight trough between six and eight months and a further increase at the end of the first year. Thereafter, rough-and-tumble play remained at a fairly high level until the end of the second year, when it started to decline. Rhesus monkey males are also known to engage in more rough-and-tumble play than females (Harlow and Harlow, 1962).

Less detailed studies of play have been carried out in several other primate species. Kaufmann and Rosenblum (1969) present data for the age changes in the duration of social play in infant pigtailed and bonnet macaques. Bonnets play more than pigtails, though both species (as in baboons and rhesus) reach a peak of play around one year of age. In squirrel monkeys, males play more than females and reach a peak in play frequency at 18 months, compared with a peak at one year of age for females (Baldwin, 1969). Chimpanzees reach a peak in the frequency of play sessions at 2 - 4 years old (Van Lawick-Goodall, 1965). Examples of the ages at which play begins and ceases in some other primate species are given by Hinde (1971), but apart from

those species mentioned above, few quantitative accounts have been published concerning the age distribution of play in primates. It appears that there is considerable variation between species in the age distribution of play. This is to be expected considering the differences between species in rates of development, behavioural repertoire and social structure. Many monkey species, however, seem to show a peak in play frequency around one year of age.

I shall now discuss some aspects of the causation and function of the age changes and sex differences in the amount of play observed in baboons, though further insight into these problems will come in later sections.

In rhesus monkeys it is known that the rough-and-tumble play of infants may be increased following injection of testosterone propionate into the mother during pregnancy (Young et al., 1964). This indicates that testosterone levels may in part be the basis of the sex differences in the amount of play in rhesus. The close similarity between baboon and rhesus play suggests that the same may be true for baboons.

Some of the fluctuations in the amount of play with age may have been related to the infant's relationship to its mother. The trough in the amount of play around eight months of age in male baboons roughly coincides with the second peak in the frequency of rejections by the mother of the infant's attempts to gain the nipple (Fig. 1.2). It seems likely that this disturbance in the mother-infant relationship was instrumental in depressing the amount of play. After being rejected, infants tended to follow their

mothers closely, attempting to jump on their mother's backs or regain the nipple, and the trend towards spending an increasing amount of time off the mother with age was temporarily halted (Fig. 1.8). Infants were preoccupied with trying to regain contact with their mothers rather than leaving them to join play groups.

Studies of other primate species lend support to this hypothesis. Harlow (1962) has shown that blasts of air ejected from a surrogate mother caused infants to cling to the surrogate more closely, rather than be driven away from her. Hinde (1971) found that six days of maternal deprivation in 5, 6 or 7 month old rhesus infants induced symptoms of distress similar to those caused by maternal rejection, and that the amount of rough-and-tumble play decreased markedly during and for some time after separation. An orphaned wild chimpanzee infant also showed a decline in playful behaviour (Van Lawick-Goodall, 1968).

It has been suggested that play behaviour is practised for its own sake, because it is pleasurable or because the animals possess surplus energy (see Beach, 1945; Leyhausen, 1965). Behaviour patterns appearing in play are generally divorced from their original motivation (Lorenz, 1956) and play occurs in the absence of physiological pressures such as the need for food, drink, sleep or a sexual partner (Loizos, 1967). Most descriptions of play behaviour have concerned domesticated or zoo animals whose primary needs are looked after, and this has given backing to the idea that animals play because there is 'nothing else to do' (see Thorpe, 1966). These considerations raise two

questions.

1. Does preoccupation with more primary needs in free-living baboons reduce the frequency of play to such an extent that it can no longer be important in behavioural development?

A play frequency reaching up to 5 minutes per hour (8 percent of time) of either physical contact or chasing suggests a fairly important role of play in development. It is known that the opportunity to interact with peers for only 20 minutes per day is adequate for the development of normal social behaviour in captive rhesus monkeys (Harlow and Harlow, 1962).

2. Do baboons play most at an age when they are most dependent on their mothers and other troop members for providing their primary needs: i.e. is the amount of play determined largely by the extent of an animal's need to engage in other types of behaviour?

Although it is true that play was largely confined to young animals which enjoyed emancipation from certain adult activities (such as maternal behaviour and protection of the troop), the highest peak in play behaviour occurred at 15 months of age (for males), at which time infants were largely independent of their mothers for food and transport. The position of this peak suggests that play behaviour in baboons was not simply behaviour that occurred in the absence of anything else; other factors were involved. Strong evidence in support of such a view comes from experiments by Mason (1965), in which chimpanzees were deprived of food for 15 hours and then allowed to choose

between being fed, petted or played with. In 40 percent of cases the chimpanzees preferred to play.

A certain amount of play was also observed in adult baboons of both sexes. Play has previously been described in adult chacma baboons (Hall, 1962, b), and adult play must be taken into account when considering the function of play. However, adult baboons played comparatively little compared with some other primate species such as bonnet macaques and chimpanzees (Simonds, 1965; Van Lawick-Goodall, 1968). It is conceivable, however, that social play has a somewhat different function in different age groups and in different species. Thus the fact that adults play is not inconsistent with the view that one of the functions of social play may lie in the development of motor coordination and social behaviour.

6. The time characteristics of play bouts

(a) The frequency distribution of bouts of different lengths.

Methods

Selecting pairs of animals of the same sex near to each other in age, I classified the play bouts between them according to their lengths in seconds, those of more than 15 seconds being lumped into one category. Pairs of animals representing different ages and sexes can thus be compared with one another.

Results

Males. (Fig. 2.2)

In every sample, the mode of the play bout lengths was one second. (A higher value than that for the one second category was obtained for the >15 seconds category in the oldest sample, but if the actual bout lengths of the long bouts were plotted separately, this would not be the case).

The frequency distribution of bout lengths was similar for all five age groups, but there was a tendency for bouts of one second to become relatively less frequent with age though the differences between the different pairs of animals were not significant. In the oldest sample there was a large increase in the percentage of bouts of more than 15 seconds ($p < 0.01$; Chi square test, comparing youngest and oldest pair).

Females. (Fig. 2.3)

As was the case for males, the mode of bout lengths was one second in every sample. There was a larger percentage of bouts of one second in length in female play than in play between males ($p < 0.05$; Mann-Whitney U test). With

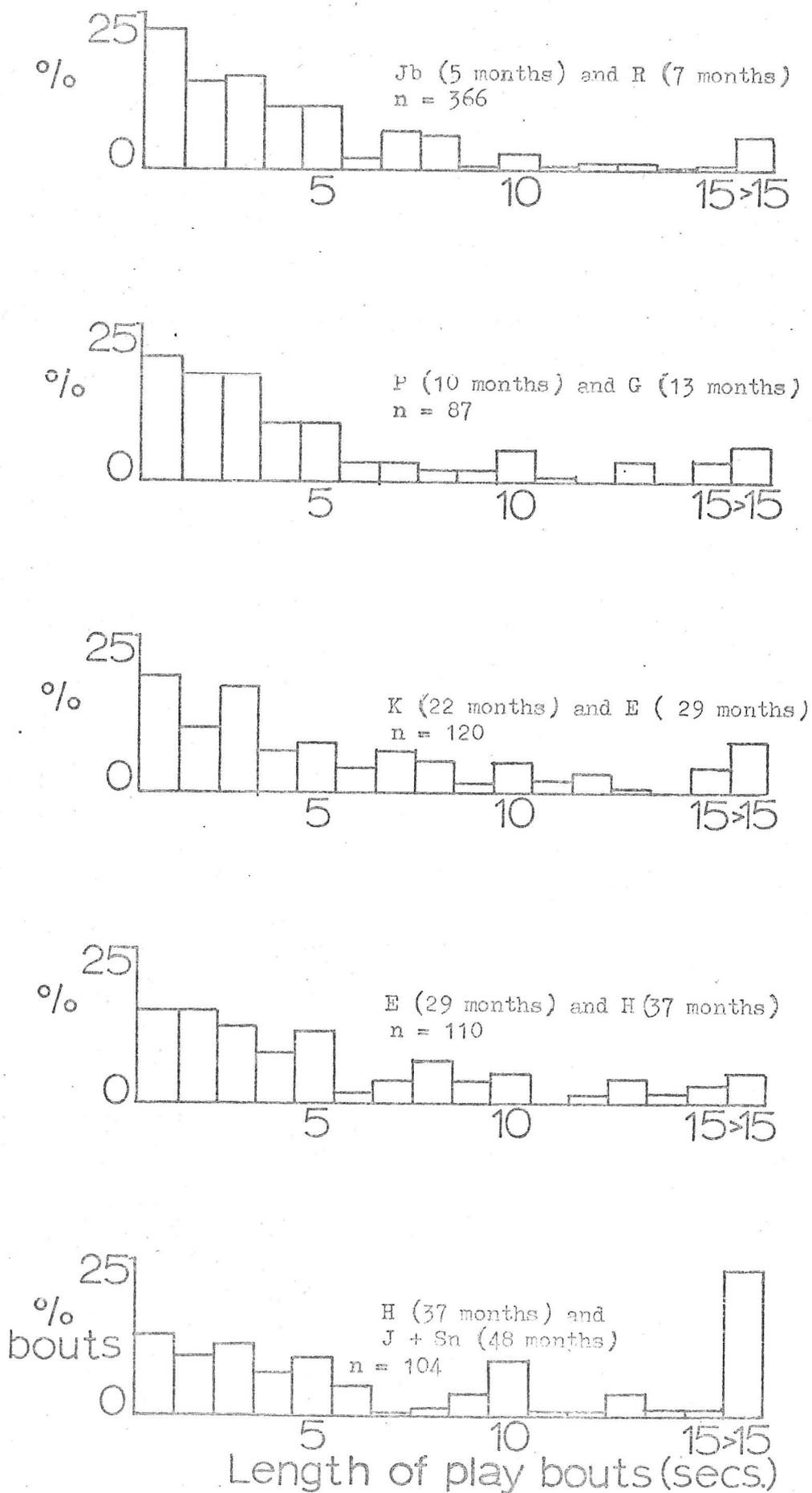


Fig. 2.2. The frequency distribution of play bout lengths for males. The ages beside the individuals' symbols indicate their mean ages during the recording period of three months from which the data are taken.

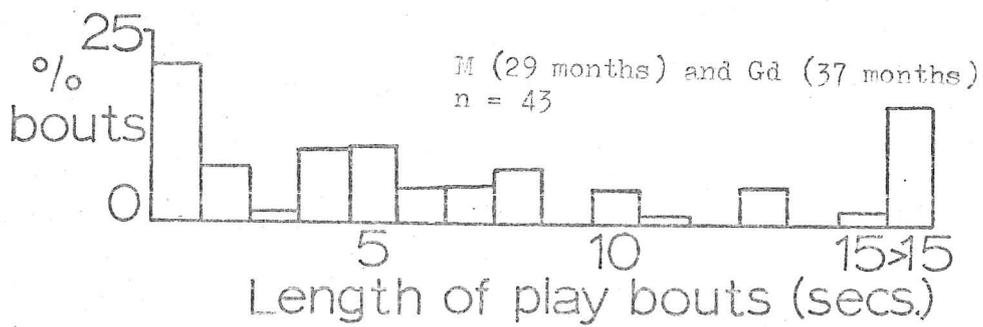
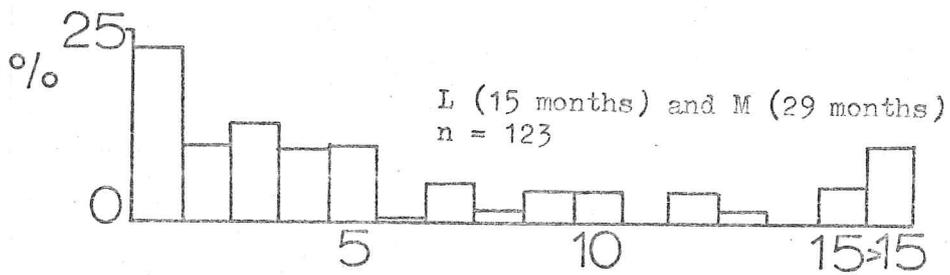
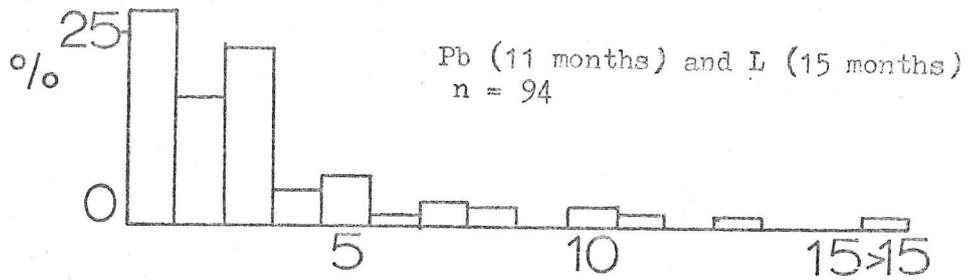
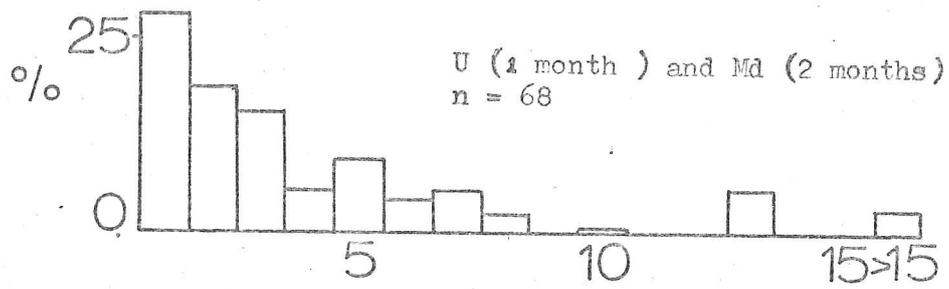


Fig. 2.3. The frequency distribution of play bout lengths for females. Legends as for Fig. 2.2.

increasing age, bouts of 1, 2 and 3 seconds tended to form a smaller percentage, and bouts of 4, 5 and 15 seconds to form a larger percentage ($p < 0.001$ in both cases; Chi square test, comparing the youngest and oldest pair).

(b) The mean length of play bouts

For each individual, the mean length of all play bouts was calculated (regardless of the age or sex of the partner) and plotted against the individual's mean age during the recording period. I considered it reasonable to consider means rather than medians since the numbers involved were very large. Play bouts were taken from a recording period of between 2 and 4 months depending on the individual; see Fig. 2.4.

As would be predicted from the frequency distribution data, the mean bout length increased with age ($p < 0.01$ for both sexes; Spearman rank correlation coefficient) and tended to be higher for males than for females.

Discussion

From these results it is apparent that part of the sex difference in the amount of play was due to the fact that males engaged in longer bouts than females, though the sex difference in bout length was not large enough to account for all the sex difference in the amount of play. Thus males engaged in more and longer bouts than females. Also, as animals of both sexes became older, they engaged in fewer but longer bouts. It may have been the case that males were less fearful than females, and older animals were less fearful than younger ones of their play partners, and for this reason their play bouts were more sustained.

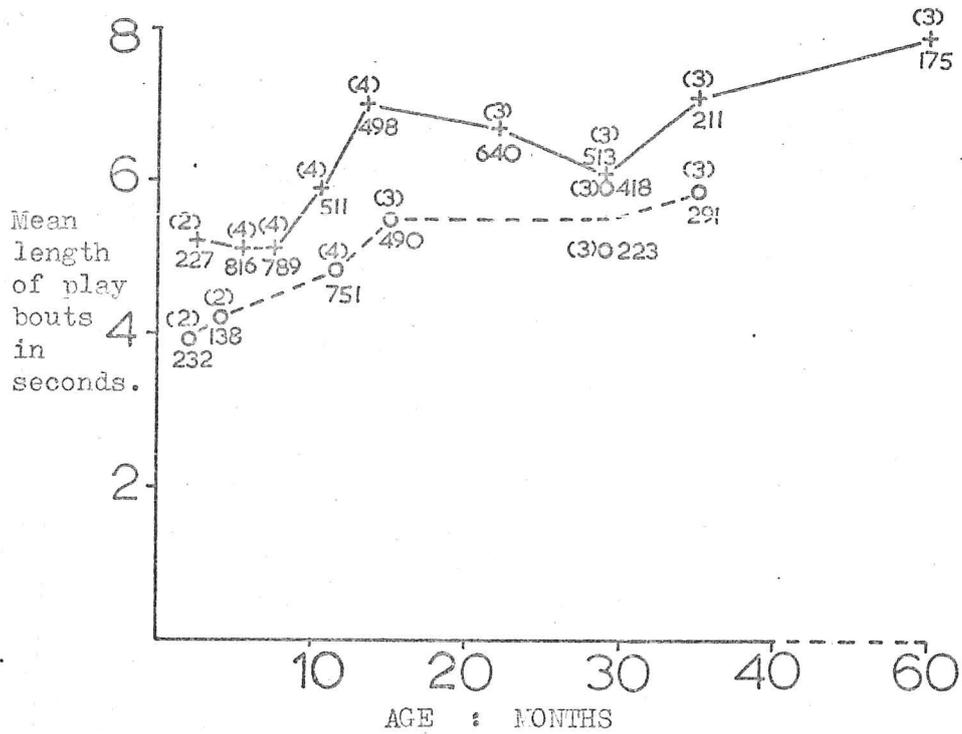


Fig. 2.4. The age changes in the mean length of play bouts. Numbers beside points indicate the number of bouts from which the figure is derived. Numbers in brackets indicate the length of the recording period, in months, from which the point is calculated. Each point represents a different individual.

7. The age changes and sex differences in the movement patterns seen in play

1. Methods

2. Aggressive Play

(a) Rough-and-tumble play

Wrestling

Mauling

Sparring

Mock biting

Conclusions

Discussion

(b) Approach-withdrawal play

Total approach-withdrawal play

Chasing

Being chased

Dodging

3. Maternal and paternal play

Results

Discussion

7. The age changes and sex differences in the movement patterns seen in play

1. Methods

The relative frequencies of the different movement patterns of play were calculated in terms of the number of times that the movement pattern occurred per 100 seconds play. It was common for more than one type of movement pattern to occur within one bout of play, and for the same pattern to recur within a bout. Thus the figures do not refer to whole play bouts comprised solely of a particular movement pattern, but to individual instances, many of which comprised only a part of a play bout. The figures reveal the frequency of a movement pattern compared with other movement patterns, but say nothing about its absolute frequency. From such figures it should be possible to assess the relative importance of the different types of play at different ages and in the two sexes.

In most of the figures referred to below, all the points were calculated from one months records, except for the four youngest animals, for which data for two months were lumped in order to give a large enough sample. The number of seconds play from which the points were calculated varies between 296 and 7,121. In the remaining figures the data used for the four youngest animals were again from two months records, but for the older animals data for three months were lumped, and the mean age during the three months is plotted. This gives a clearer picture of the age changes by smoothing out some of the erratic points, and figures were plotted in this way when matched-pair statistical

tests were not required.

2. Aggressive Play

(a) Rough-and-tumble play

Wrestling

Fig. 2.5 shows the frequency of wrestling play in males and females, plotted against age. No very marked age changes are apparent, but there was a tendency for wrestling to be more common in males than in females; the figures for males fluctuated around 10 instances and for females around 7 instances per 100 seconds play. ($p < 0.01$; Wilcoxon matched-pairs test)

Mauling

Although one animal was sometimes passive throughout a long play sequence, a large proportion of non-mutual play consisted of a brief hitting, grabbing or pulling movement lasting no more than a second.

There was a tendency for both active and passive mauling to be relatively more common amongst females than amongst males ($p < 0.01$ in both cases; Wilcoxon matched-pairs test; Figs. 2.6 and 2.7). This is consistent with the finding that males engage in relatively more wrestling play than females. It is also in harmony with the conclusion in Section 6 that females have more short play bouts than do males.

In males, active mauling showed little change in relative frequency with age (Spearman rank correlation coefficient, $r_s = 0.11$; $p > 0.05$) but passive mauling decreased significantly ($r_s = -0.94$; $p < 0.01$). In females, active

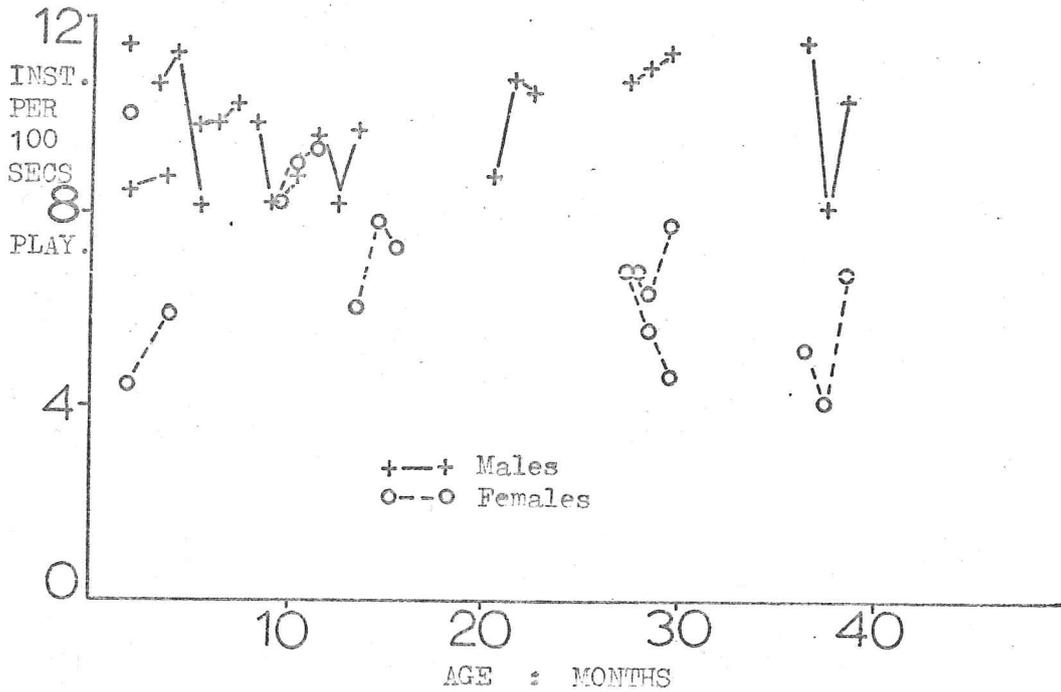


Fig. 2.5. Instances of wrestling per 100 seconds play. Lines link points derived from one individual. Each point is derived from one months records except for those for the four youngest animals, which are derived from two months records (see also p. 70).

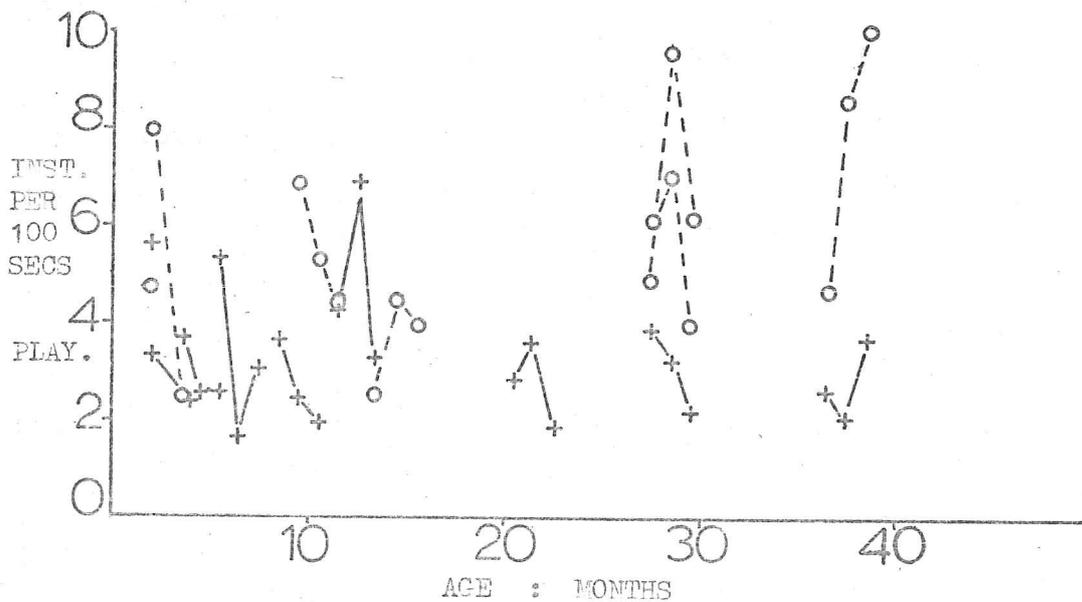


Fig. 2.6. Instances of active mauling per 100 seconds play. Legends as for Fig. 2.5.

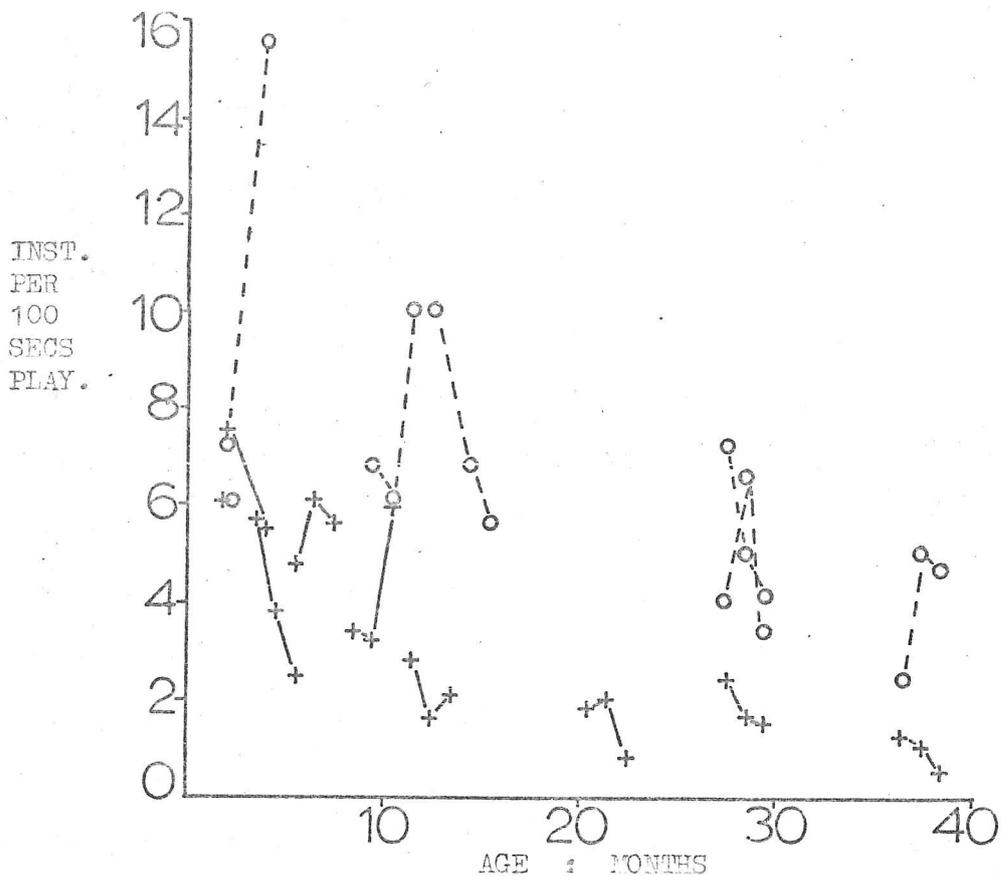


Fig. 2.7. Instances of passive mauling per 100 seconds play. Legends as for Fig. 2.5.

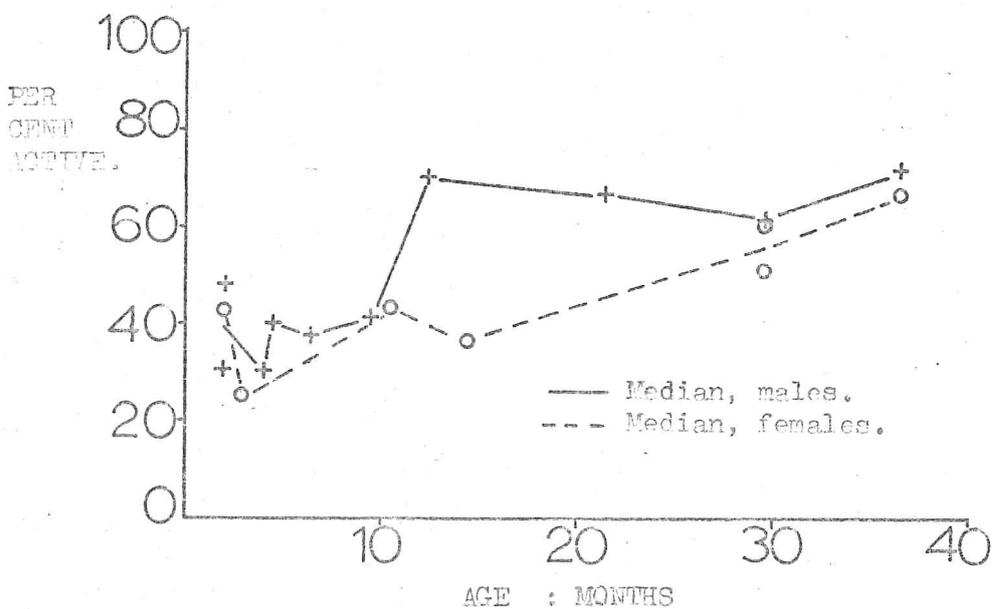


Fig. 2.8. The percent of instances of mauling play which were active. Each point represents one individual. The mean age during the recording period (which lasted 2, 3 or 4 months) is plotted.

mauling increased and passive mauling decreased, but in neither case significantly ($r_s = 0.60$ and -0.66 respectively; $p > 0.05$ in both cases).

In both sexes, the percentage of instances of mauling play in which animals took the active role increased with age (Fig. 2.8), significantly for males ($r_s = 0.83$; $p < 0.05$) but not significantly for females ($r_s = 0.67$; $p > 0.05$). There was no clear difference between the sexes in the percentage of instances which were active up to the age of about one year. After one year, the figures for males were somewhat higher than those for females. Males were more often passive than active up to about one year old. Females were more often passive than active up to at least 15 months old.

From these results one can conclude that older animals tend to maul younger ones.

Sparring

At all ages, males engaged in more sparring play than females ($p < 0.01$; Wilcoxon matched-pairs test), and in both sexes sparring became relatively more common with age ($r_s = 0.89$; $p < 0.01$ for males and 0.97 ; $p < 0.01$ for females; see Fig. 2.9a).

Considering sparring play between animals of the same sex only (Fig. 2.10), the difference between males and females was even more marked, reaching over 4 instances per 100 seconds play in males, compared with a maximum of 0.4 instances in females. Male-male sparring increased significantly with age ($r_s = 0.86$; $p < 0.01$). Female-female sparring also increased, but not significantly with age ($r_s = 0.74$; $p > 0.05$), and stayed at the same level after

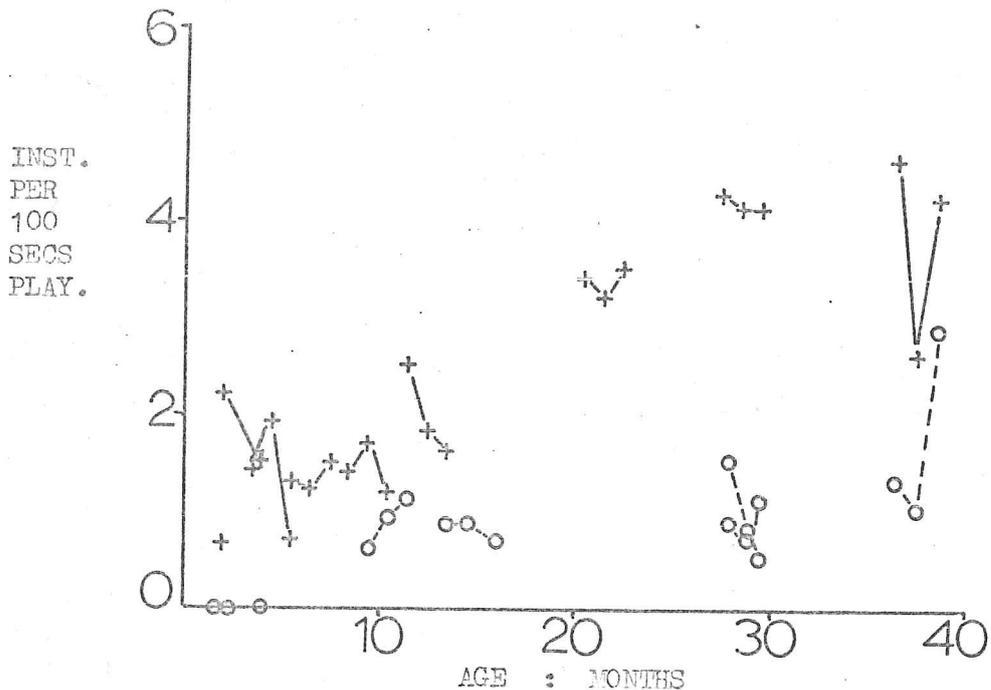


Fig. 2.9 a. Instances of sparring per 100 seconds play. Legends as for Fig. 2.5.

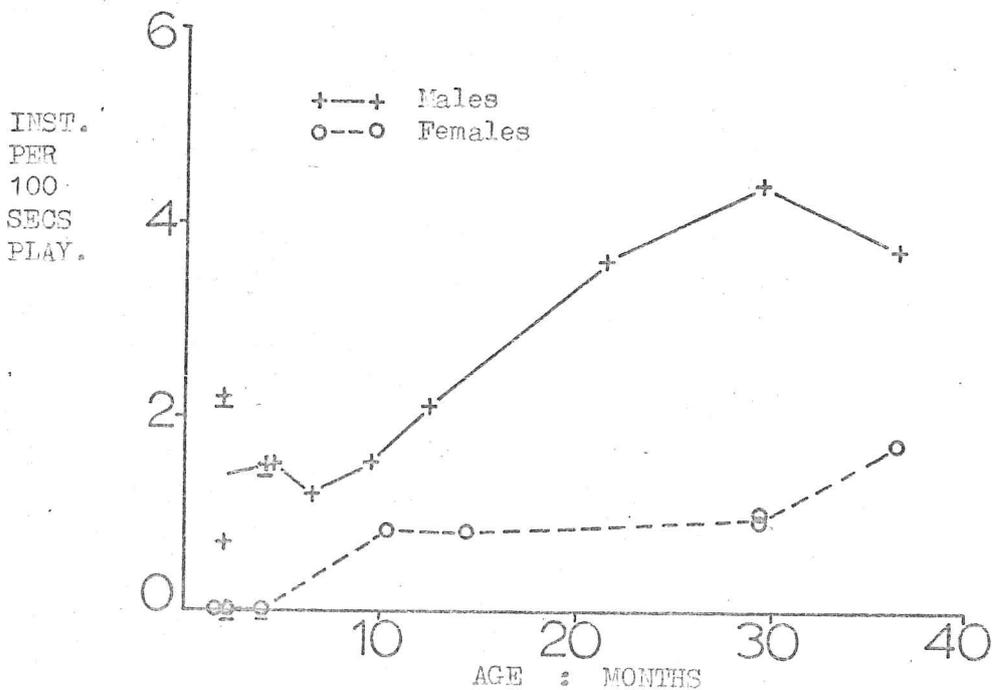


Fig. 2.9 b. Instances of sparring per 100 seconds play (same data as Fig. 2.9.). Each point represents one individual except for the four points underlined which represent one male and one female only. All points are derived from 3 months records except for the points for the four youngest animals which are derived from 2 months records. The mean age during the recording period is plotted in each case. (See also page 70).

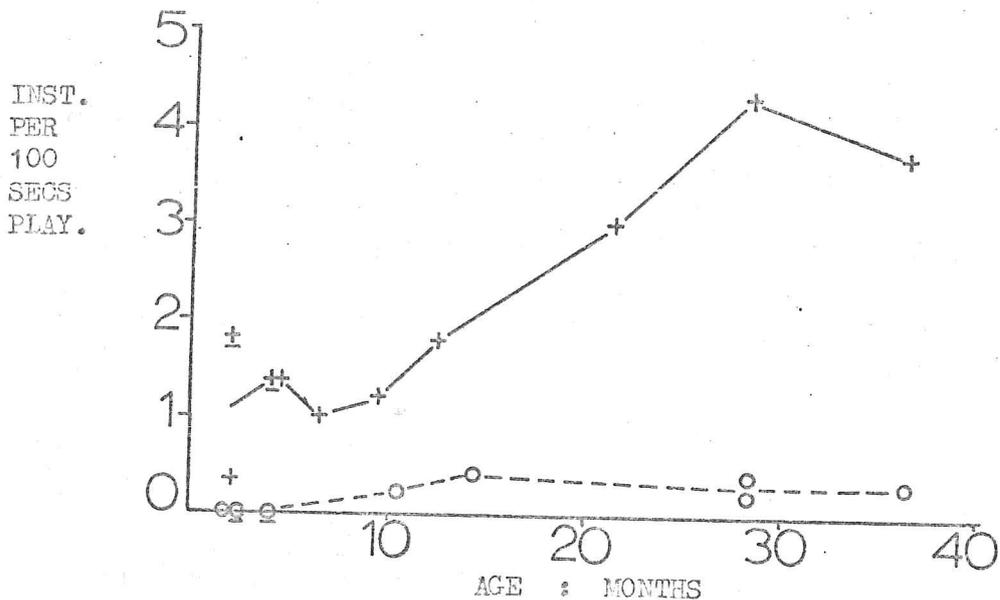


Fig. 2.10. Instances of sparring between animals of the same sex per 100 seconds play. Upper line male-male sparring; lower line female-female sparring. Otherwise legends as for Fig. 2.9 b.

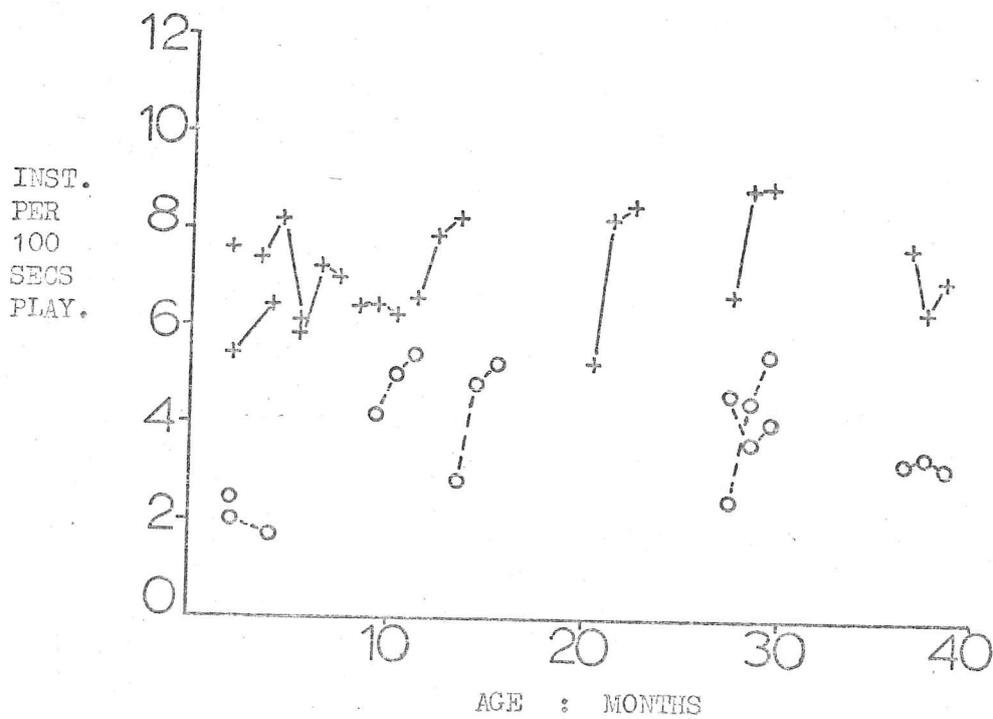


Fig. 2.11. Instances of mutual mock biting per 100 seconds play. Legends as for Fig. 2.5.

15 months. More than half of the sparring by females was with a male partner: nearly all male sparring was with a male partner. By comparing Figs. 2.9b and 2.10 it is apparent that, in sparring between males and females, females tended to sparr with males which were younger than themselves. (The difference between the positions of the points in Figs. 2.9b and 2.10 is most marked amongst the females in the oldest animals; the points for the two oldest males show little difference in the two figures, but there is some difference in the position of the points in the younger males.)

Mock biting

Mutual mock biting was relatively more common in males than in females (Fig. 2.11; $p < 0.01$; Wilcoxon matched-pairs test). This is to be expected since males engaged in relatively more mutual rough-and-tumble (wrestling) play than did females. (By definition, mutual biting could only take place during mutual rough-and-tumble play.) In males there was little change in the frequency of mutual biting with age, and the frequency fluctuated around 7 instances per 100 seconds play. In females, mutual biting was relatively rare before 5 months of age (around 2 instances per 100 seconds play). After 10 months the level fluctuated around 4 instances per 100 seconds play.

In Fig. 2.12 I have plotted the number of instances of mutual biting as a percentage of the number of instances of wrestling (Fig. 2.11 as a percentage of Fig. 2.5). The data indicate that more wrestling instances of males included mutual biting than did wrestling instances of females ($p < 0.01$; Wilcoxon matched-pairs test), the

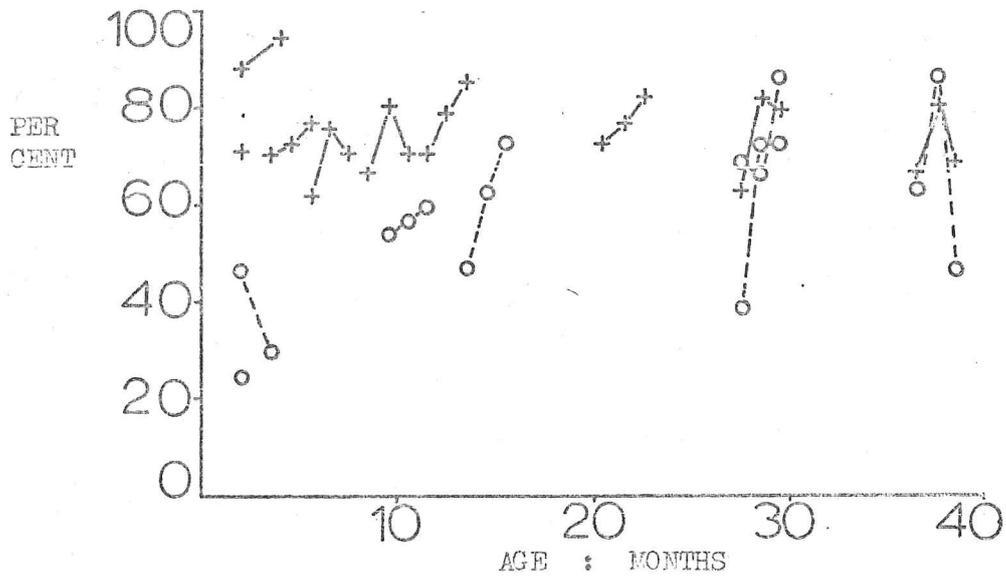


Fig. 2.12. The percentage of instances of wrestling play in which mutual mock biting occurred. Legends as for Fig. 2.5.

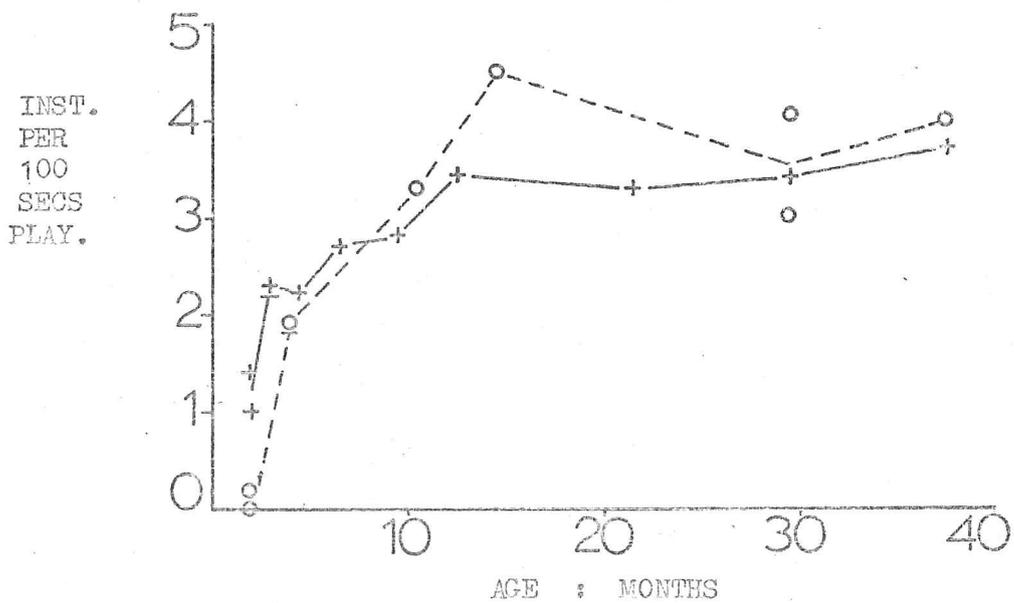


Fig. 2.13. Instances of approach-withdrawal per 100 seconds play. Legends as for Fig. 2.9 b.

difference being particularly marked during the first five months when the amount of female biting was very low. In females, mutual biting tended to become a more common component of wrestling instances with age, though the increase was not significant ($r_s = 0.77$; $p > 0.05$). In males there were no marked age changes, biting occurring in 70 - 80 percent of wrestling instances at all ages.

(b) Approach-withdrawal play

Total approach-withdrawal play

In both sexes, the total number of approach-withdrawal instances increased with age relative to other types of play patterns ($r_s = 0.94$; $p < 0.01$ for males and $r_s = 0.83$; $p < 0.05$ for females: Fig. 2.13). All the increase took place during the first 15 months of life. There was a marked difference between the sexes in the relative frequency of approach-withdrawal play in the youngest animals. At two months of age, males engaged in much more approach-withdrawal play than females, and there is some indication that males started to chase other animals at an earlier age than did females (Table 2.2). After ten months of age however, females tended to engage in relatively more approach-withdrawal play than males.

Table 2.2

Ages at which males and females were first seen to chase another animal

<u>Sex</u>	<u>Age at which first chase seen</u>
Male	1½ months
Male	2½ months
Female	2½ months
Female	4 months 1 week

Approach-withdrawal play appeared later than rough-and-tumble play, which was first seen at 2 weeks of age. This difference is probably largely a reflection of the development of the infant's locomotor ability.

Chasing

Being the chaser in approach-withdrawal play became relatively more common with age in both sexes ($r_s = 0.88$; $p < 0.01$ for males and $r_s = 1.00$; $p < 0.01$ for females: Fig. 2.14). This is consistent with the conclusion that animals also more often had an active role as they got older in mauling play.

Up to at least one year of age males did relatively more chasing than females.

Being Chased

The frequency of being chased increased during the first year, but after this age showed no clear trends (Fig. 2.15). Between 5 and 15 months females were chased more than males.

Dodging

Sometimes animals appeared to invite another one to chase them by making a bouncy leaping movement away from the partner (often accompanied by a hit, especially to the head). I have called this behaviour dodging.

If the partner responded by chasing the animal that dodged away, the animal characteristically waited for it to catch up, then dodged away again, and so on. In Fig. 2.16 I have plotted the number of instances of dodging per 100 seconds play. Dodging was absent in animals up to 5 months old. Thereafter it was far more common amongst females than

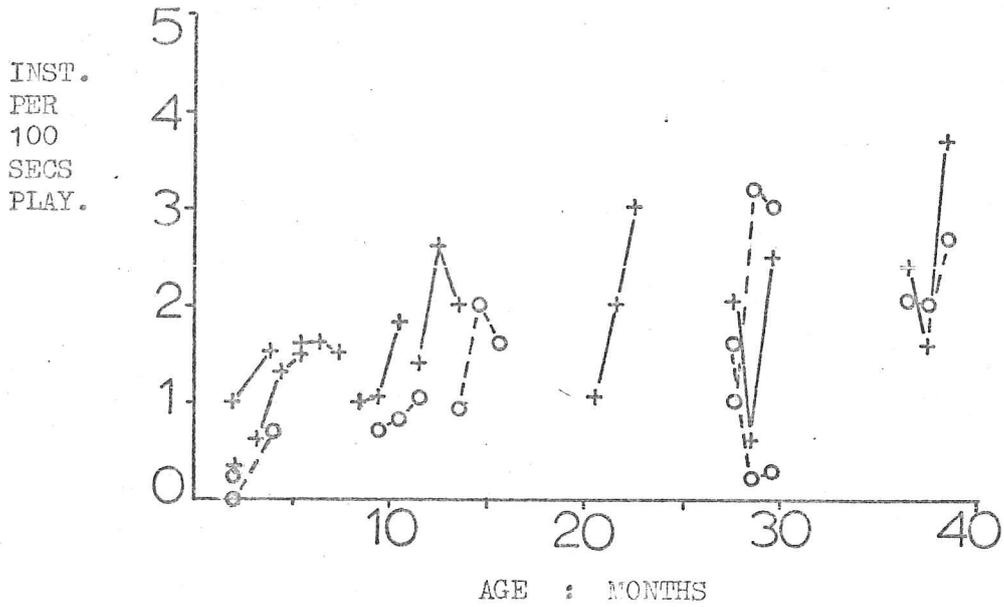


Fig. 2.14. Instances of active chasing per 100 seconds play. Legends as for Fig. 2.5.

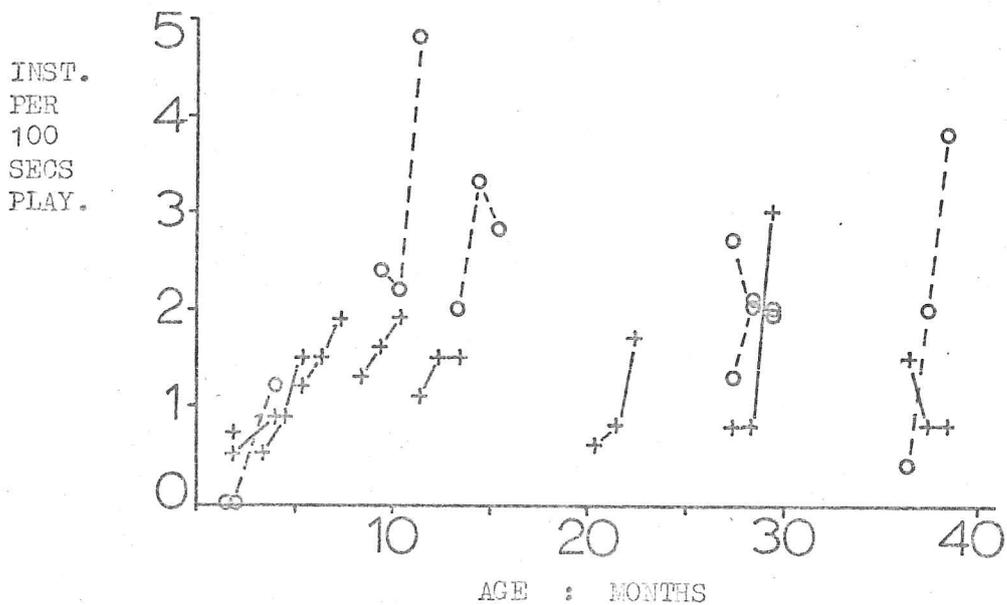


Fig. 2.15. Instances of being chased per 100 seconds play. Legends as for Fig. 2.5.

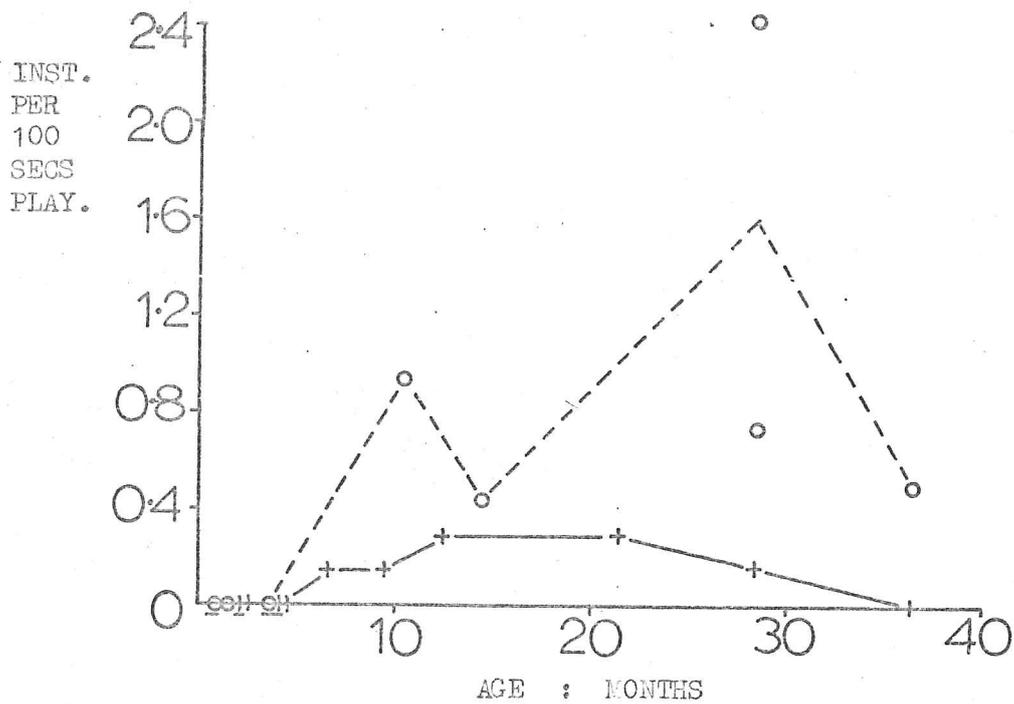


Fig. 2.16. Instances of active dodging per 100 seconds play. Legends as for Fig. 2.9 b.

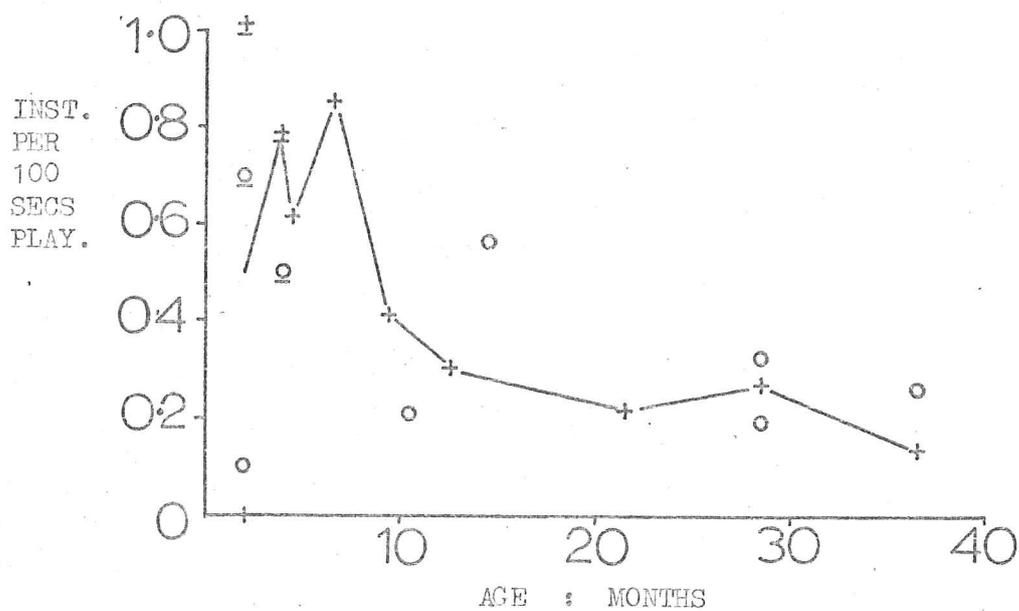


Fig. 2.17. Instances of being dodged from per 100 seconds play. Legends as for Fig. 2.9 b.

amongst males (there were not enough matched pairs to do a statistical test) Fig. 2.17 indicates that it is the youngest animals which are most often dodged from, and in males being dodged from decreased significantly with age. ($r_s = 0.83$, $p < 0.01$) Females showed no significant age changes.

Dodging is thus behaviour characteristic of females over 5 months of age and is most often directed towards infants of less than 5 months of age. It appears as if the females are 'encouraging' infants to engage in chasing play.

In dodging it is generally the larger animal that does the withdrawing and the smaller one that does the approaching. This is the reverse of what is true for other approach-withdrawal play. (See Section 8)

Conclusions

Sex differences

When males participated in rough-and-tumble play they were more likely to engage in wrestling (mutual) play than were females: females were more likely than males to engage in mauling (non-mutual) play. Insofar as the proportion of mauling instances which were active was similar for the two sexes (Fig. 2.8) one can say that, altogether, males were more likely to engage in active rough-and-tumble than were females, which were more likely to be passive participants. Males also had the active role more often than females in approach-withdrawal play.

In wrestling play, males were more likely to engage in mutual biting with their partner, and were more likely to sparr. Thus males tended to be rougher and more vigorous

in play than females.

Age changes

In both sexes, animals increasingly tended to take the active role in mauling play with age, and became more likely to be the chaser rather than the chased in approach-withdrawal play. Approach-withdrawal patterns appeared later than rough-and-tumble patterns and increased in frequency relative to rough-and-tumble during the first year. Sparring became a more frequent component of male play with age, indicating that male play tended to become more vigorous.

Discussion

There is no previous information concerning sex differences or age changes in the component movement patterns of social play in baboons, though an increase in the roughness of rough-and-tumble play has previously been described in two to three year old males (Hall and DeVore, 1965).

Comparable data are available however for captive rhesus monkeys. Hinde and Spencer-Booth (1967, b) found that rough-and-tumble patterns comprised around 85 percent, and approach-withdrawal 15 percent of total play in rhesus during the first 6 weeks. At the end of 6 weeks approach-withdrawal increased and thereafter remained at 20 - 50 percent of total play, the increase perhaps being due to the increased fearfulness of infants at the approach of others. (In contrast, Harlow and Harlow, 1965, have described rough-and-tumble and approach-withdrawal play in rhesus as developing in parallel, and occurring with about equal frequency during the first six months). In baboons, however, approach-withdrawal increased relative to

rough-and-tumble throughout the whole of the first year of life. In both species, the proportion of play which was active increased with age, and males were generally more active than females in both rough-and-tumble and approach-withdrawal. In rhesus monkeys, females engaged in relatively more approach-withdrawal than males. The reverse was true for baboons up to 5 months old, but after 10 months, females did engage in somewhat more approach-withdrawal than males.

The results in this section offer no firm proof that social play in baboons is important in the development of movement patterns or social relationships. However, they are compatible with such an hypothesis. The execution of the movement patterns described above clearly gives animals practice at fighting ability (for example the orientation of bites and proficiency at chasing and fleeing). The possibility of taking active or passive roles gives an opportunity for practicing both roles and for learning to adopt a particular role with a particular individual or sex. Age changes and sex differences in the use of different movement patterns and in taking active and passive roles may be a reflection of the age changes and sex differences in the ability to execute different movement patterns, in the complexity of play sequences in which an animal is able to participate, and in social relationships between individuals.

Further insight into the function of social play in the development of movement patterns will come in Section 9 in which play movement patterns are compared with those in aggression.

3. Maternal and Paternal Play

Results

This category of play was relatively infrequent, the highest rate recorded being 1.6 instances per 100 seconds play (see Fig.2.18). However, instances of carrying/riding lasted somewhat longer than other movement patterns, about 20 per cent of instances lasting more than 15 seconds.

As would be expected, older animals generally carried younger ones. Animals older than 15 months were not seen to be carried and animals younger than 15 months were not seen to do any carrying. There was no marked difference between the sexes in the roles of carrying and riding. It might have been expected that were there a sexual element in riding dorsal, then males would ride dorsal more than females, but this was not the case.

Males often carried their younger siblings, sometimes rescuing them from rough play. Of eight cases in which infants which had an older sibling were carried or rode on an older male, in five cases the older male was their sibling.

Carrying by young animals was often clumsy and the carrier sometimes walked on three legs whilst supporting the infant with one hand. Older juveniles and adolescents were more proficient however (perhaps in part because of their increased size and strength) and infants would cling to them more confidently.

Infant carrying occasionally developed into a game in which two or three juveniles, nearly always females, competed for possession of an infant. Characteristically one juvenile female would chase another who carried an infant ventrally,

INST.
PER
100
SECS
PLAY.

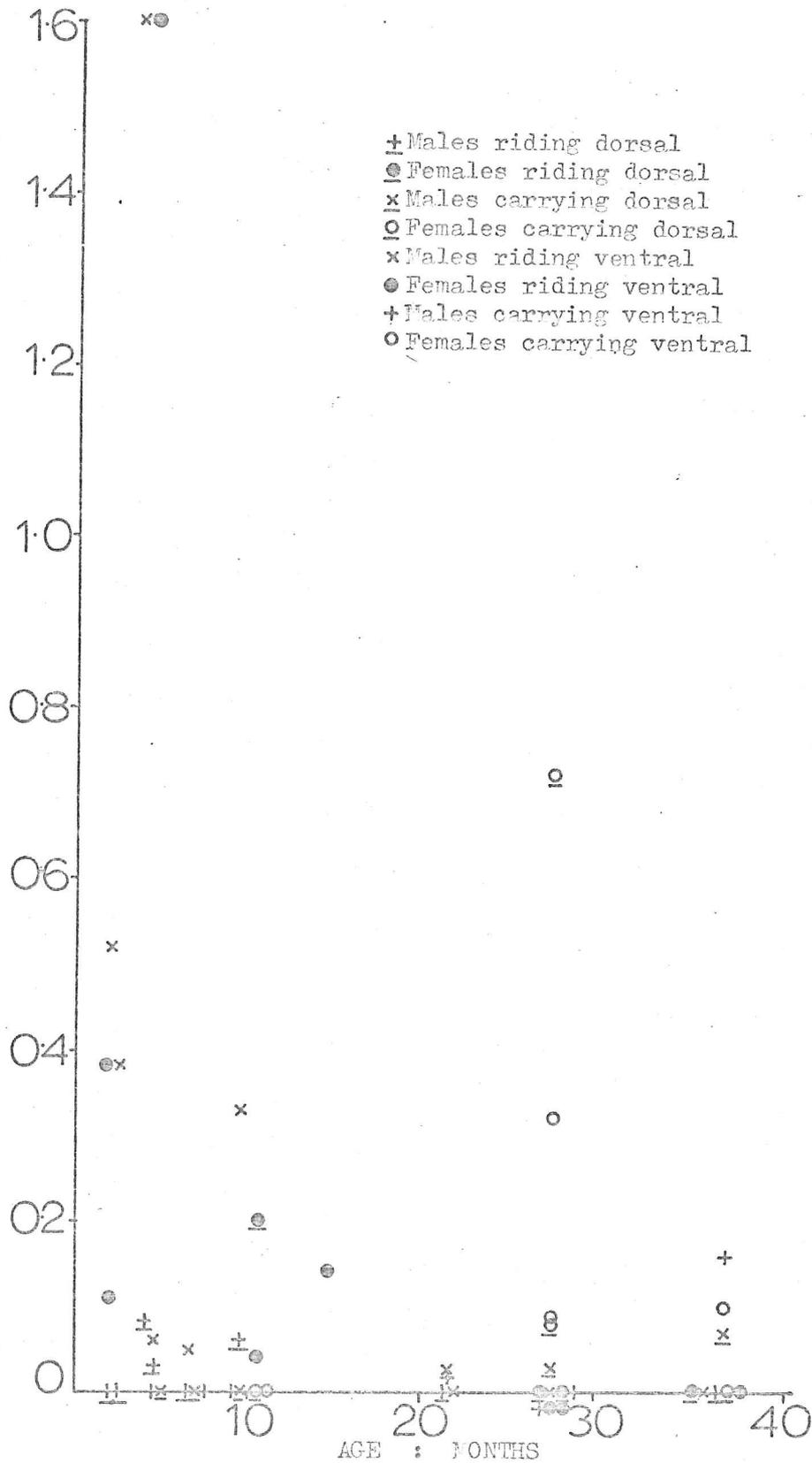


Fig. 2.18. Instances per 100 seconds play of carrying and riding, ventral and dorsal. Points are derived from 2 or 3 months records and mean age during the recording period plotted.

and rough-and-tumble play sometimes followed. Usually the infant continued to cling during rough-and-tumble but sometimes it joined in. When it did so, this often gave the other juvenile a chance to seize it and carry it away herself. Between play bouts and often during rough-and-tumble play the infant would be groomed intensely by the female in possession.

In addition to carrying infants, older juvenile females often approached and handled small infants whilst they were on their mothers. This was frequently a prelude to grooming. Adult females also handled infants, but very rarely carried them. Whether or not a female was able to approach and handle an infant appeared to be determined by the relative status of the female and the mother.

Although handling of infants whilst on their mothers could be regarded as maternal play, I was not able to collect any quantitative data on this category of behaviour.

Discussion

The great attraction of infants for juvenile and sub-adult female olive baboons has been described by DeVore (1963), and Hall (1962, b) mentions infant carrying by chacma baboon females other than the mother. Bolwig (1959) observed competitiveness of young chacma baboons of both sexes for the possession of infants, but suggests that such behaviour may be simply 'possessive' rather than 'parental' since it is sometimes shown to inanimate objects.

Handling of infants by juvenile or adolescent females also occurs in many other species of monkeys and apes

(Hamburg, 1969), and its frequency in different species is probably determined largely by species differences in the permissiveness of mothers (Hinde, 1971). Mothers are also known to be more permissive towards the infant's siblings than to other group members of similar age in rhesus monkeys (Spencer-Booth, 1968) and in chimpanzees (Van Lawick-Goodall, 1968). This may have been the reason why infant baboons were carried by their older siblings more than other group members, the permissiveness of mothers towards their older offspring's approaches to their new infant perhaps helping to establish an affectional bond between the siblings.

Several authors have suggested that experience at mothering is important in the development of maternal motor skills. In ⁿlargurs, for example, mothers allow their infants to be passed around and held by other adult females shortly after birth. Females who have had experience of their own infants are better at keeping infants quiet and are able to hold them longer than inexperienced females (Jay, 1963). Play mothering in vervet monkeys has been studied in some detail by Lancaster (1971) who suggests that the opportunity to interact with infants provides juvenile females with practice at motor skills and also helps them to learn to accept the role of mother towards the infant. Evidence that social experience with infants is important in the development of the appropriate attitude of the mother towards its infant comes from experiments with rhesus monkeys (Harlow, et al., 1966). Females brought up in social isolation were rejecting and aggressive as mothers, but their maternal behaviour improved towards their second infant.

Thus one may speculate that carrying infants by juvenile female baboons may be important in the development of at least three aspects of maternal behaviour:

1. The motor patterns of carrying the infant and keeping it comfortable (e.g. learning to ensure that the infant is oriented properly and is not knocked against obstacles etc.).
2. Learning (during games) to protect the infant from interference from other troop members. The object of such games would not necessarily have to be an infant in order for it to be effective in the development of such skills. Learning during games with objects could be generalised to parental behaviour (cf. Bolwig cited above).
3. Learning to accept the maternal role and not be rejecting or aggressive.

Adult male olive baboons at the Gombe are known to carry infants in a variety of social contexts including protective and agonistic situations (Ransom and Ransom, 1971). Thus it is also necessary for males to acquire skills of carrying and care of the infant and to adopt the appropriate attitude towards infants. It seems reasonable to speculate that paternal behaviour in play may have a similar function to maternal play.

8. Relationships between individuals in play

A. Factors affecting choice of partner

1. Play with same/opposite sex.
2. Amount of play/age difference of partners.
3. Partner preference.
4. Relationships between siblings.
5. Discussion.

B. Active and passive roles in play

1. Initiation and termination of play.
2. Vocalisations in play.
3. Roles in non-mutual play.
4. Discussion.

8. Relationships between individuals in play

A. Factors affecting choice of partner

1. Play with same/opposite sex

In Fig. 2.19 I have plotted the number of seconds play with the same sex as a percentage of the total number of seconds play.

Males played mostly with their own sex, but females played mostly with males. This difference can be explained at least in part by the fact that males played more than females and the fact that there were more males than females during the main study period (9 males and 5 females). The results do not thus necessarily imply any selection by the animals for a particular sex.

The two oldest males (29 and 37 months old) played somewhat more with their own sex than did younger males. This increase is consistent with the conclusions about the frequency of movement patterns in the two sexes; males engaged in relatively more sparring play as they became older, a pattern which was characteristic of male-male play.

Only the youngest females (two months old) played more with their own sex than did males. This may be explained by the factors controlling the availability of play partners. The other animals which an infant of this age met was determined largely by the mother's behaviour. It so happened that the mother of one of the two female infants associated largely with a mother which also had a female infant (not included in the study), and the mother of the other female infant associated with a female juvenile at this stage. A similar argument applies to the male infants of this age.

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A. Factors affecting choice of partner

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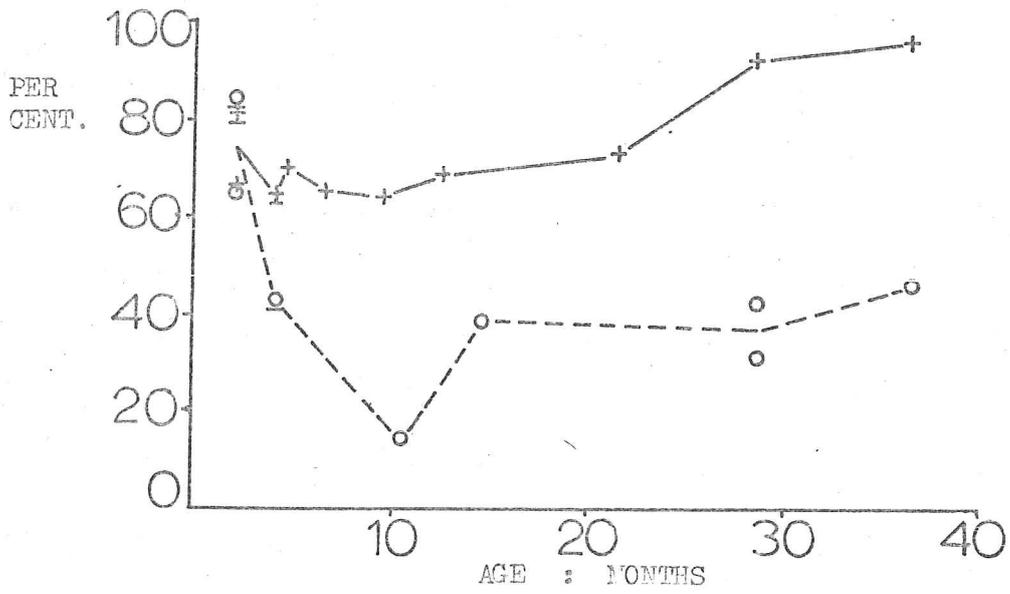


Fig. 2.19. The percentage of time spent playing which was with an animal of the same sex. Legends as for Fig. 2.9 b.

2. Amount of play/age difference of partners

The calculations of the amount of play between each pair of animals were based on three months observations, and the age given on the figures is the animal's mean age during the recording period. The data are based on totals of between 12 and 24 hours observation for each individual.

Males

In play between males, most play tended to occur between those individuals near to each other in age (Fig. 2.20). One exception to this rule was that P played with Jb more than he played with R. This may have been because Jb was bigger than R at this stage, despite being two months younger. Nevertheless, G played more with R than with Jb, and also less than would be expected with P. Two pairs of siblings, E and Jb and H and P played slightly more than might be expected considering their age differences (see Part 4).

Females

Amongst females the same generalisation is true if one individual, D, is omitted. D played very little with the females nearest to her in age for reasons which are not clear. One possible explanation was that, being the daughter of the highest ranking female in the troop, she was more able to gain access to black infants, and perhaps spent much time grooming such infants rather than playing with peers.

Male-female

In play between males and females, most play again occurred between age mates, but the situation was somewhat confused by the fact that older females played quite a large

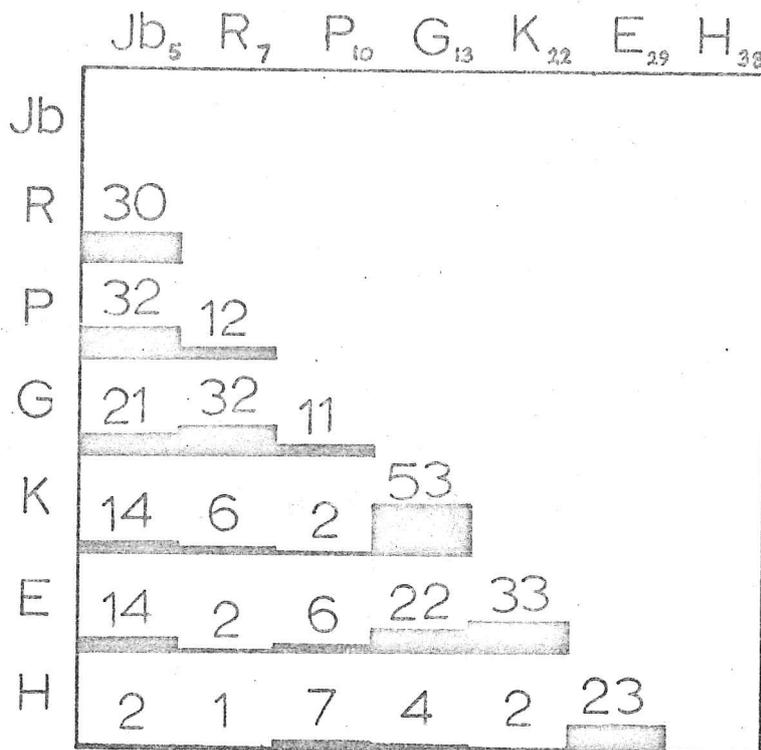


Fig. 2.20. Seconds per hour spent playing between pairs of individual males. The data are derived from three months records. The mean age in months of each animal during the recording period is indicated by the numbers beside the initial letters of each animal at the top of the figure.

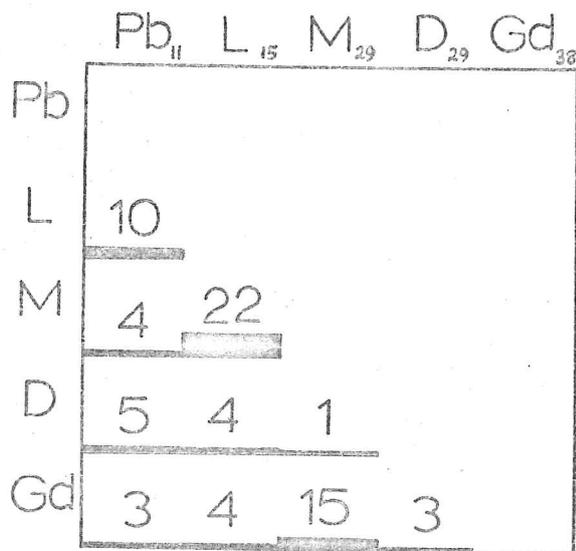


Fig. 2.21. Seconds per hour spent playing between pairs of individual females. Legends as for Fig. 2.20.

		FEMALES				
		Pb ₁₁	L ₁₅	M ₂₉	D ₂₉	Gd ₃₈
MALES	Jb ₅	16	10	17	7	3
	R ₇	20	9	6	6	7
	P ₁₀	8	10	4	3	6
	G ₁₃	25	17	4	5	3
	K ₂₂	15	6	10	1	6
	E ₂₉	2	2	2	3	8
	H ₃₃	1	1	1	1	1

Fig. 2.22. Seconds per hour spent playing between individual male-female pairs. Legends as for Fig. 2.20.

amount with young males.

3. Partner preference

One may now ask whether animals play most with those nearest to them in age because they associate with them most (i.e. because they are most often available for play), or because they most prefer them as partners (or both).

In order to assess partner preference (i.e. which partners would be played with most were all partners equally available) I selected 5 animals representing the two sexes and different ages. For convenience of analysis, I then examined for each of the five animals in turn, those play bouts in which they took part in which only two other individuals came within five metres during the bout. The following example for animal 'A' shows the way in which each of the five animals was treated.

There were 13 partners with which A might play and therefore many combinations of 4 animals (A + partner + 2 nearby) which could occur for one play bout. Taking all the play bouts in which a particular combination of 4 occurred (regardless of which of the three played with A and which were nearby) I counted the number of bouts and the number of seconds that each of the three partners was played with by A. The scores for the three animals then gave an indication of which animal was preferred to which as a play partner by A (i.e. was played with more per time they were all available for play). Lumping together all the information about the rank order of preference of all the trios, I compiled an overall rank order of partner preference for the

13 possible play partners (data were omitted for which the rank order of a trio as judged by the number of bouts of play did not agree with that judged by the number of seconds play).

For all five animals a linear rank order of partner preference could be established. There was no consistent effect of the presence of one animal on another's choice of partner. Results which did not fit into the rank order were generally those for which the data were few (see Fig. 2.23). The rank order of partner preference was then compared with the rank order of the amount the five animals actually played with each of the 13 partners (data from Figs. 2.20 - 2.22), using Spearman rank correlation coefficients. In all five cases there was a significant positive correlation between the two ranks (Table 2.3).

This means that the amount of play between any two animals was not determined simply by how much they were together. Selection of like-aged animals for play would have taken place even if all animals were equally available.

The next question that can be asked is: do animals associate most at times when they are not playing with those individuals they play with most? For the same five individuals I added up the number of minutes watched in which each of the other individuals came within three metres of the animal in question (the data were obtained from the mother-infant check sheet), and from this worked out a rank order of association. There was a significant correlation between the rank order of the amount of play and that of association (Table 2.3). This indicates that animals did tend to associate most with those animals they played with most.

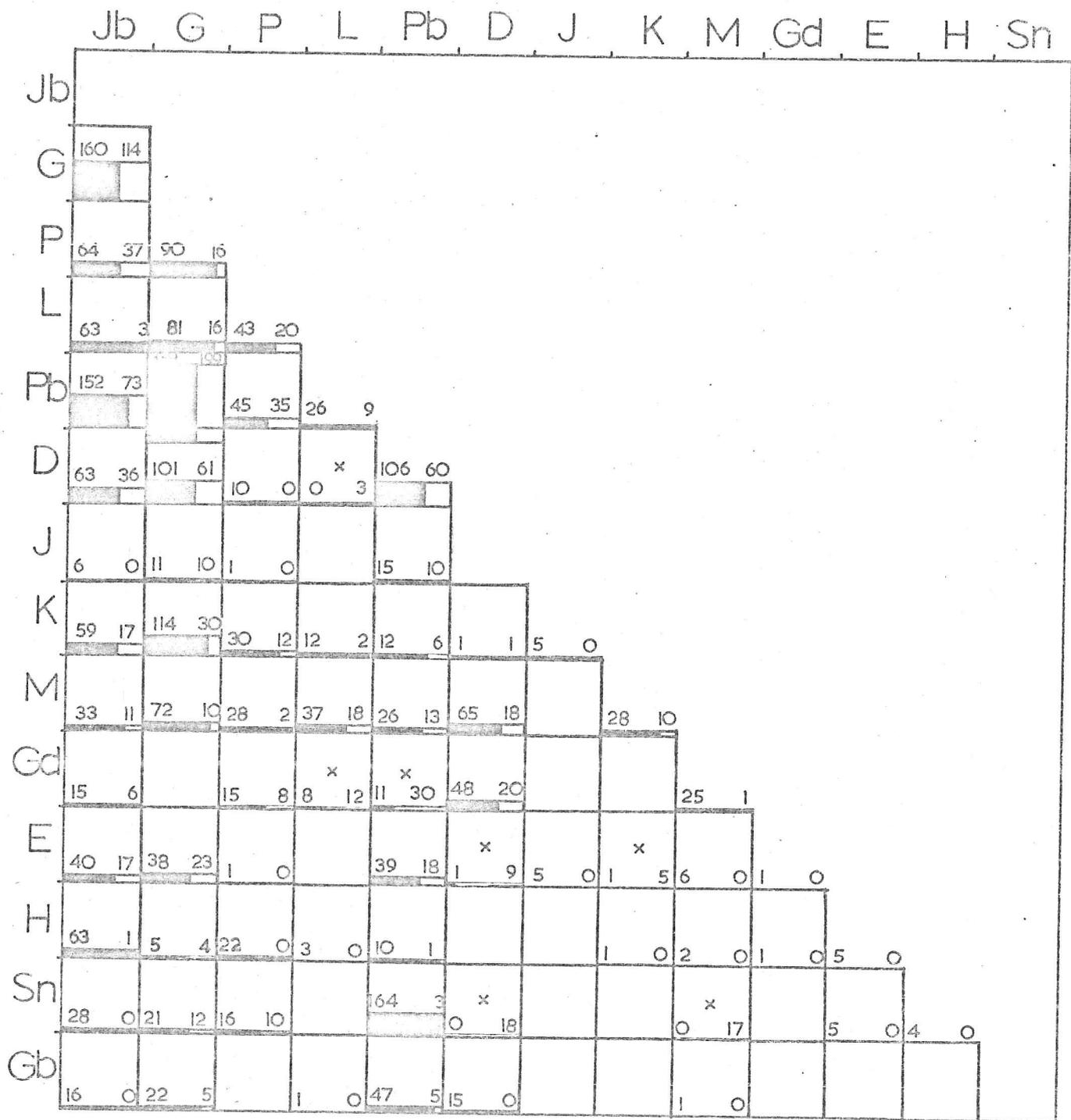


Fig. 2.23. Partner preference in play for one individual 'R'. Symbols representing individual animals are arranged in a rank order of partner preference across and down the figure. The form of the figure can be illustrated by reference to one square. For example, the top square indicates that R played with Jb for a total of 160 seconds (black area) when G was nearby and R played with G for a total of 114 seconds (white area) when Jb was nearby. Thus R prefers Jb to G. The crosses indicate results which do not fit the rank order presented. The vertical scale represents N, ie. the total number of seconds play from which each ratio is deduced (ie. 160 + 114 = 274 seconds in the case of R, Jb and G). The vertical height of one square represents 500 seconds.

However, in all five animals in Table 2.3, the correlation between play and association was less good than for play and partner preference. This suggests that animals did in fact have to select preferred play partners to some extent from those animals which were nearby. The difference between the two sets of r_s values gives a rough measure of the extent of this selection.

Table 2.3

Spearman rank correlation coefficients (r_s)
between rank orders of the amount of play with
the rank orders of partner preference and of association

	<u>Jb</u> 5	<u>R</u> 7	PB 11	M 29	<u>E</u> 29
Play/partner preference	0.83**	0.81**	0.78**	0.64*	0.74**
Play/association	0.50*	0.73**	0.66*	0.60*	0.48*

N = 13

** = $p < 0.01$

* = $p < 0.05$

Names underlined are males.

Numbers beside names = mean age in months during the recording period.

4. Relationships between siblings

Methods

There were three known pairs of siblings in the troop. In order to further understand the factors affecting partner choice in play it would be useful to know whether siblings play together more than expected, taking into account their age difference.

In Table 2.4 I have presented:

- (a) The amount that each pair of siblings played with each other (in seconds per hour) during three separate months.
- (b) The amount that each sibling played with the two animals of the same sex nearest in age to its sibling (one older and one younger). The mean of these two figures gives an indication of the amount that each of the siblings would be expected to play with the other were they not siblings. The figures for the expected amount of play can then be compared with the figures actually obtained.

Results

For Jb and E (both males) the figures obtained were greater than expected in 5 cases and tied once. For P and H (both males) the figures obtained were higher than expected in every case ($p < 0.05$; Mann-Whitney U test for both pairs of siblings). For M and J (female and male) too little play occurred between them to be conclusive.

Thus two out of three pairs of siblings played together more than would be expected were they not siblings. The associations data from the partner preference section indicate that siblings also associated a large amount with each other. E was the animal third on Jb's rank order of association and Jb was top of E's list. J was fifth on M's rank order and although M and J did not play very much together, they did groom a great deal.

In both the pairs of male-male siblings, there was a tendency for the male immediately younger than the older sibling to play a large amount with the younger brother (K with Jb and E with P; Fig.2.20). By so doing they were often

able to initiate play with the older sibling which came to its younger brother's defence.

Table 2.4

Seconds per hour spent playing by three pairs of siblings and by each of the siblings with the two partners nearest in age to its sibling during three separate months

Sibling pairs	Play in seconds per hour		
	August	September	October
Jb and E (Two males, aged 5 and 29 months)	Jb and E 8 R and E 4) P and E 5) 4.5 K and Jb 4) H and Jb 1) 2.5	22 1) 4 7) 4 19) 11 3) 11	11 2) 7.5 13) 7.5 21) 11 1) 11
P and H (Two males, aged 10 and 37 months)	P and H 12 R and H 0) G and H 5) 2.5 J and P 1) E and P 5) 3	7 1) 1 1) 1 1) 4 7) 4	8 0) 3.5 7) 3.5 0) 6.5 13) 6.5
M and J (Female and male aged 29 and 48 months)	M and J 0 M and Sn 0) M and H 1/2) 0.25 J and D 0) J and Gd 0) 0	0 0) 0 0) 0 1) 0.5 0) 0.5	2 0) 1 2) 1 0) 0 0) 0

5. Discussion

In this discussion I shall be concerned with some of the factors which influenced partner choice in play and their effects on behavioural development.

Sex of partner

The data presented in Fig. 2.19 left the question open

as to whether animals selected play partners of their own sex in preference to partners of the opposite sex. The data on the amount of play with different partners and on partner preference however do indicate that this was generally the case. In 7 males and 3 females (out of a total of 7 males and 5 females) the partner who was played with most was of the same sex (Figs. 2.20 - 2.22). It was demonstrated in part 3 that the amount of play with different partners was highly correlated with partner preference. Thus one may assume that the 12 animals mentioned above would largely have had the same animal as their top play partner even if one allowed for the different availability of the various partners. One must, however, also allow for the fact that males played more than females: even if males played more with males when males and females were equally available, this might have been because male partners were more ready to play than female partners. However, 3 out of 5 females played more with a female partner than with any male, despite this bias. The case of female D who was one of the exceptions to this rule has already been discussed; the other exception, Pb will be discussed below.

The preponderance of play between animals of the same sex occurs in a number of other primate species, for example hamadryas baboons (Kummer, 1968) and langurs (Jay Dolhinow and Bishop, 1970).

Age of partner

The conclusion that most play in baboons occurred between age mates is consistent with previous reports for baboons (e.g. Hall, 1962, b; Kummer, 1968) and for many

other primate species, for example Japanese macaques (Itani, 1954, cited Fady, 1969), crab-eating macaques (Fady, 1969), rhesus monkeys (Altmann, 1962; Southwick, Beg and Siddiqi, 1965), bonnet monkeys (Simonds, 1965), Langurs (Jay, 1965), squirrel monkeys (Baldwin, 1969) and chimpanzees (Van Lawick-Goodall, 1965).

It has been suggested (Altmann, 1962; Fady, 1969) that when animals choose partners of approximately equal weight and strength, play is less likely to break down, because both partners have a chance to direct or dominate the playful interaction. When age differences are too great, the smaller animal soon gets caught in a chase or cannot catch up if it is the chaser, and may drop out of rough-and-tumble play because it is too rough. Thus the choice of age mates as play partners probably gives animals the maximum opportunity to practice skills of combat. Ellefson (cited Jay et al., 1970) suggests that the lack of play in young gibbons may be due to the absence of partners of similar size and strength in the family unit. The greater roughness of males in play may have been one of the reasons why baboons tended to choose their own sex to play with, and the same explanation may hold for *Hamadryas* baboons and langurs in which males are also said to be rougher in play than females (Kummer, 1968, a; Jay Dolhinow and Bishop, 1970). But as Altmann points out, stability may be temporarily achieved between animals differing in size by the self-handicapping or restraint of the larger partner. Self-handicapping occurs in all studied primate species in which rough-and-tumble play occurs (Bertrand, 1969).

Although most play occurred between age mates, play between partners widely differing in age may also have had an important function in the social development of the younger partner. During play with older partners, animals may learn to adopt their more sophisticated play behaviour. Furthermore, Baldwin (1969) has suggested that, in the social context of play, young squirrel monkeys may be led by older monkeys into situations into which they would otherwise fear to go, and in this way they are able to overcome their fears.

Maternal club

One of the factors affecting choice of partner according to Fady (1969) is the 'maternal club' to which animals belong; animals are more likely to play together if their mothers habitually associated with each other. Mothers with newborn infants at the Gombe generally formed friendships with other new mothers, forming grooming clusters during periods of rest, and I have already discussed (Part 1 of this section) the importance of the mothers' associations in determining the amount of play between infants of about 2 months of age. Mothers and daughters also often associated with each other. It is possible that some affectional ties between infant baboons may have been established in this way which persisted after the infants became independent of their mother's movements, and which were reflected in the amount that they played with each other. For example, R's and G's mothers were almost certainly mother and daughter, and associated with each other much more than with other females. R and G played with each other more than with some of the partners which were nearer to them in size (see Part 2) when they were

7 and 13 months old respectively. The mothers of G and Pb also associated with each other a great deal when G and Pb were black infants (up to about 6 months old) and at 11 months of age Pb played with G more than with any other animal. R was Pb's second most frequent partner, with the female nearest to her in age, L, coming only 5th in the list, perhaps because Pb's ties to G drew her into male play groups. Maternal groupings are also important in determining the amount of play between infant chimpanzees (Van Lawick-Goodall, 1968).

It is possible that such affectional ties, established between animals in infancy and maintained during play, may form the basis of adult relationships, for example, the attachments which mothers with newborn infants form to an adult male (see Ransom and Ransom, 1971 and section below on siblings).

Siblings

As in baboons, rhesus monkey and chimpanzee siblings play more with each other than with other group members of similar age (Southwick, Beg and Siddiqi, 1965; Van Lawick-Goodall, 1968), though in other species such as langurs this may not be the case (Jay Dolhinow and Bishop, 1970).

The establishment of affectional ties between siblings or between members of a maternal club makes possible more complex social interactions of a 'tripartite' nature in which "three individuals simultaneously interact in three essentially different roles, and each of them aims its behaviour at both of its partners". (Kummer, 1967). For example, one animal often protected another from rough play

by carrying it away from its partner, or by playing with the partner itself (see also Section 7, Part 3, and Part 4 of this section). Tripartite interactions were sometimes also seen in juvenile aggression (often following similar interactions in play), and when adult males protected infants, juveniles or adult females from attack. Interactions in which a sub-adult or young adult male hamadryas baboon protected one juvenile from the rough play of another have been described by Kummer, who has stressed the importance of learning in the development of tripartite relations. It seems probable that play between siblings or members of the same maternal club were important in learning to participate in such complex social interactions. Furthermore, particular pairs of adult male olive baboons often supported each other in aggression (cf. Hall and DeVore, 1965 and Saayman, 1971), and it is possible that these supportive relationships (not strictly tripartite) have their origins in the affectional bonds described above.

In chimpanzees it is known that adult males who are brothers support each other in agonistic encounters (David Bygott, personal communication).

B. Active and Passive Roles in Play

1. Initiation and termination of play

The data on partner preference tell nothing about the relative contributions of the partners in maintaining the relationship. One way of looking at this is to examine the relative amount that partners initiated and terminated play bouts with each other.

(a) Initiation of bouts

For each of the possible pairs of playing animals I counted the number of bouts initiated by each partner.

Male-male. Fig. 2.24

In Fig. 2.24 seven males are considered. This means that there are 6 pairs of males adjacent to one another in age along the diagonal of the figure. In five out of the six pairs, the older animal initiated the higher proportion of bouts. In the sixth case (Jb and R), Jb initiated more than 50 percent of bouts with R, although Jb was 2 months younger than R. However, as mentioned before, Jb was larger than R at this stage.

As the age difference between partners became greater (towards the bottom left of the figure), the older animal tended to initiate a progressively smaller proportion of bouts, until with very large age differences the larger animal usually initiated fewer bouts than the smaller one. This suggests that males were more afraid of partners slightly larger than themselves than they were of animals which were much larger, and indicates that larger males may have restrained themselves more the greater the size difference between them and their partners. Adult males

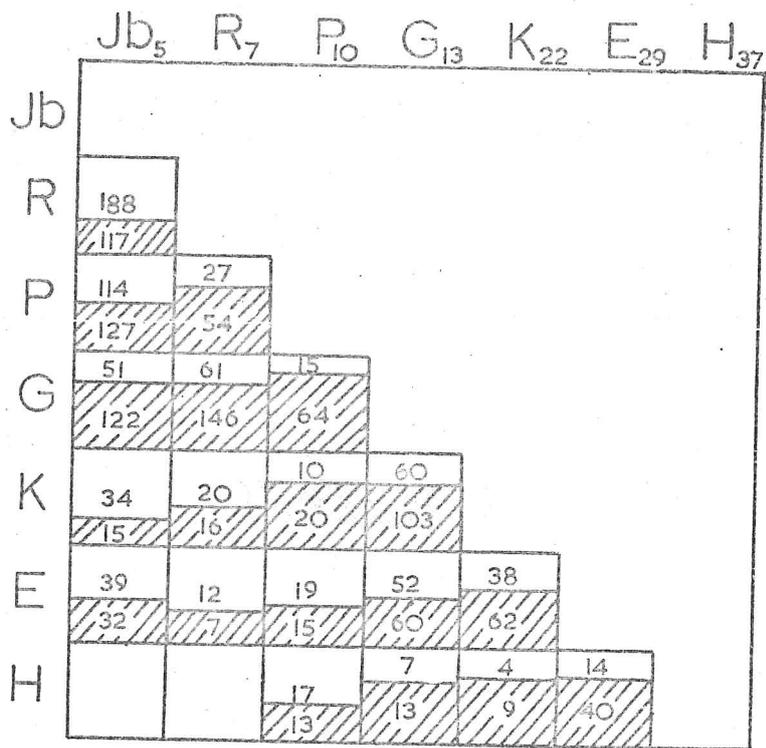


Fig. 2.24. Play initiation between individual male-male pairs. The numbers in the shaded portions of the boxes indicate the number of play bouts initiated by the animal whose initial is written in the column down the left side of the figure. The numbers in the unshaded portions of the boxes indicate the number of play bouts initiated by the animal whose initial appears in the row along the top of the figure. Data are from 3 months records. The mean age (in months) of each animal during the recording period is indicated next to the names in the row. Data for which N = 10 are omitted.

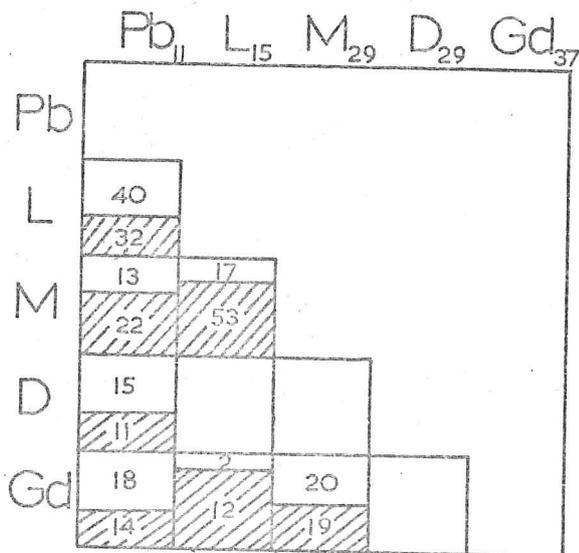


Fig. 2.25. Play initiation between individual female-female pairs. Legends as for Fig. 2.24.

frequently intervened if an infant was hurt and caused to scream during play. Thus larger males tended to be gentle and were perhaps reluctant to initiate play with infants, especially when adult males were nearby. When large juveniles did initiate play with infants their intention to handicap themselves was often made clear before play started through play invitation gestures. Characteristically, juveniles bent their forearms to bring their head and shoulders down to the ground or else rolled on their backs, looking at the partner.

Female-female. Fig. 2.25

In play between females there appeared to be no consistent patterns. One female, L, initiated less than 50 percent and another, M, more than 50 percent of play bouts with all the 3 partners for which there are data.

Male-female. Fig. 2.26

Males initiated more than 50 percent of play bouts with all females which were younger than themselves (to the bottom left of the thick black line dividing the figure) and also with those which were slightly older than themselves (above and to the right of the black line and close to it). As one moves towards the top right hand corner of the diagram the age difference between the partners becomes progressively greater, and there is a tendency for males to initiate a progressively smaller proportion of the bouts. Up to about five years old there was no noticeable size difference between animals of the same age but of different sex. A probable explanation of the results is that males played more roughly than females and consequently females were

FEMALES

		Pb ₁₁	L ₁₅	D ₂₉	M ₂₉	Gd ₃₇
MALES	Jb ₅	112 87	22 21	12 17	60 43	13 7
	R ₇	130 111	32 40	21 19	25 21	47 10
	P ₁₀	42 59	32 46	17 15	26 13	43 10
	G ₁₃	78 203	15 65	17 28	17 49	16 13
	K ₂₂	69 27	15 2	3 7	11 18	5 11
	E ₂₉	0 11		9 9	9 9	5 11
	H ₃₇					

Fig. 2.26. Play initiation between individual male-female pairs. Legends as for Fig. 2.24.

		Jb ₅	R ₇	P ₁₀	G ₁₃	K ₂₂	E ₂₉	H ₃₇
Jb								
R	84 57							
P	41 32	12 22						
G	33 32	15 48	10 27					
K	17 4			27 24				
E	11 17		9 5	17 11	17 33			
H			9 5			5 21		

Fig. 2.27. Play termination between individual male-male pairs. Legends as for Fig. 2.24.

afraid to initiate play even with males which were somewhat smaller than themselves.

Small males tended to initiate less than 50 percent of bouts with much larger females, but more than 50 percent of bouts with much larger males. This could either be because large females did not restrain themselves as did large males, or because they played in a way which was unattractive to small males for other reasons.

(b) Termination of bouts

It was often not possible to decide which partner was responsible for terminating a bout, and for this reason the data are rather few. They were treated in the same way as the data for play initiation.

Male-male. Fig. 2.27

A similar pattern emerged to that seen in play initiation. Four out of 6 males terminated more than 50 percent of bouts with the individual nearest to them in age but younger than themselves. Jb and R were again an exception, Jb terminating more bouts than R, and G terminated slightly more bouts than K.

The smaller of a pair of playing animals would often try to leave its partner but be prevented from doing so by the larger one. Thus the fact that the younger partner did not so often terminate a bout does not necessarily mean that it was not trying to do so.

In conclusion one can say that in male play between preferred partners (i.e. those near to each other in age), the larger animal had the greater role in determining the amount of play that occurred. Although fewer data are

available for less preferred partners (widely differing in age) it was generally the case that the smaller partner terminated more bouts than the larger.

Female-female. Fig. 2.28

For the four cases of play between females for which there are enough data, the proportion of bouts terminated by each partner was roughly similar to the proportion of bouts initiated by each partner.

Male-female. Fig. 2.29

The data for termination of bouts between males and females are somewhat variable. In 9 out of 16 pairs of animals for which there are data, the animals which initiated more than 50 percent of bouts also terminated more than 50 percent. In 5 cases this was not true, and in 2 cases each animal terminated exactly 50 percent of bouts.

2. Vocalisations in play

Three types of vocalisations were distinguishable in play.

Laughing: a staccato panting noise characteristic of vigorous play and which never occurred outside play.

Gecking: expressed mild discomfort or fear.

Screaming: expressed more intense discomfort of pain and was often accompanied by the facial expressions of fear.

Laughing was not very loud, and probably sometimes occurred but was not recorded; gecks and screams were always audible.

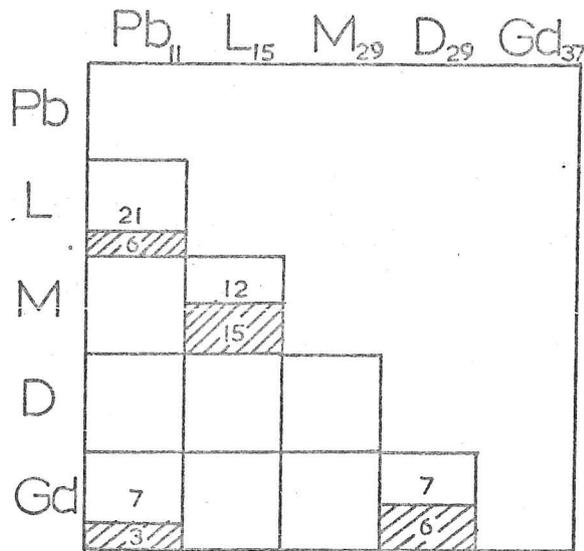


Fig. 2.28. Play termination between individual female-female pairs. Legends as for Fig. 2.24.

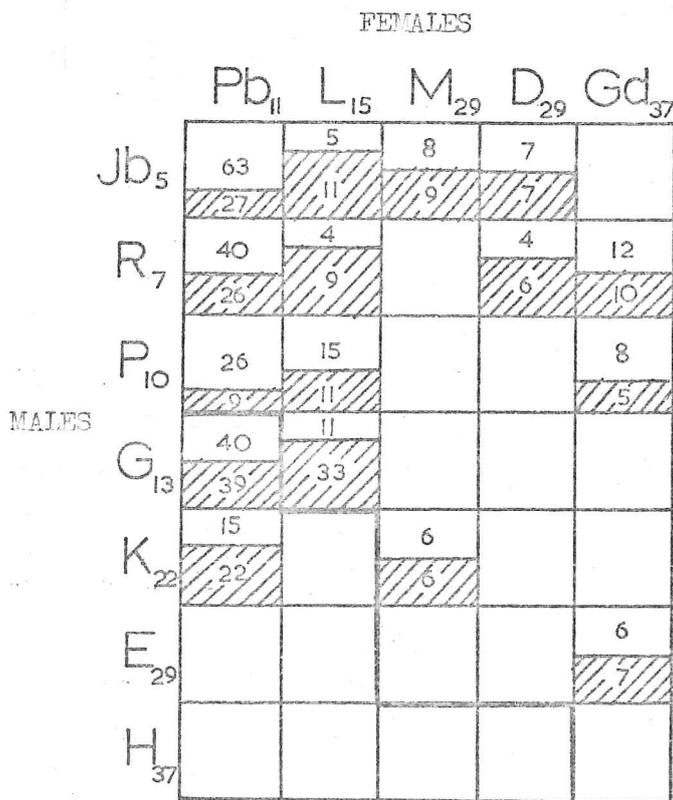


Fig. 2.29. Play termination between individual male-female pairs. Legends as for Fig. 2.24.

Laughing

Laughing occurred more often in the younger of a pair of playing animals than in the older (41 times compared with 12, Fig. 2.30), but the older animals sometimes laughed when play was rough. Laughing was equally common in the two sexes in proportion to the amount of play observed (Table 2.5).

Table 2.5

The total number of laughs per 100 seconds play observed in the two sexes

	No. of laughs	Total seconds play observed	Laughs per 100 seconds play
Male	37	34,816	0.1
Female	15	14,099	0.1

Gecks and screams

These two vocalisations occurred with about equal frequency. I have lumped them together in this analysis as they both seemed to be expressions of discomfort or fear, and differed only in that they expressed emotions of different intensity. In Figs. 2.31, 2.32 and 2.33 I have plotted gecks and screams in play between males, between females and between males and females. Most vocalisations were made by the younger partner and by the individual which initiated less than 50 percent of the play bouts (Table 2.6).

	Jb	R	<u>P</u>	<u>Pb</u>	G	L	K	M	D	E	<u>Gd</u>	H	J	Sn
Jb	/		3							4				
R		/												
<u>P</u>			/		1	1								
<u>Pb</u>				/	1								3	
G	1	1			/		8			2				
L			1			/	2	2						
K					1		/			3				
M								/			2			
D									/		1			
E	1				3					/	3	4		1
<u>Gd</u>			1				1			1	/			
H												/		
J					1								/	
Sn														/

Fig. 2.30. Laughing during play between individual pairs of animals (of both sexes). The symbols representing each animal are written in order of increasing age across and down the figure: names of females are underlined. The numbers in the boxes indicate the number of play bouts during which the animal in the column laughed during play with the animal in the row. Data are from three months records. The mean age of the animals during the recording period is the same as in the preceding figure .

	Jb	R	P	G	K	E	H
Jb	/		4	26			3
R		/		38	2		
P	1		/	8	2	3	2
G				/	10	2	10
K					/		2
E						/	13
H							/

Fig. 2.31. Gecks and screams during play between individual male-male pairs. Numbers in the boxes indicate the number of play bouts in which the animal in the column gecked or screamed during play with the animal in the row. Other legends as for Fig. 2.30.

	Pb	L	M	D	Gd
Pb	/		1	2	1
L	1	/	4		
M			/	1	1
D				/	
Gd					/

Fig. 2.32. Gecks and screams during play between individual female-female pairs. Legends as for Fig. 2.31.

		FEMALES				
		Pb	L	M	D	Gd
MALES	Jb	1				
	R	1		1		2
	P		1	2	2	
	G	11	2	3		1 1
	K	12	5	3		
	E	3			1	
	H	3	1	1		

Fig. 2.33. Gecks and screams during play between individual male-female pairs. Numbers in upper halves of boxes refer to females, and those in the lower halves of boxes to males. Details of recording period as for Fig. 2.30.

		Jb	R	P	G	K	E	H
Jb								
R	54							
P	17	33						
G	8	32	16					
K	7	38	4	19				
E	11	6	4	44	28			
H						10		
						20		
						3	7	
						14	8	
						15	6	17
							8	8
								3
								8

Fig. 2.34. Active and passive roles in mauling play between individual male-male pairs. Numbers in boxes indicate the number of instances of mauling play during which each of the partners had the active role. Numbers in the shaded portions refer to animals in the column, and numbers in the unshaded portions to animals in the row. Recording period as for Fig. 2.30. Data omitted for pairs for which $N < 10$.

Table 2.6

The proportion of gecks and screams made by the younger partner and by the individual which initiated less than 50 percent of bouts

	Male-male	Female-female	Male-female
Gecks + screams by younger partner.	$\frac{125}{126}$	$\frac{10}{11}$	$\frac{46}{57}$
by the individual which initiated less than 50 percent of bouts.	$\frac{118}{126}$	$\frac{5}{11}$	$\frac{55}{57}$

In male-male play, gecks and screams were about twice as frequent as in female-female play (Table 2.7). In male-female play however, females gecked or screamed 48 times and males only 9 times. This again suggests that males played more roughly than females.

Table 2.7

The total number of gecks and screams per 100 seconds play for male-male and female-female play

	No. of gecks+screams	Total seconds play observed	Gecks+screams per 100 seconds play
Male-male	126	24,285	5.2
Female-female	11	4,114	2.7

3. Roles in non-mutual play (mauling and approach-withdrawal)

For both mauling and approach-withdrawal play I counted for each of the possible pairs of play partnerships, the

number of instances in which each partner had the active role (Figs. 2.34 - 2.39). Those individuals which more often initiated play (see Figs. 2.24 - 2.26) usually more often had the active role in mauling and approach-withdrawal (Table 2.8).

Table 2.8

The proportion of pairs of play partners in which the individual that initiated more than 50 percent of play bouts also had an active role in more than 50 percent of instances of mauling or approach-withdrawal play

	Male-male	Female-female	Male-female	Total
Mauling	$\frac{12}{15}$	$\frac{8}{8}$	$\frac{39}{40}$	$\frac{59}{63}$
Approach-withdrawal	$\frac{10}{10}$	$\frac{2}{3}$	$\frac{8}{10}$	$\frac{20}{23}$

(Note that N varies because pairs of partners for which N = less than 10 were omitted from the analysis.)

Conclusions for parts 1, 2 and 3

1. Relationships between individuals in play were largely determined by size. The larger of two play partners generally had the greater role in controlling the amount of play that occurred, more often had the active role, and vocalised less often. These generalisations are not true for play between males widely separated in age, possibly because the larger males restrained themselves.
2. Males played the role characteristic of the larger partner when playing with females which were slightly larger than themselves, perhaps because males played more roughly than females.

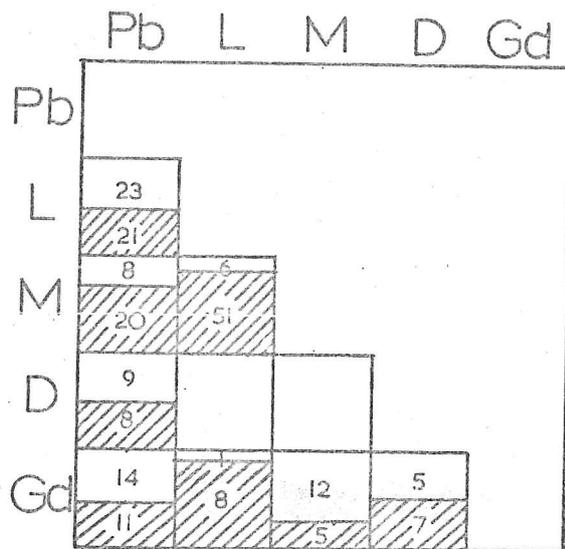


Fig. 2.35 a. Active and passive roles in mauling play between individual female-female pairs. Legends as for Fig. 2.34.

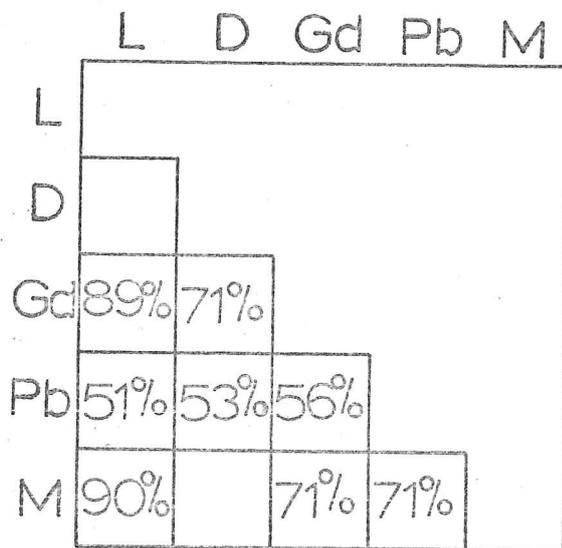


Fig. 2.35 b. Data from preceding figure are rearranged. Percentages in boxes indicate the percent of instances of mauling play in which the animal in the column had the active role during play with the animal in the row. The animals are ordered in a hierarchy such that percentages are all greater than 50 percent.

FEMALES

		Pb	L	M	D	Gd
MALES	Jb	81	21	24	13	10
		46	11	21	10	1
	R	90	31	19	18	51
		65	31	15	10	10
	P	20	17	21	17	26
		29	26	27	4	8
	G	34	9	10	11	16
		125	37	34	11	7
K	11	17	7	2		
	43	7	9	7		
E					4	
					11	
H						

Fig. 2.36. Active and passive roles in mauling play between individual male-female pairs. Legends as for Fig. 2.34.

		Jb	R	P	G	K	E	H
MALES	Jb							
	R	29						
		19						
	P	19	8					
		17	10					
	G	5	19	3				
		10	20	18				
	K				13			
				33				
E				5	15			
				8	13			
H						8		
						25		

Fig. 2.37. Active and passive roles in approach-withdrawal play between individual male-male pairs. Explanation as for Fig. 2.34.

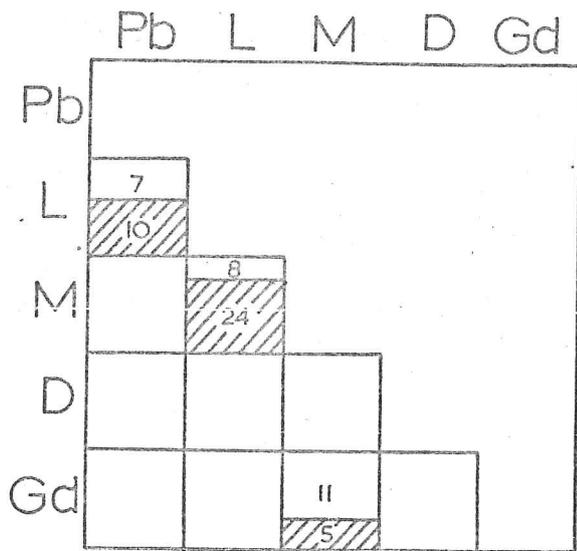


Fig. 2.38. Active and passive roles in approach-withdrawal play between individual female-female pairs. Explanation as for Fig. 2.34.

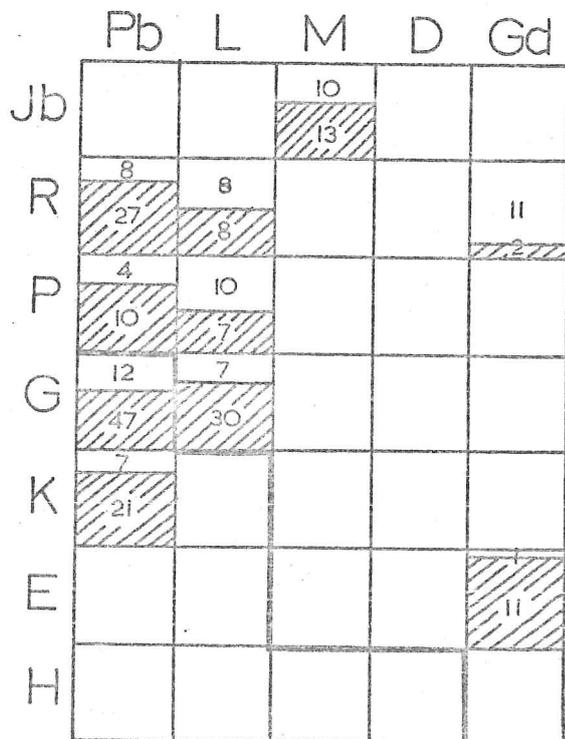


Fig. 2.39. Active and passive roles in approach-withdrawal play between individual male-female pairs. Explanation as for Fig. 2.34.

4. Discussion

No quantitative studies concerning the roles of individuals in primate play have previously been carried out. It is known however that in rhesus monkeys males initiate more play than females (Harlow, 1962; Hinde and Spencer-Booth, 1967).

It has also been shown for rhesus monkeys that the ability to take an active role in aggression or play is influenced by the extent of social experience with peers. Totally isolated rhesus monkeys 6 months old tested with semi-isolated infants of the same age were unable to threaten or play with the semi-isolates, they simply accepted abuse and would not fight back (Rowland, 1964, cited Harlow, 1965). Mason (1961) has carried out similar experiments, keeping monkeys socially isolated for three years and then observing the interactions between them. Isolated monkeys were more aggressive compared with controls owing to their lack of communicative skills which prohibited the establishment of stable aggression hierarchies. Early social isolation also causes social retardation in dogs (Melzack and Thompson, 1956). Isolated dogs were unable to accept or reciprocate approaches by a man or effectively compete with controls for food. More subtle effects of social experience may influence future agonistic relations. In a comparison of rural and urban living rhesus monkeys, Singh (1968) found that the urban monkeys were more aggressive and dominated the rural ones in aggressive encounters.

Thus it is possible that the amount and nature of play experience may influence an animal's ability to take an

active role in future play or aggression. It was shown that, out of those pairs of baboons which played most together (near to each other in age), the larger partner more often had the active role, and was more likely to initiate play. Thus animals were more likely to initiate play with those animals near to them in age if they could dominate the playful interaction and (if the conclusions about rhesus monkeys apply to baboons) the more they played, the more likely they were to be able to dominate future interactions. Thus inherent differences, including sex differences, between individuals in 'personality', size, and predisposition to play may be emphasised through play experience, and may gradually lead to the establishment of stable individual relationships.

I shall discuss further the relevance of roles in play to the development of individual relationships in Section 10.

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9. Aggressive behaviour: comparison with aggressive play.

1. Introduction

As explained in Section 1, I have separated aggressive behaviour proper from aggressive play by the criterion of threat, those sequences which included gestures of intense threat being classed as aggression. I do not claim that there was a clear-cut distinction between the two classes of aggression so defined, they were merely two ends of a spectrum of different ways of organising a common 'pool' of behaviour patterns. Behaviour at one end of the spectrum (aggression proper) was characterised by its greater intensity and was nearly always accompanied by intense threat. The immediate functional consequence of the behaviour was clear. By biting the opponent or threatening to do so it served to establish precedence over other individuals to a desired object or place. Behaviour at the other end of the spectrum (aggressive play) was characterised by a lack of intense threat and hard biting, and was often accompanied by different social signals, such as the play face. Play did not appear to have any immediate functional consequence.

This is as far as it is possible to go with a qualitative description. In this section I shall make a quantitative comparison of play and aggression in an attempt to assess in greater detail the difference between the way the behaviour patterns are organised in the two categories, and the differences in the relationships between individuals in the two classes of behaviour. This will show the extent to which the use of the criterion of threat does separate the two types of aggression and may throw light on the importance of

play in the development of the organisation of movement patterns and individual relationships.

2. Aspects of aggressive behaviour relevant to check sheet design.

Apart from threatening behaviour patterns, all the movement patterns which were seen in aggressive play also occurred in aggression proper. Movements were generally more intense in aggression (for instance chases and the hitting movements made in sparring were generally faster), but it was difficult to make any quantitative assessment of this difference using check sheet methods, because the movements made were too fast to follow. For this reason I have confined my attention to the frequency of the different categories of movement pattern in aggression rather than the frequency of the component movements within one category of movement pattern.

As in play, aggressive interactions usually occurred in dyads.

3. Check sheet methods and design

In order that I could make a quantitative comparison of aggression with aggressive play, I recorded aggression on check-sheets which had some of the same measures as the play check-sheet. Time did not allow such a detailed study of aggression as of play, so the check-sheet used was a simplified form of the play check-sheet.

Thus I recorded:

- (a) The length of aggressive sequences (using a stop watch).

A bout of aggression was defined as an aggressive sequence uninterrupted by a break of one second or more (cf. definition of play bout). It was clear from observations of aggressive behaviour between adult males that chases often lasted much longer than did chases in juvenile play. Thus, rather than measure the length of whole aggressive bouts, I considered it would be more meaningful to time aggressive rough-and-tumble (R-and-T) and approach-withdrawal (Ap-W) instances separately, even if both occurred in one bout, and compare the length of these two classes of movement pattern with the length of the same two classes of movement pattern in play. In the play study I had measured only the length of whole play bouts, which often included both R-and-T and Ap-W movement patterns. Thus, in order to obtain data comparable to those for aggression, I selected for analysis those play bouts in which only R-and-T or only Ap-W patterns occurred. There seemed no reason to suppose that the length of such instances of R-and-T and Ap-W should not be representative of the rest.

- (b) The movement patterns which occurred in each bout.
- (c) The names of the animals involved in each bout.

Aggression was recorded on a tape recorder and later transcribed to the check sheet.

4. The length of instances of rough-and-tumble and approach withdrawal movement patterns in aggression and play.

Shown in Figs. 2.40 and 2.41 are the frequency distributions of the length of R-and-T movement patterns in aggression and play uninterrupted by a break of more than

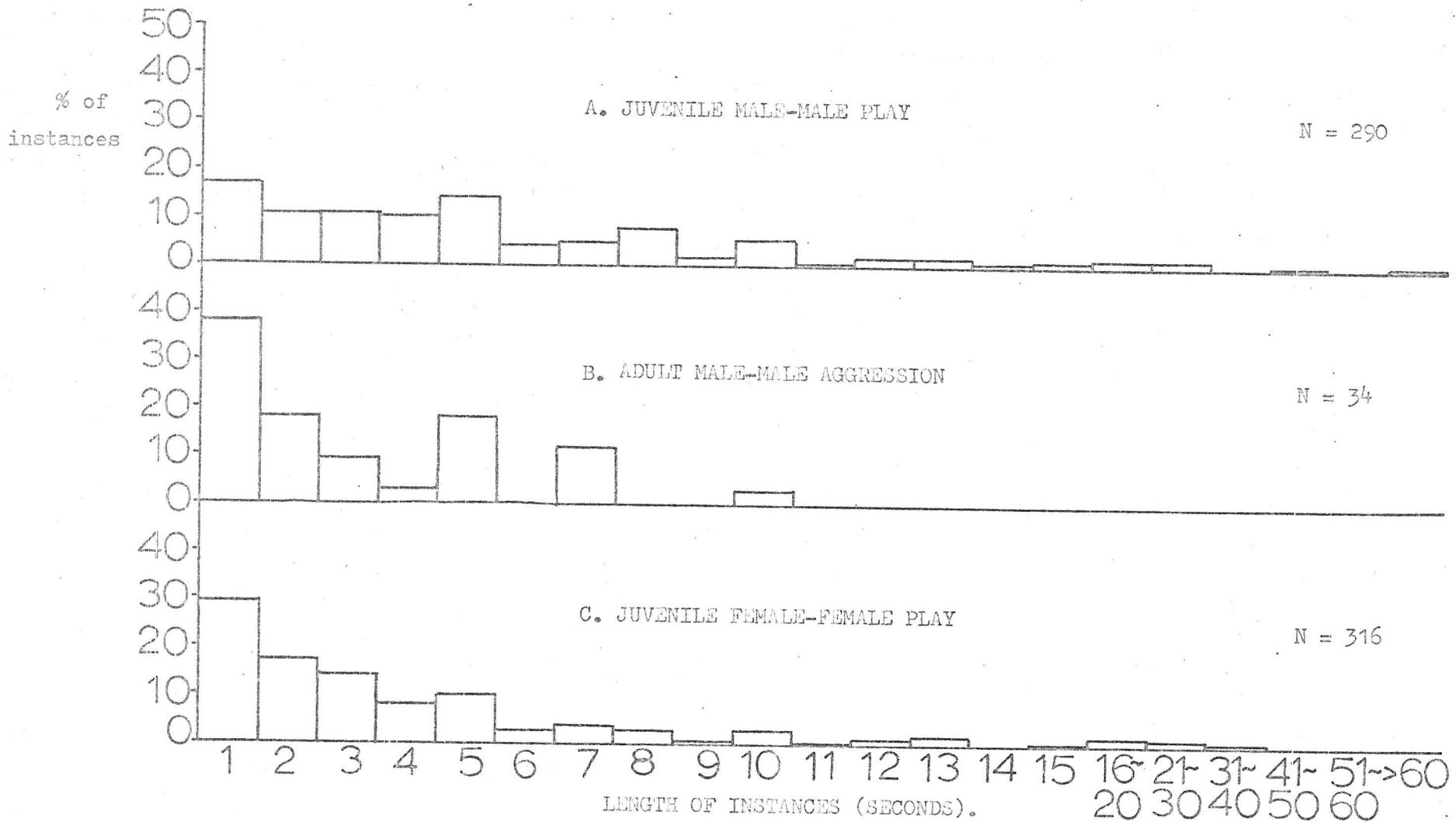


Fig. 2.40. The frequency distribution of the duration in seconds of instances of rough-and-tumble movement patterns in play and aggression. See text for further explanation.

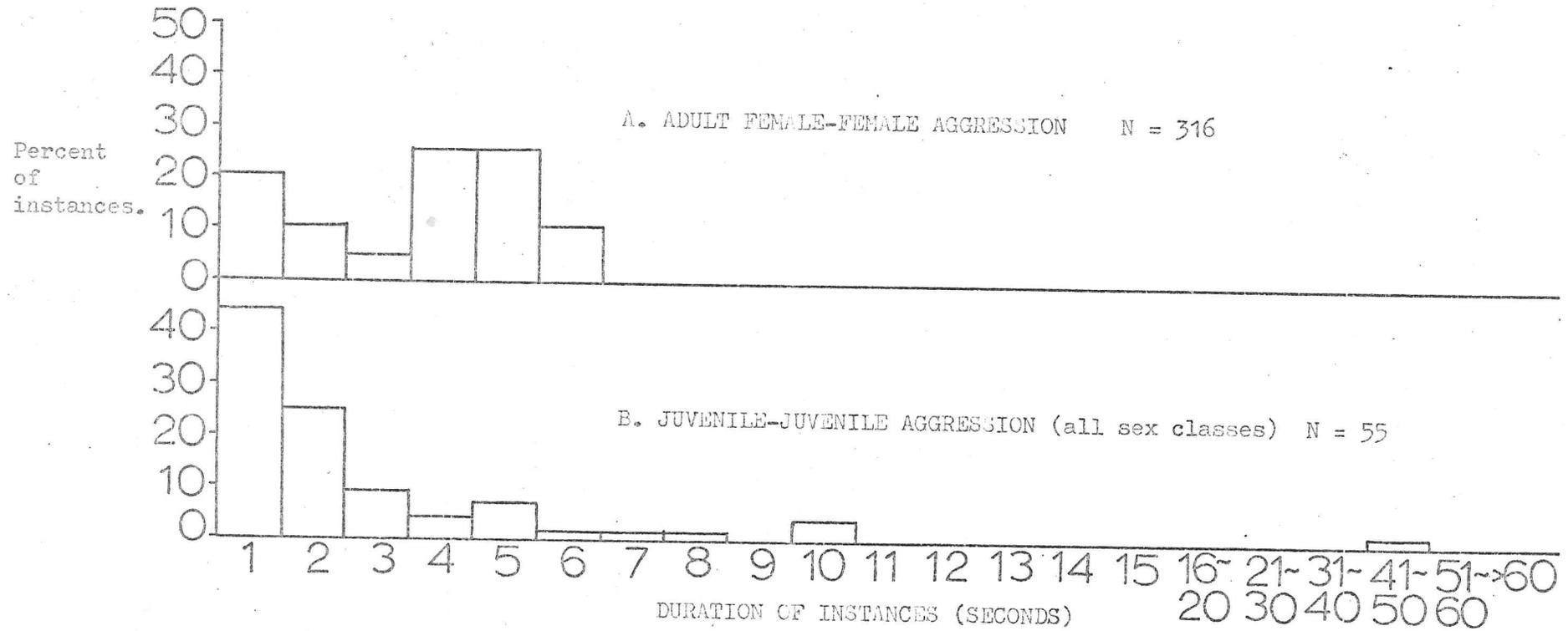


Fig. 2.41. The frequency distribution of the duration, in seconds, of instances of rough-and-tumble movement patterns in play and aggression (contd.).

one second or by Ap-W movement patterns. Figs. 2.42 and 2.43 show the equivalent data for Ap-W movement patterns.

The data for play (2.40A and 2.41A) were obtained from a sample of four individuals for each sex representing different ages from 2 to 37 months. They will be referred to collectively as juveniles in this section for convenience.

I have not separated the data for juvenile-juvenile aggression (Fig. 2.41B-2.43) into male-male, female-female and male-female classes because the data are rather few. About 65 percent of the measurements are for male-female aggression, but those data for the other two classes had a similar frequency distribution, so I have lumped them together.

The mode, the mean and the median length of instances of R-and-T and Ap-W movement patterns in juvenile male-male and juvenile female-female play and in adult male-male, adult female-female and juvenile-juvenile aggression are shown in Table 2.9.

Table 2.9

The mode, the median and the mean length of instances of rough-and-tumble and approach-withdrawal movement patterns in aggression and play

	Rough-and-Tumble				Approach-Withdrawal			
	Mode	Median	Mean	N	Mode	Median	Mean	N
Juvenile male-male play.	1	13	6.0	290	2	5	3.1	79
Adult male-male aggression	1 and 5-7	7	3.1	34	5	10.5	12.8	27
Juvenile female-female play	1	8	4.6	316	2	5	3.0	60
Adult female-female aggression	1 and 4-5	2.5	3.6	19	2	2	1.9	16
Juvenile-juvenile aggression	1	7	3.3	55	1	4	2.7	32

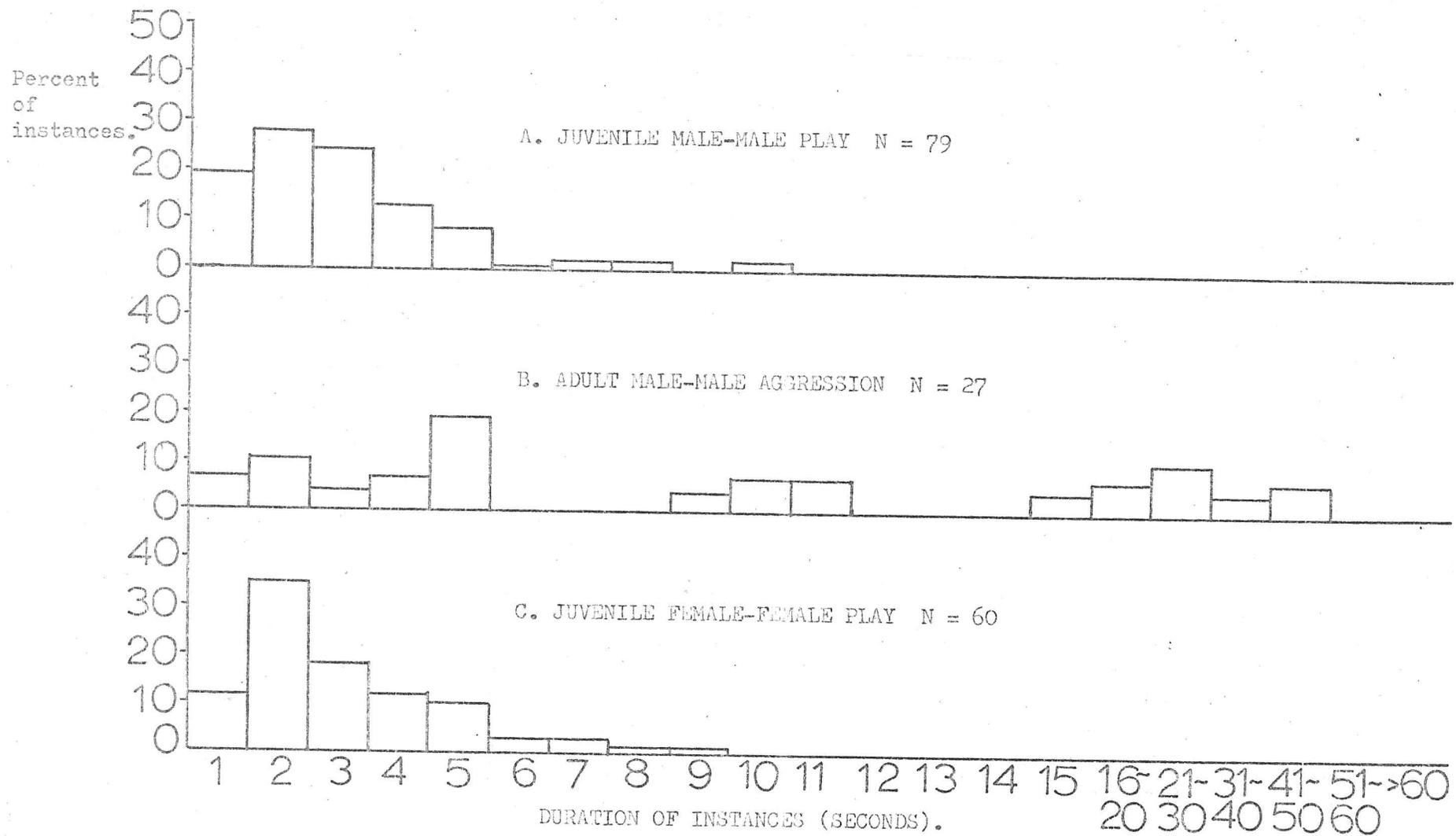


Fig. 2.42. The frequency distribution of the duration, in seconds, of instances of approach-withdrawal movement patterns in play and aggression.

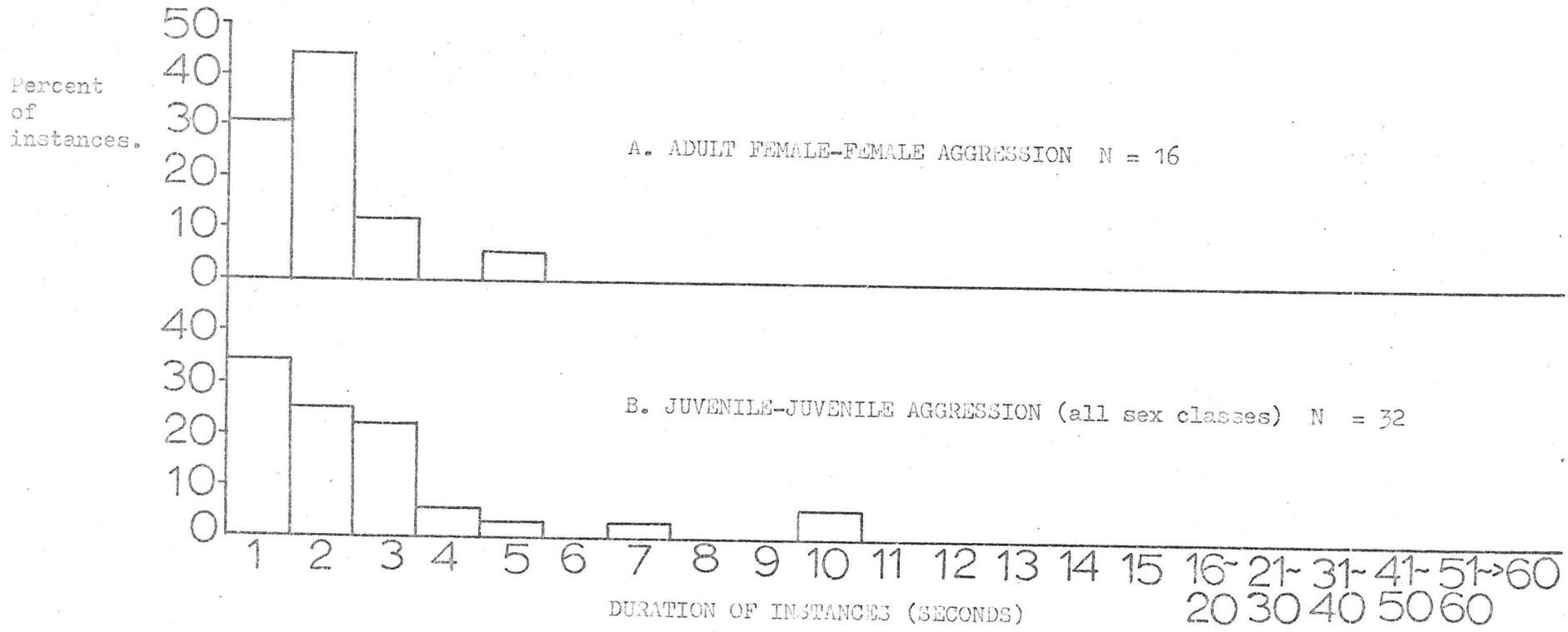


Fig. 2.43. The frequency distribution of the duration, in seconds, of instances of approach-withdrawal movement patterns in play and aggression (contd.).

(a) Rough-and-tumble movement patterns

Looking at medians and means, R-and-T instances tended to last longer in the play of both sexes than in any of the three categories of aggression, there being many more long bouts in play than in aggression ($p < 0.01$; Median test). Instances of R-and-T tended to be longer in male-male play than in female-female play; there were fewer bouts of less than 4 seconds in males than in females ($p < 0.001$; Chi square test). There was no clear difference between the sexes in adult aggression, nor between juvenile and adult aggression. In adult aggression in both sexes, the frequency distribution appeared to be bimodal, but in juvenile aggression and play it was unimodal.

(b) Approach-withdrawal movement patterns

Again looking at medians and means, adult male-male Ap-W instances tended to be much longer than those of any other category, 30 percent of chases lasting more than 15 seconds ($p < 0.001$; Chi square test). Adult female-female chases lasted for a shorter time than any of the other four age/sex categories, a larger proportion of chases lasting less than 3 seconds ($p < 0.01$ in three of the four comparisons by the Chi square test, but the difference between adult females and juveniles in aggression was not significant). Chases in play were about the same length in the two sexes, and somewhat longer (though not significantly so) than in juvenile-juvenile aggression.

Looking at modes, adult male-male chases were again the longest, but the mode for juvenile-juvenile aggression was the shortest, and for the other three categories it was equal.

In adult male aggression, chases tended to be longer

than R-and-T instances, but the reverse was true for adult female aggression and both classes of play ($p < 0.01$ in all cases; Median test).

(c) Discussion

In R-and-T play, baboons experienced more physical contact than in R-and-T patterns in aggression; this was particularly true for males. Juvenile baboons had little physical contact with peers other than through play. Grooming was infrequent compared to adults especially in males and the contact between peers during play may have been an important aspect of the socialisation process.

The long chases characteristic of adult males were probably a reflection of their fear of engaging in physical contact with one another. Even during the brief fights which did occur, wounds were often inflicted with the canine teeth (see below).

In adult females chases in aggression were very short because the aggressee tended to stop and present in submission to the aggressor (see Part 5).

Play chases were shorter than those in adult male aggression, probably because the chaser more often caught up with its partner due either to the disparity in size between the participants (this also applies to juvenile-juvenile aggression) or to the fact that the chasee slowed down to allow the chaser to catch up, or turned to face its oncoming partner.

5. The movement patterns in aggression and play

Introduction

In this section I shall compare male-male and female-female interactions in aggression and play in order to answer the questions:

- (a) Are the sex differences in the relative frequency of movement patterns in play also seen in aggression?
- (b) Are there differences in the relative frequency of movement patterns between aggression and play within one sex?
- (c) If so, does play become more like aggression as animals get older?

For this analysis I have considered 6 classes of movement pattern, namely: mutual biting, sparring, and wrestling other than sparring (mutual categories), and non-mutual biting, chasing and mauling (categories in which one partner has an active and the other a passive role). For each of these patterns I counted the number of times it occurred and expressed the number as a percentage of the total number of movement patterns of all categories observed. This procedure was carried out for male-male and female-female play, juvenile male-male and juvenile female-female aggression and for adult male-male and adult female-female aggression. For play, animals representing different ages were treated separately. It should be noted that the 6 categories of movement pattern are not all mutually exclusive; biting could occur at the same time as other patterns. Thus the figures indicate the number of times each pattern was used relative to other patterns. The results are shown

in Figs. 2.44 and 2.45.

(a) Are the sex differences in the relative frequency of movement patterns in play also seen in aggression?

In Table 2.10 are presented the sex differences in the extent to which the six movement patterns contributed to play and aggression and the probability values for each of the differences. In play, the proportion of movement patterns which were mutual was greater for male-male play than for female-female play ($p < 0.001$; Mann-Whitney U test, comparing 8 males with 6 females). The same sex difference holds true for adult aggression ($p < 0.001$; Chi square test). In juvenile aggression the same tendency appears but the difference was not significant, and chasing was much commoner in juvenile male aggression than in juvenile female aggression.

Thus there was much similarity between the sex differences in play and those in aggression, particularly those in adult aggression.

Table 2.10

Sex differences in the extent to which the six movement patterns contributed to play and aggression (from inspection of Figs. 2.44 and 2.45)

	Play	Aggression	
		Juvenile	Adult
Non-mutual categories	Mauling -23.5**	- 4.0	- 5.0*
	Chasing - 3.5*	+12.0	+ 3.0
	Non-mutual biting - 1.0	-20.0**	-43.0**
Mutual categories	Wrestling + 7.5*	+ 1.0	+ 2.0
	Sparring + 5.0**	+ 9.0	+35.0**
	Mutual biting +16.5**	+ 1.0	+ 9.0**

+ Occurred more in males than in females by percent indicated
 - Occurred less in males than in females by percent indicated
 For each movement pattern in play, the median for each sex of all age groups is compared.

* $p < 0.05$. ** $p < 0.01$.

(Mann-Whitney U test for play; Chi square test for aggression)

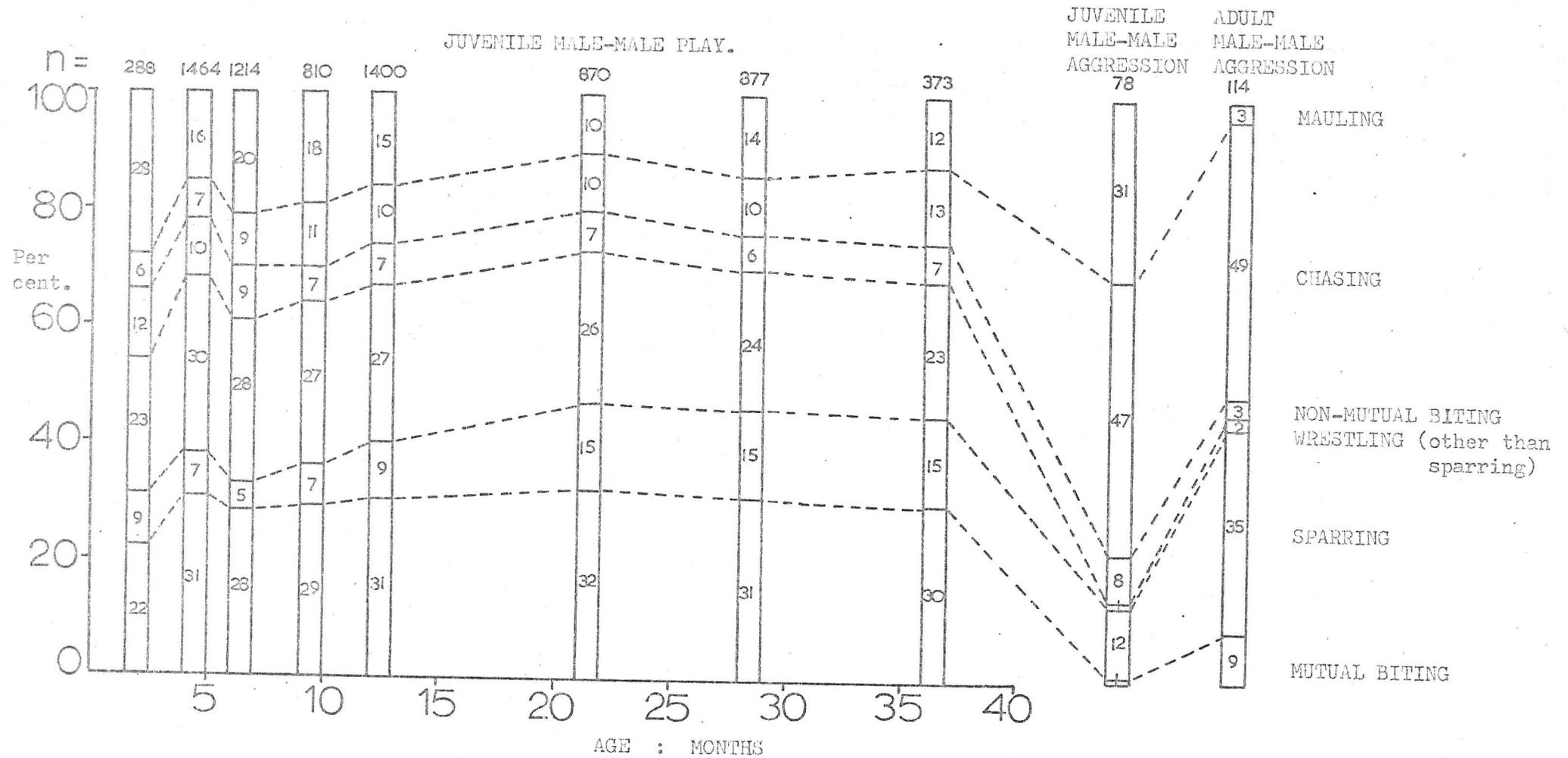


Fig. 2.44. The percentage contribution of six movement patterns to play and aggression between males of different age classes. Data for play are from three months records, and the mean age during the recording period is plotted. See text for further explanation.

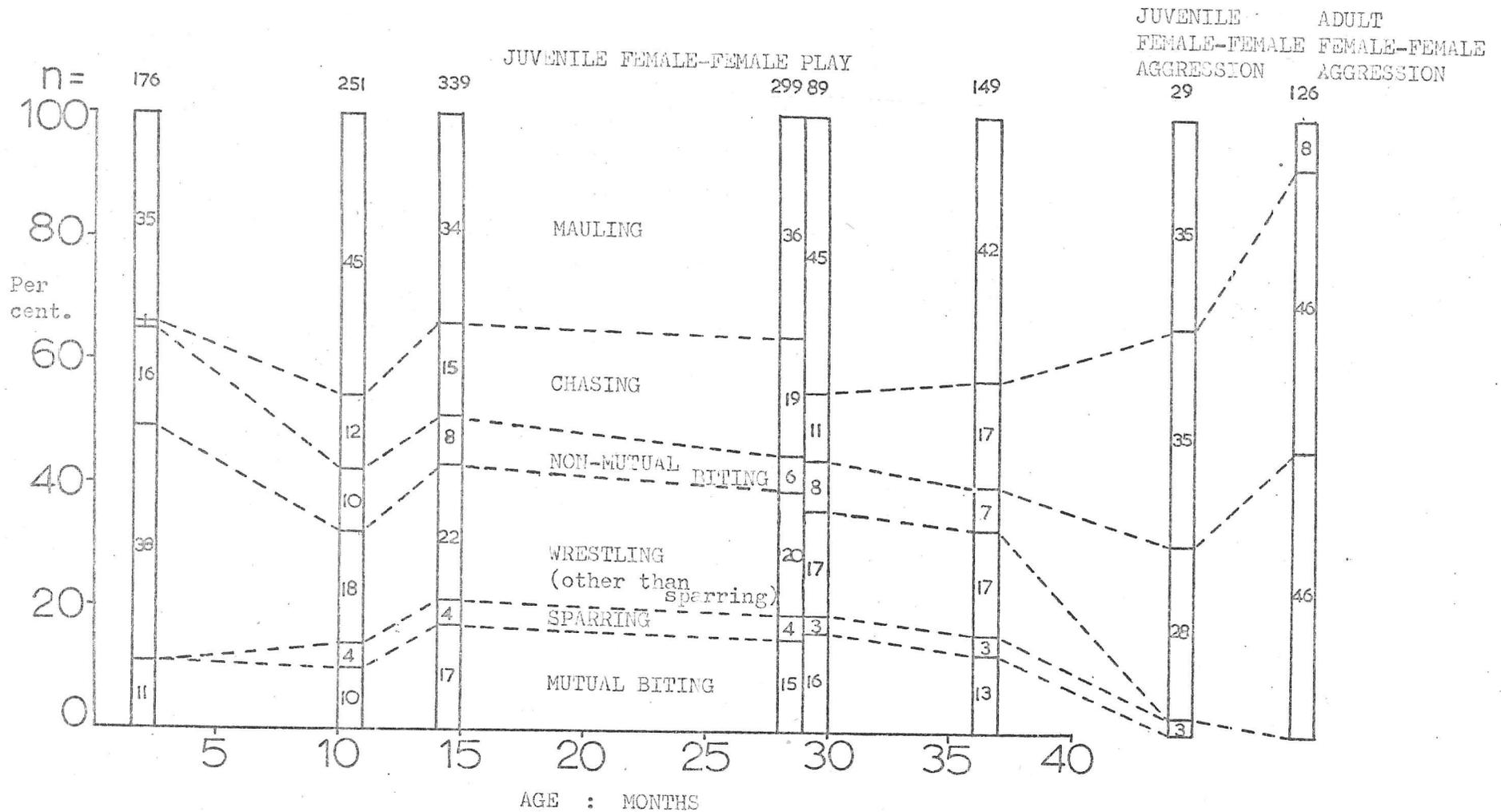


Fig. 2.45. The percentage contribution of six movement patterns to play and aggression between females of different age classes. Other details as for Fig. 2.44.

Although the signs of the sex differences in the relative frequency of the different movement patterns were largely consistent between play and aggression, the sizes of the differences were less consistent. All six patterns were present in both male and female play, but some patterns present in male-male aggression were absent from female-female aggression. Thus wrestling and mutual biting occurred in juvenile male-male aggression but not in juvenile female-female aggression. Wrestling, sparring and mutual biting occurred in adult male-male aggression but not in adult female-female aggression (thus there were no mutual patterns at all in adult female aggression). The sex difference in the relative frequency of non-mutual biting was greater in both classes of aggression than in play (in which there was only 1 percent sex difference), but the reverse was true for mauling (see Table 2.10).

- (b) Are there differences in the relative frequency of movement patterns between aggression and play within one sex?
- (c) If so, does play become more like aggression as animals get older?

Males

Table 2.11 compares the relative frequency of the six movement patterns in male-male play with those in juvenile male-male aggression and with those in adult male-male aggression.

Table 2.11

Differences in the percentage contribution of the different movement patterns to play and aggression in males (from inspection of Fig. 2.44)

		Play/Juvenile aggression	Play/Adult aggression
Non-mutual	Mauling	-17.5**	+12.5**
	Chasing	-37.0**	-39.0**
	Non-mutual biting	- 1.0	+ 4.0*
Mutual	Wrestling	+25.5**	+24.5**
	Sparring	- 3.0	-26.0**
	Mutual biting	+29.5**	+21.5**

+ occurred more in play than in aggression by percent indicated.

- occurred less in play than in aggression by percent indicated.

Medians of figures for all age groups of play are used.

* $p < 0.05$)
 ** $p < 0.01$) Chi square test.

In play, mutual patterns comprised a median over all age groups of 66 percent of total patterns, whereas the equivalent figure for juvenile aggression was 14 percent and for adult aggression 46 percent. In this sense one could say that juvenile male play was more like adult aggression than juvenile aggression.

If one looks at individual movement patterns, this generalisation does not hold true. Differences between play and juvenile aggression and between play and adult aggression were similar for chasing, wrestling and mutual biting. Sparring and non-mutual biting occurred about equally in play and juvenile aggression, but both occurred more frequently in adult male aggression than in play.

Mauling was relatively more frequent in juvenile aggression than in play but less frequent in adult aggression than in play.

One may now ask whether the relative frequency of patterns in play became more like those in aggression as males became older (see Fig. 2.44).

There was no tendency for the total contribution of mutual (and non-mutual) patterns to change with age. Mutual biting and wrestling showed no age changes, but sparring became relatively more common with age ($r_s = 0.75$; $p < 0.05$), and in this respect play became more like juvenile and adult aggression. Non-mutual biting tended to decrease ($r_s = -0.88$; $p < 0.01$) and chasing to increase ($r_s = 0.98$; $p < 0.01$) and in respect to these patterns too, play became more like juvenile and adult aggression with age. Mauling tended to decrease with age ($r_s = 0.86$; $p < 0.01$), play thus becoming more like adult aggression but less like juvenile aggression. (See also Section 7 in which similar conclusions concerning play movement patterns were reached.)

Although there was a tendency for the relative frequency of some play patterns to become more like those of aggression with age, they did not always approach the same absolute proportions as those in juvenile or adult aggression by the age of 37 months (the limit to which my data go). Thus sparring reached 15 percent in play compared with 12 percent in juvenile and 37 percent in adult aggression, chasing reached 13 percent in play compared with 47 percent in juvenile and 49 percent in adult aggression and mauling declined to 12 percent in play compared with 3 percent in

adult aggression.

Overall, the proportions in which the movement patterns were used in juvenile aggression were somewhat more like the proportions in adult aggression than were the proportions in which the patterns were used in play (Fig. 2.44). Thus, although the proportions in which the patterns were used in play became more like those in adult aggression with age, one cannot conclude that play was important in the development of the use of the patterns in such proportions because they were already being used in such a way, to some extent, in juvenile aggression.

Females

Table 2.12 compares the relative frequency of the six movement patterns in female-female play with those in juvenile female-female aggression and with those in adult female-female aggression.

Table 2.12

Differences in the percentage contribution of the different movement patterns to play and aggression in females

		Play/Juvenile aggression	Play/Adult aggression
Non-Mutual	Mauling	- 4.0	+31.0**
	Chasing	-21.5**	-32.5**
	Non-mutual biting	-20.0**	-38.0**
Mutual	Wrestling	+19.0**	+19.0**
	Sparring	+ 1.0	+ 4.0
	Mutual biting	+14.0*	+14.0**

Legends as for Table 2.11.

As in males, mutual patterns comprised a larger proportion of play than aggression (37 percent of play compared with 3 percent of juvenile aggression and 0 percent of adult aggression, $p < 0.001$ in both cases by the Chi square test). Thus, with respect to the ratio of mutual to non-mutual patterns used, female play resembled juvenile and adult male aggression more closely than juvenile and adult female aggression.

All three mutual patterns were commoner in play than in both juvenile and adult aggression (though the difference was significant in only four of the six comparisons, see Table 2.12). Mutual patterns were absent from female aggression with the exception of a small amount of sparring in juveniles. Mauling was also more common in play, the difference being greater for adult than for juvenile aggression in which the difference was not significant. Chasing and non-mutual biting were much more frequent in juvenile and adult aggression than in play.

There was no indication from the data that play tended to become more like aggression with age. The total contribution of mutual patterns did not decrease, nor did any of those patterns relatively more common in aggression than play become more common in play with age (see Fig. 2.45).

As in males, the proportions in which the patterns were used were more similar between juvenile aggression and adult aggression than between play and juvenile aggression or play and adult aggression (Fig. 2.45).

Discussion

The similarity of the sex differences in the proportion

in which the movement patterns were used in aggressive play and aggression supports the concept that play and aggression are different ways of organising a common pool of behaviour patterns, and indicates that they share certain causal factors.

The comparison of the component patterns of aggressive play and aggression within each sex indicated that there were clear cut differences between the two types of aggression. However the data offered little evidence that play was important in the development of ways of organising the component patterns, since patterns in juvenile aggression were more like those in adult aggression than were those in play in both sexes.

There was a tendency for some male (but not female) play patterns to approach proportions more like those in adult aggression with age. The increasing 'roughness' of play has previously been described in baboons by Hall and DeVore (1965) and in langurs by Jay Dolhinow and Bishop (1970) from subjective impressions. The latter authors' statement in their review that play in baboons and langurs becomes "progressively more involved in dominance interactions" with age seems meaningless however.

6. Biting in aggression and play

In order to compare further the movement patterns in play with those in aggression I have analysed the extent to which different parts of the body are bitten in aggression and mock-bitten in play. Since the difference between aggression and aggressive play hinges on the 'seriousness'

or otherwise of the behaviour (i.e. whether hard biting is intended or not), a comparison of the parts bitten in aggression and play should throw light on the function of play.

A. Methods

Data about the parts mock bitten in play were collected separately from the main play study owing to the limits imposed on recording by the speed with which play occurred.

In order to record play biting I followed the troop until I saw any animals start playing, then I watched one of the playing animals for one bout at a time and wrote down the names of the partners and all the parts that received bites from the animal I was watching during the bout, regardless of the length of time that each part was bitten. I then waited for the start of another bout and repeated the procedure. Sometimes a bout or bouts would be missed whilst writing on the recording sheet. By selecting animals at random I was able to obtain a sample representing all age groups. I divided the body arbitrarily into 20 anatomical regions and used a symbol to represent each region for the purpose of recording.

The places bitten in aggressive interactions between adult females and between juveniles were recorded on the aggression check sheets.

It was not possible to record the parts bitten in aggression between adult males directly because biting was usually too fast and too brief to see. Instead I recorded wounds received by adult males (both flesh wounds and pieces of fur removed). It is most unlikely that such

wounds would be inflicted other than by an adult male baboon. Other members of the troop were never observed to bite an adult male during aggression, and only adult males have long canines capable of inflicting wounds. It is possible that some of the wounds might have been inflicted during fights with predators (for instance chimpanzees), but such fights were never observed to result in wounding and were relatively very infrequent. Only one of the 35 wounds recorded was observed at the time it was inflicted and the others were mostly seen up to two weeks afterwards.

B. Results

The results are presented in Figs. 2.46, 2.47 and 2.48. The number of bites to each region of the body is expressed as a percentage of the total number of bites observed.

(a) Play mock biting

In the time available I was not able to collect enough data to be able to compare male-male and female-female mock biting separately. The results presented in Fig. 2.46 represent (a) males biting males and females (over 95 percent of the data are for males biting males), and (b) females biting males and females (over 95 percent of the data are for females biting males).

Both males and females directed about 75 percent of bites to the anterior regions of the body (head, neck, shoulders, arms and hands), but some biting occurred in all regions. Females bit the side of the neck and the cheeks less than did males, and the shoulders, top of the head, back of the neck and the hands somewhat more.

The side of the neck was the place most frequently

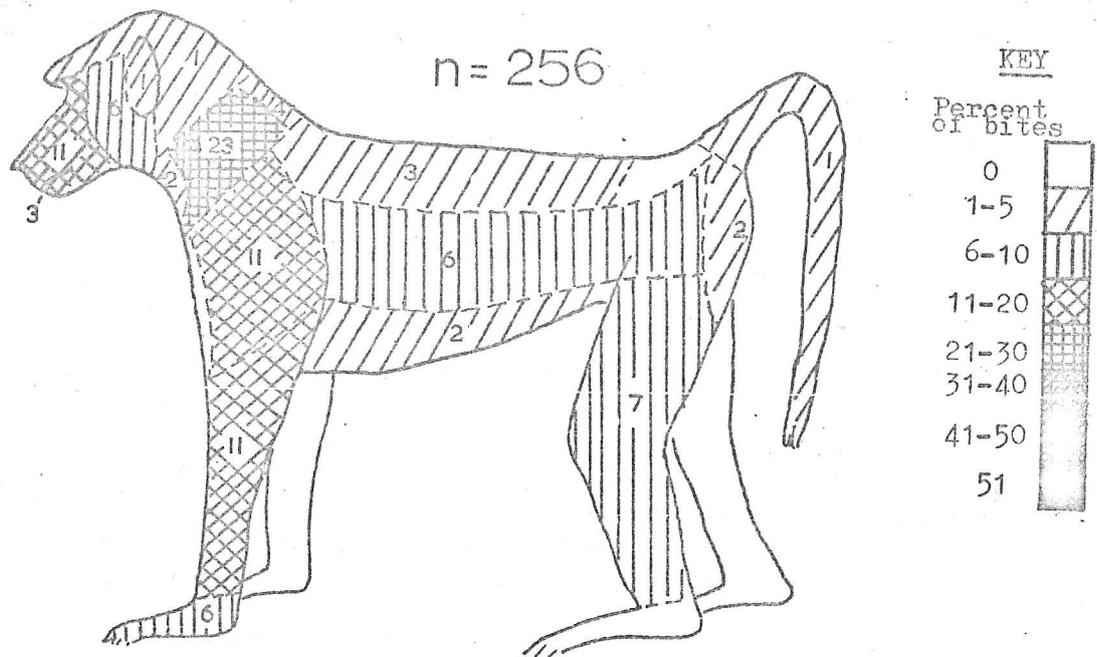


Fig. 2.46 a. Regions of body mock bitten by males in play. Numbers indicate the percentage of bites oriented to the various regions of the body. The pattern of biting is also shown by the degree of shading of the different parts, those parts most often bitten being most heavily shaded (see key). For further explanation see text.

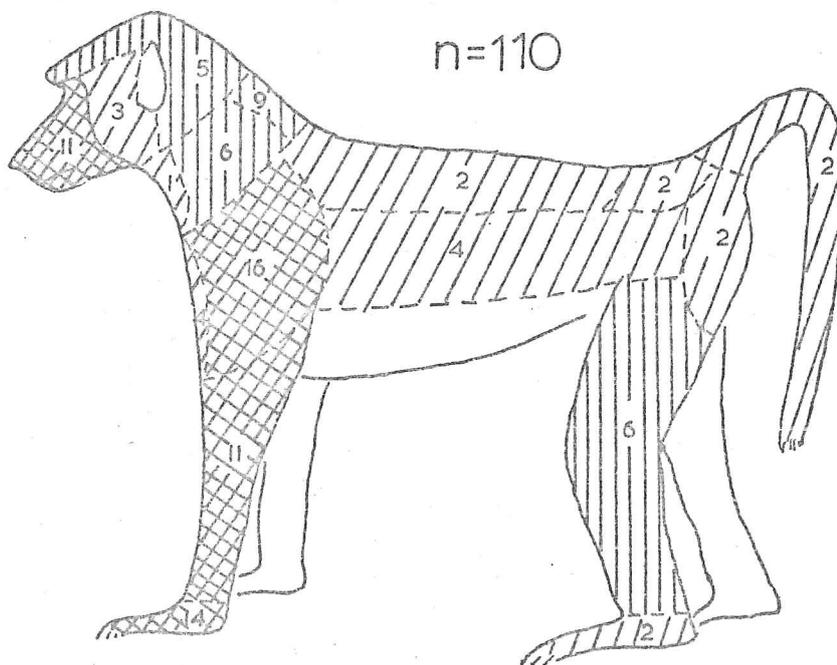


Fig. 2.46 b. Regions of the body mock bitten by females in play.

bitten by males, but it was difficult for two baboons to bite each other on the side of the neck simultaneously. When females played with males it sometimes looked as if the male was able to bite the side of the female's neck, but the female was obliged to bite other parts of the male (such as the shoulders, arms and hands). If males passively allowed females to bite them, the sex difference in the regions bitten might not be so marked.

Although I have few quantitative data, females appeared to bite females in play largely in the same regions as females bit males.

(b) Biting in aggression

Adult male wounds (Fig. 2.47a)

Wounds occurred in most regions of the body, but more than 50 percent were on the face. The bare face is much more likely to be wounded than are parts of the body covered by fur. The neck and shoulders of adult males are protected by a thick mane and the number of wounds observed in this region probably does not reflect the extent of biting. One can say however that most wounds were inflicted on the anterior part of the body. This is to be expected since nearly all fighting between adult males was in the form of sparring (in which the partners stand facing each other). Wounds on the rump were probably inflicted during chases.

Adult female-female biting (Fig. 2.47b)

In aggression between adult females biting was confined to the back of the neck, back, lower back and tail. Aggressive interactions between adult females appeared to be more stereotyped than those between adult males and

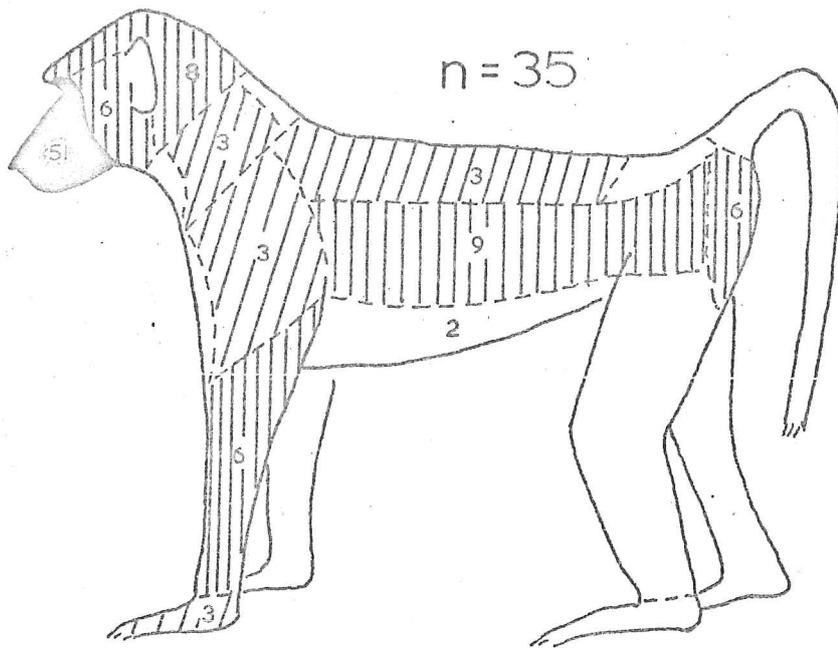


Fig. 2.47 a. Regions of the body in which wounds were received during adult male-male aggression. Legends as for Fig. 2.46.

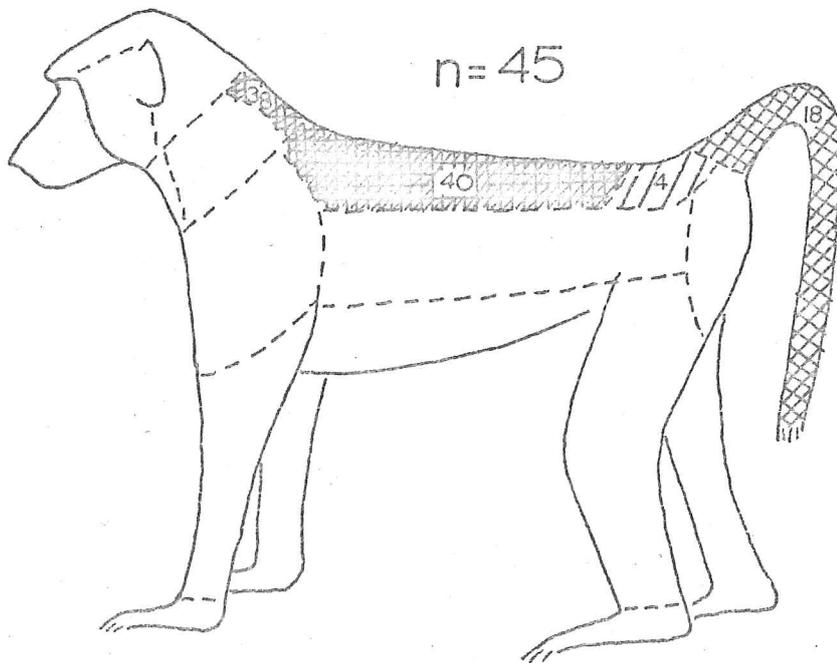


Fig. 2.47 b. Regions of the body bitten during adult female-female aggression.

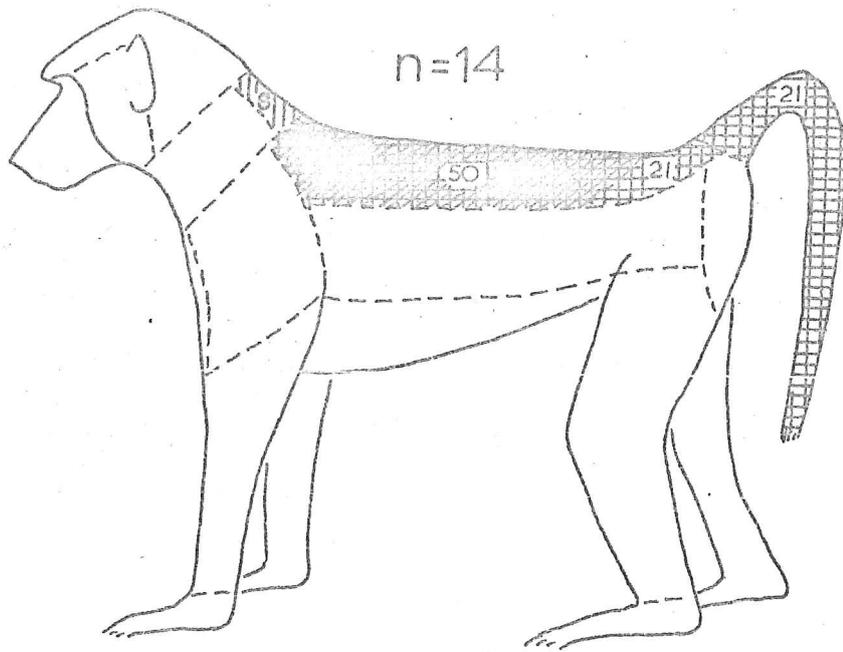


Fig. 2.48 a. Regions of the body bitten by males during juvenile-juvenile aggression. Legends as for Fig. 2.46.

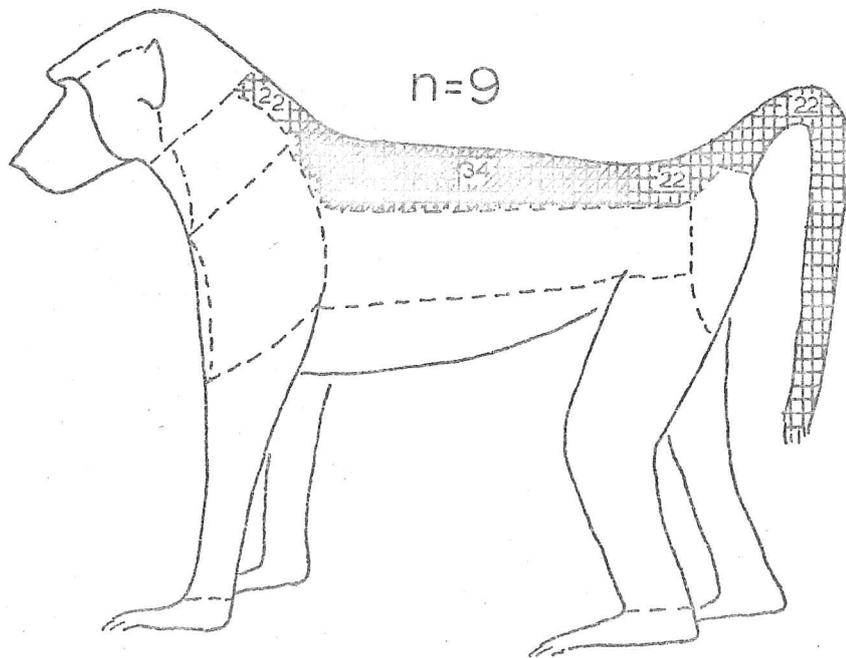


Fig. 2.48 b. Regions of the body bitten by females during juvenile-juvenile aggression.

involved a 'punishing' bite by the aggressor from behind, often following a short chase. The aggressee usually adopted a submissive posture, turning her rump towards the aggressor and crouching. (Note that non-mutual biting occurred in adult female aggression but mutual biting did not. Fig.2.45).

Juvenile-juvenile aggression (Fig. 2.48a and b)

The data for this class of aggression are rather few, but they are enough to show that biting by both male and female juveniles followed a very similar pattern to that amongst adult females. Biting was confined to the back of the neck, back, lower back and tail.

One can conclude that the parts bitten in the play of both sexes resembled those in adult male aggression much more closely than those in adult female or juvenile aggression.

7. The relationships between individuals in aggression

In this section I shall attempt to make an assessment of the relationships between individuals in aggression, looking separately at adult male-male, adult female-female, juvenile male-male, juvenile female-female and juvenile male-female interactions.

Examining each of the above five categories in turn I looked at bouts of aggression (recorded on the aggression check sheet) between all the possible pairs of individuals, and counted the number of times each of the two partners of every pair had an active or passive role, looking at instances of mauling, chasing and non-mutual biting movement patterns. In some bouts, only mutual movement patterns

occurred, e.g. sparring, and these bouts were ignored for the purpose of this analysis. Also included in the analysis were interactions in which one animal threatened another as it walked towards it, and the other animal retreated (not classed as a chase because the animals were not running, but classed as aggression because it involved threat). Aggressive interactions were recorded whenever possible whilst doing the mother-infant and play records throughout the period of study (March - November 1970 and April - August 1971).

1. Juvenile aggression: comparison with play

(a) Male-male

In Fig. 2.49a the results are presented in a matrix with the animals in age order. In 67 cases out of 68 the older animal had the active role and the younger the passive role (though there are very few data for the three youngest males). It should be added that the ages of J and Sn were not known exactly, and they both appeared to be the same age, but Sn always had the active role in interactions between them.

It was shown that in play, males could be arranged in a linear hierarchy according to age in which in 12 out of 15 pairs of animals the older partner more often had the active role than the younger partner (Fig. 2.34). Thus, so far as the data for pairs of individuals overlapped, the same hierarchy existed in aggression and play. In all 15 pairs of animals for which there are data for play however, both partners sometimes had the active role, and the larger partner had the active role in only 301 cases out of 480.

	Jb	R	P	G	K	E	H	J	Sn	Gb
Jb	/									
R		/								
P			/							
G		1		/						
K				2	/					
E				1	8	/	1			
H	2			5	4	14	/			
J			3	2	1	2		/		
Sn				3	3	1	2	12	/	
Gb										/

Fig. 2.49 a. Roles in aggressive interactions between juvenile males. Numbers indicate the number of times the animal in the column down the left side of the figure had the active role during aggression with the animal in the row. Ages of animals range between 0 - 85 months. See text for further explanation.

	Pb	L	M	D	Gd
Pb	/	2			
L		/			
M		2	/		
D	2	4	4	/	1
Gd		1	2	1	/

Fig. 2.49 b. Roles in aggressive interactions between juvenile females. Ages range between 0 - 48 months. Legends as for Fig. 2.49 a.

	Pb	L	M	D	Gd
Jb	1	1	1		
R	1	1		1	
P	1	1		1	1
G	3	1	3		
K	2	4	9	2	1
E		1	5	5	1
H	2	4	3	3	4
J	2	1		3	4
Sn	1	1		4	
Gb					

Fig. 2.50. Roles in aggressive interactions between juvenile male-female pairs. Numbers in boxes indicate the number of times each animal had the active role with every other animal. Numbers in lower halves of boxes refer to males (in column), and those in upper halves of boxes to females (in row). Ages range from 0 - 85 months. See text for further explanation.

Thus one can say that roles were more often reversed in play than in aggression ($p < 0.001$; Chi-square test).

(b) Female-female

A similar matrix for females is shown in Fig. 2.49b. In 16 cases out of 19, the older animal had the active role and the younger the passive. D was only about 2 weeks older than M however. Thus females roughly fall into a hierarchy determined by age (as in males).

No hierarchy determined by age emerged from the interactions between females in play (Fig. 2.35), and in only 3 pairs of individuals out of 6 for which there are data for both play and aggression did those individuals which more often had the active role in play also have the active role in aggression. Thus the data do not indicate any strong resemblance between play and aggression in the relationships between individuals.

In all 8 pairs for which there are play data, both partners sometimes had the active role, and the larger animal had the active role in only 131 instances out of 209. If the order of Pb and L were reversed in Fig. 2.49b, there would only be one role reversal out of 19 instances of aggression. Thus, as in males, roles were more often reversed in play than in aggression ($p < 0.01$; Chi-square test).

(c) Male-female

In 47 out of 82 instances of aggression between males and females the larger animal had the active role, and in 76 instances out of 82 the male had the active role (Fig. 2.50). In 13 out of 19 pairs of individuals for which

there are data for both play and aggression, the individual which had the active role more often in play also had the active role in aggression. Thus there was some resemblance between play and aggression in individual relationships.

In all 25 pairs of animals for which there are play data, both partners sometimes had the active role (Fig. 2.36). In 31 out of 34 pairs of animals for which there are aggression data, only one of the pair was ever seen to have the active role. In the three pairs of animals in which roles were reversed, there was only one instance of role reversal in each case. Thus roles were again more often reversed in play than in aggression ($p < 0.001$; Chi square test).

2. Adult aggression

(a) Male-male

Role reversal was frequent in aggression between adult males (see below), but I have attempted to work out a linear hierarchy (Fig. 2.51) of the same type as those presented for play (Figs. 2.34 - 2.36) in which for any pair of animals, the individual higher on the list had the active role more often than the individual lower on the list.

The males could be ordered in such a way that, in 24 pairs out of 36 pairs of animals for which I have data, the animal higher in the hierarchy had the active role more often than the animal lower in the hierarchy. In four pairs the reverse was true, but there was only one instance of aggression recorded for each of the four pairs. In eight pairs both partners were active in aggression an equal number of times. Thus the relationships between

	LO	CT	SP	MD	SY	CS	NT	SK	HC	KT	MK	GF	Q
LO													
CT	1												
SP	1	1											
MD													
SY	3	1	1	1									
CS	1	4	1	1	1								
NT	2	4			6	2							
SK	1			1	2			1					
HC	1	2		1				1	1				
KT	1	4	1			1	2	2	1	1			
MK	3	2					2	2					
GF		1		2	1					1			
Q						1							

Fig. 2.51. Roles in aggression between individual adult male-male pairs. Numbers in boxes indicate the number of times each male had the active role during aggression with every other male. Numbers in the lower halves of boxes refer to animals in the column down the left side of the figure, numbers in the upper halves of the boxes refer to animals in the row. See text for further explanation.

	LO	CT	SP	MD	SY	CS	NT	SK	HC	KT	MK	GF	Q
LO													
CT	1												
SP	1	1											
MD													
SY	3	1	1	1									
CS		4		1	1								
NT	2	4			6	2							
SK	1			1				1					
HC	1	2		1				1	1				
KT	1	4	1			1	2	1	1				
MK	3	2					2						
GF		1					2			1			
Q						1							

Fig. 2.51. Roles in aggression between individual adult male-male pairs. Numbers in boxes indicate the number of times each male had the active role during aggression with every other male. Numbers in the lower halves of boxes refer to animals in the column down the left side of the figure, numbers in the upper halves of the boxes refer to animals in the row. See text for further explanation.

adult males in aggression could be described fairly adequately by a linear hierarchy of a similar type to those presented for play. In the adult male hierarchy however, the high-ranking animals were not necessarily the oldest (the relative ages of adult males could be estimated approximately by the extent to which their teeth were worn down).

(b) Female-female

Adult females could be ordered in such a way that higher-ranking animals nearly always had the active role in aggressive interactions with lower-ranking animals (Fig. 2.52). There were only 2 instances out of 190 in which roles were reversed with respect to the hierarchy.

3. Discussion

In juvenile-male-male and juvenile male-female interactions the relationships between individuals were similar in aggression and play with respect to their ranking in hierarchies. In juvenile female-female interactions this was not the case, hierarchies in aggression and play were different. In juvenile male-male and juvenile female-female interactions, role reversal was more frequent in play than in aggression with respect to the hierarchies which best described the data in each case (Table 2.13). In adult aggression, role reversal was frequent amongst adult males, but infrequent amongst adult females. (Rowell (1966) also reports that approach-retreat interactions amongst adult female baboons in a captive group showed more consistency of direction than in the group as a whole). Thus, with regard to the extent of role reversal, the way in which animals of both sexes interacted in play more

	PK	PY	A	U	ET	LZ	LK	GT	KG	LD	NY	JO	MY	KA
PK	/	12	9	4	4	2	2	3	2	1	3		3	
PY		/	9	3	14	1	4	3	2	2		3	2	2
A			/	7	1		2	5	3	4	2	1	2	2
U				/	1	2	1	1	1	1	1	3	1	1
ET					/	2	3	2	6	2	1	2	1	
LZ						/	1	1	2	1	1	1		1
LK							/	1	3			1	2	4
GT				1				/			1	1		
KG					1				/	1	2	3	1	1
LD										/				1
NY											/	1	1	2
JO												/		3
MY													/	
KA														/

Fig. 2.52. Roles in aggression between individual adult female-female pairs. Numbers indicate the number of times the animal in the column had the active role during aggression with the animal in the row.

closely resembled the way animals interacted to adult male aggression than the way they interacted in either adult female-female or juvenile male-male or juvenile female-female aggression.

This conclusion can be compared with the conclusions about the parts bitten in play (Table 2.13). In those age/sex classes of aggression or play in which roles were most predictable, i.e. there was little role reversal, the parts bitten were confined to the neck, back and tail, whereas in those classes in which roles were less predictable, the parts bitten included nearly all regions of the body.

Table 2.13

The extent of role reversal (the percentage of instances of aggression or play in which the animal that had the active role was the lower ranking in the hierarchy presented) compared with parts bitten in aggression and play and the percentage of movement patterns which were mutual, in six age/sex classes

	Percent role reversal	N	Parts bitten	Percent mutual movement patterns
Male-male play	37	480	All parts	66
Female-female play ¹	31	209	All parts	37
Adult male-male aggression	29	76	Nearly all parts	46
Juvenile male-male aggression	1	68	Neck, back & tail only	14
Juvenile female-female aggression ²	5	19	Neck, back & tail only	3
Adult female-female aggression	1	190	Neck, back & tail only	0

1 This figure is calculated from the hierarchy presented in Fig. 2.35b.

2 The data better fit a hierarchy different from the one presented in Fig. 2.49b in which the order of Pb and d is reversed. In such a hierarchy there would only be one reversal out of 19 (i.e. $\frac{1}{19}$ percent).

This parallel might be expected since, in those classes of interactions in which the relationship between partners is very predictable, the passive partner did not usually attempt to retaliate, but tended to present in submission to or run away from the active partner, which then often gave a 'punishing' bite to the neck, back or tail. Such bites seemed to be a ritualised reaffirmation of an existing relationship. In less predictable relationships, by definition, the passive partner more often retaliated, and instead of always presenting to or running away from the active partner, often turned and faced it, and so more biting to the anterior part of the body would be expected (see Plates XIII and XIV).

These observations are consistent with the conclusions about the movement patterns in play and aggression. The percentage of movement patterns which were mutual was higher in juvenile play and adult male aggression than in juvenile aggression and adult female aggression (see Figs. 2.44 and 2.45 and Table 2.13).

The close similarity in the nature of male interactions in play and adult aggression (and the dissimilarity between male play and juvenile male aggression) suggests that play could be important to males in the development of ways of interacting socially which they will later use in aggression towards their own sex. This idea will be elaborated later. There is no evidence that the individual relationships established in male play are maintained into adulthood. In male play (and in juvenile male aggression) roles were largely determined by age, but, as I have stated earlier,



Plate XIII. Aggressive sparring between two adult males (on left). The nearer male's erect tail implies extreme fear. Two other adult males look on, one of them threatening one of the fighting pair by raising the mane, flattening the ears and showing the white eyelids by raising the brows.



Plate XIV. Aggression between two adult females. The female on the right bites the tail of the lower ranking female on the left, and threatens her by showing the white eyelids. The aggressee crouches in submission and her facial expression suggests extreme fear (mouth open and lips withdrawn to expose teeth and gums).

this was not the case in adult males.

In females, play differed from adult female aggression in the extent of role reversal (and more resembled adult male aggression). Thus there is no suggestion that play might be important to females in the development of ways of interacting which they will later use as adults in aggression towards their own sex. Unlike the case in males however, the rank order in female play differed from the rank order in juvenile female aggression (which was determined largely by age). The adult female hierarchy was also not determined by age (as in adult males, relative ages could be estimated by the condition of teeth). Thus it is conceivable that individual relationships between females are established in play and are maintained in adulthood. There was no correlation between the relative ranks of juvenile females in play and the relative ranks of their mothers in aggression (Table 2.14) as has been found for macaques (e.g. Koford, 1963; Marsden, 1968; Sade, 1967).

Table 2.14

Comparison of the rank order of female juveniles determined by age, interactions in play and aggression and the rank of their mothers

	<u>Age</u>		<u>Play</u>	<u>Aggression</u>	<u>Mothers</u>
Oldest	Gd	Highest ranking	M	Gd	D
	D		Pb	D	Pb
	M		Gd	M	M
	L		D	Pb	L
Youngest	Pb	Lowest ranking	L	L	Gd

I will now discuss more fully the possible relevance of the nature of relationships in play to adult aggressive relationships in the two sexes.

Males

Relationships between juveniles up to about $3\frac{1}{2}$ years old in aggression were very predictable and determined largely by the size (age) of the participants. Relationships between adults were less predictable and not determined by age. There must therefore have been a stage between $3\frac{1}{2}$ years and adulthood when the nature of male-male aggressive interactions changed, relationships becoming more like those in play. My data do not cover this age range, and further observations are required to determine exactly how aggressive and play patterns develop during this time. The frequent reversal of roles in adult male aggression indicates that the relationship between any two animals was somewhat flexible. Although one of the pair may have more often been the aggressor in an aggressive encounter, roles could change if, for example, a third animal supported one of the participants. As supportive relationships changed (for example when a new male joined from another troop, as frequently happened), so then would relationships between individuals in aggression change. Social rank also varied with age: it was generally males which had reached full maturity which were at the top of the aggression hierarchy; older males gradually lost their position. By reversing roles, males were able to reassess the strength and fighting ability of their partner, and take account of the support given by other males. Flexibility in roles in aggressive interactions was thus a reflection of the continual readjustment which took place in adult male social relations. Male play thus offered experience and

practice at types of social interaction which are of great importance in adult life.

Females

In females, as explained above, it is possible that the social relationships of adults were determined during juvenile play. By the age at which females reached sexual maturity at 4 - 5 years old (and perhaps before) a female's social position was established, and females (unlike males) did not appear to change rank as they became older. Aggressive interactions between adult females were generally dyadic, and it was not usual for a third female to be enlisted in support of one of the participants. Troop changes by females were never observed (though one example of a troop change by an adult female and her yearling daughter is known from another Gombe troop (Leanne Nash, personal communication)). Thus adult female social relations were characterised by their relative stability and inflexibility; females accepted their status despite the fact that some large females were lower ranking than smaller, weaker-looking ones. From this point one could now argue the other way and say that, because there was little role reversal in female aggression, aggressive behaviour did not give much opportunity for the establishment of new social relationships. Thus it is probable that female social relations were established largely through play, in which role reversal was common, rather than through aggression. Rowell (1966, b) has pointed out however that the adult female aggression hierarchy in captive baboons is not completely static, and changes in rank may originate in friendly behaviour such as

grooming, in which the direction of interactions is less consistent than in agonistic behaviour.

The frequent occurrence of role reversal in primate play has been emphasised by Bertrand (1969), Jay Dolhinow and Bishop (1970) and Loizos (1967), and several authors have claimed that primate play is important in establishing social relationships between individuals, for example in baboons (Hall, 1962, b), rhesus monkeys (Harlow, 1965) and langurs (Jay Dolhinow and Bishop (1970)). No previous studies have provided evidence however as to whether relationships established in play persist into adulthood and whether play is equally important in this respect in the two sexes.

Studies of aggressive behaviour in non-primate species, for example feral goats, also indicate that interactions involving role reversal are characteristic of behaviour in which rank is being established (Shank, 1972). One class of agonistic behaviour ('rushing') is employed when a goat asserts its rank over another lower ranking (smaller) animal as it takes precedence over it in access to a desired object or place. The roles of individuals in rushing are very predictable. Another sort of agonistic pattern ('clashing') involves actual physical contact, and appears to be used solely in the determination of rank. Most clashing occurs between individuals close together in the rush hierarchy, but roles in clashing are frequently reversed and unpredictable.

10. The Development of Sexual Behaviour

- A. The frequency of sexual behaviour.

- B. The movement patterns in sexual behaviour.
 - 1. Juvenile-juvenile and juvenile-adult female interactions.
 - 2. Juvenile male-adult female and adult male-adult female interactions.
 - 3. Discussion.

- C. Relationships in sexual behaviour.
 - 1. The sex of partners.
 - 2. Relationships between individuals.
 - 3. Discussion.

10. The development of sexual behaviour

Behaviour was classified as sexual when an animal stood with its feet on the ground or clasped to the legs of its partner and with its hands on the back or haunches of its partner. Sexual behaviour patterns sometimes also included thrusting, intromission and orgasm.

As explained in the introduction, there was no criterion by which sexual behaviour could be divided into sexual play and sex proper on the basis of the movement patterns involved. Sexual behaviour patterns were frequently interspersed with aggressive play patterns. For instance a mount might be both preceded and succeeded by rough-and-tumble in one bout of play. Thus there was good reason to consider some sexual behaviour as play. However, mounts were often separated in time from rough-and-tumble play and such mounts showed no consistent differences from those which were interspersed with rough-and-tumble. For this reason I recorded all sexual behaviour regardless of whether it occurred within a play sequence.

A. The frequency of sexual behaviour

Presented in Fig. 2.53 are the age changes in the absolute frequency of sexual movement patterns (including both active and passive roles and sexual behaviour involving all classes of partners). The age changes in the frequency of sexual behaviour for both sexes were similar to the age changes in the amount of time spent playing excluding sexual play (see Section 1, B), Fig. 2.54.

There was a significant correlation between the two figures (Figs. 2.53 and 2.54) in the rank order of the different

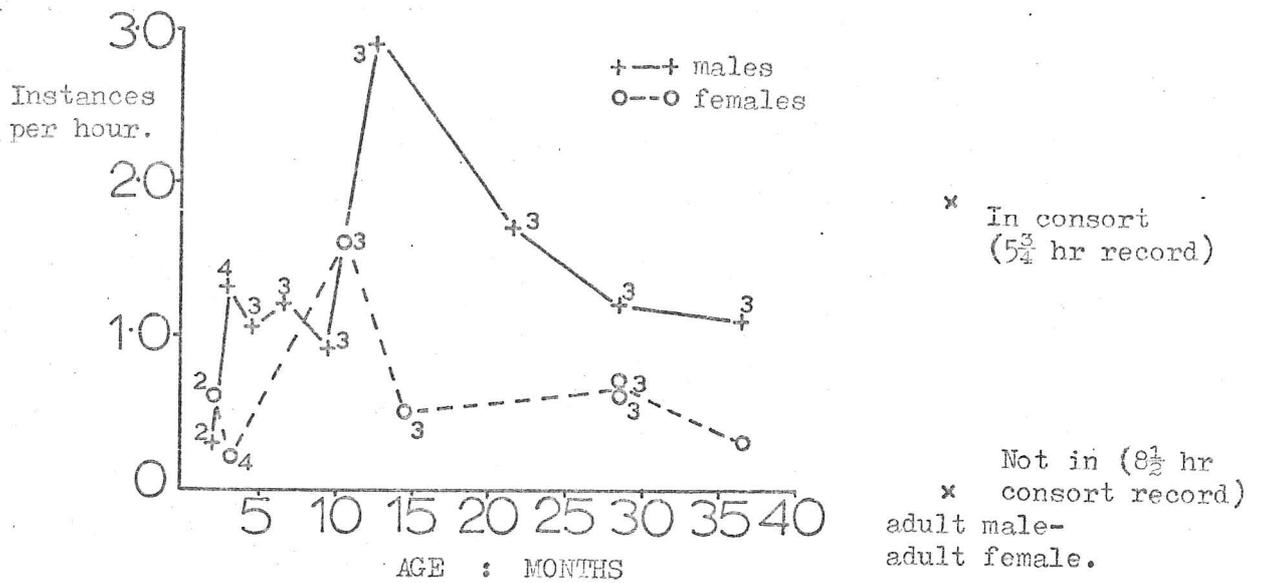


Fig. 2.53. Age changes in the frequency of sexual behaviour, including both active and passive roles. Each point represents one individual. Animals were watched for between 12 and 33 $\frac{1}{2}$ hours over a 2-4 month period. Numbers beside points indicate the length in months of the recording period for each individual. The mean age of each animal during the recording period is plotted.

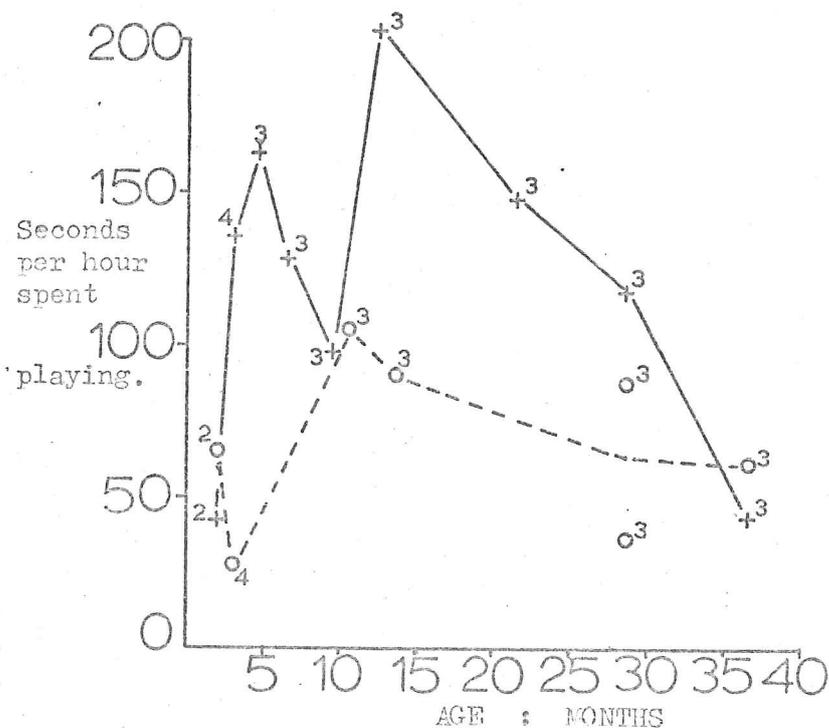


Fig. 2.54. Seconds per hour spent playing, excluding sexual play. Legends as for Fig. 2.53.

points for males ($r_s = 0.72$; $p < 0.01$; $N = 9$), but the correlation for females was not significant ($r_s = 0.77$; $p > 0.05$; $N = 6$). Also, the frequency of sexual behaviour in males relative to that in females was similar to the relative amount of time spent in play (other than sexual play) by the two sexes (Figs. 2.53 and 2.54).

This conclusion implies that sexual behaviour and play other than sexual play share a common causal basis. The common causal factors may not be confined to sexual behaviour and play; they could for instance influence the general level of activity of the animal and thus the frequency of all social interactions.

I shall now consider first the movement patterns and then the relationships between individuals in sexual behaviour and discuss whether the data can throw any light on the importance of incipient sexual behaviour in the development of sexual movement patterns and in the development of individual relationships.

B. The movement patterns in sexual behaviour

There are not enough data to be able to plot age changes in the frequency of movement patterns in sexual behaviour between juveniles¹ because the movement patterns to be discussed were rather infrequent. Instead I shall lump all the data for juvenile-juvenile interactions and compare their sexual movement patterns with those in sexual behaviour between juvenile males and adult females.

1 The term 'juvenile' is used loosely for convenience in this section to include all non-adult animals.

Table 2.15

The percentage of mounts in which four classes of movement pattern occurred
Numbers in brackets represent 'N'

Percent of mounts in which	Juvenile-Juvenile				Juv. male-Ad. female
	Male-male	Male-Female	Female-Male	Female-Female	
One or two feet were clasped	30(64)	26(74)	0(11)	9(11)	94(283)
Thrusting occurred	16(64)	18(74)	0(11)	0(11)	93(267)
Intromission occurred	0(64)	0(74)	0(11)	0(11)	68(104)
There was a pause after thrusting (orgasm)	0(64)	0(74)	0(11)	0(11)	21(87)

Secondly, I shall examine the age changes in the frequency of sexual movement patterns in juvenile male-adult female interactions and compare these with adult male-adult female interactions.

1. Juvenile-juvenile and juvenile-adult female interactions

In the normal male mounting pattern the male rests his hands on the female's hindquarters and clasps her ankles with his feet (Plate XV). Rhythmic pelvic thrusting occurs followed by a short pause during ejaculation.

Presented in Table 2.15 are the percentages of mounts in which four categories of sexual movement pattern (listed below) were observed in five classes of partnership. (The

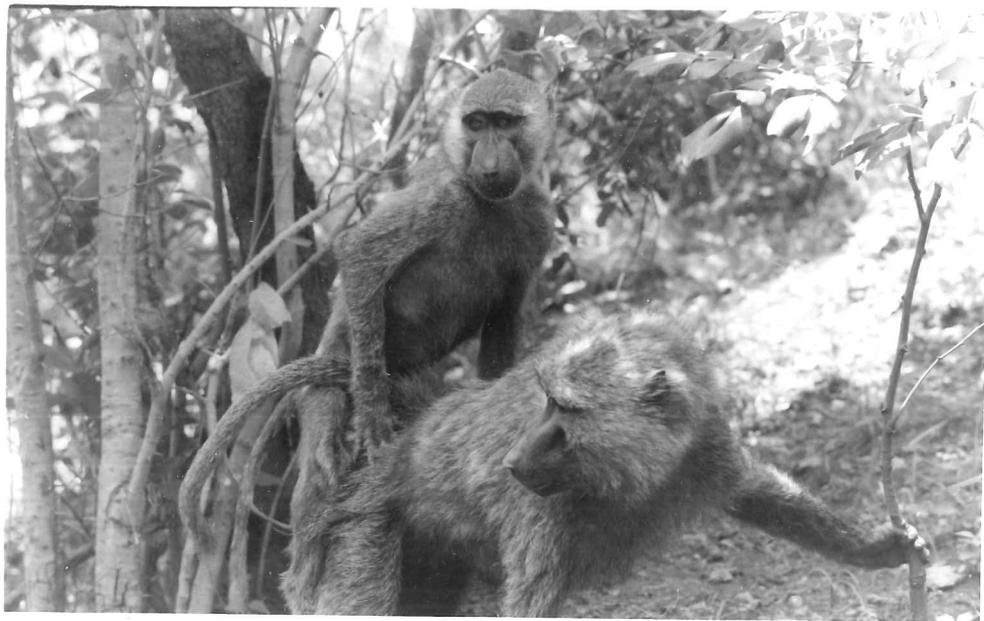


Plate XV. A two year old male mounting a young adult oestrous female. The male shows the normal adult mounting posture.



Plate XVI. A game of 'king-of-the-castle' between two eighteen month old males.

term 'mount' is used to mean any instance of sexual behaviour in any context.)

Description of movement patterns:

1. Leg clasping: usually the ankles but sometimes other parts of the leg are clasped by the feet of the mounter.
2. Thrusting: rhythmic pelvic movements.
3. Intromission: insertion of the penis.
4. Orgasm: a short pause (3-5 seconds) following thrusting was taken to be an indication of orgasm; accompanied by ejaculation in older animals.

With the exception of one instance in which a female juvenile clasped her partner's leg with one foot, none of the patterns of sexual behaviour presented in Table 2.15 were displayed by female juveniles. Juvenile males showed leg clasping and thrusting but not intromission or orgasm when mounting other juveniles of either sex. The sex of the partner had little effect on the amount of leg clasping and thrusting that occurred. When mounting adult females however, juvenile males did achieve intromission and orgasm, and showed foot clasping and thrusting on a higher proportion of occasions than when mounting either juvenile males or juvenile females ($p < 0.01$ in all cases; Chi square test).

2. Juvenile male-adult female and adult male-adult female interactions

Adult females commonly presented to newborn infants before handling or grooming them. Presenting by such 'aunts' often seemed to be oriented towards the infant rather than the mother, and from about four weeks onwards male infants sometimes responded by sniffing or manipulating

the female's anogenital region. In this way infant males gained some early sexual experience, but they did not regularly attempt to mount adult females until they were 6 months old. Infants may however have gained some experience at mounting adult females before 6 months as they climbed onto their mother's back to ride (Plate VI), but I did not include boarding the mother in this analysis.

Leg clasping

The data for the age changes in the frequency of leg clasping are not very meaningful owing to the disorientation of mounts by the youngest animals (see below) and the resulting difficulty in deciding whether or not clasping had occurred, so I will not discuss them further.

Thrusting

Thrusting did not occur regularly until six months of age and at first thrusts were arrhythmic and few in number. The mean number of thrusts per mount increased greatly between ten and fifteen months of age (Fig. 2.55). This was partly because more mounts included thrusting (there was thrusting in 50 percent of mounts in animals less than ten months old and thrusting in 91 percent of mounts in animals between 11 and 20 months old ($p < 0.01$; Fig. 2.56), and partly because mounts involving a large number of thrusts became more numerous (Fig. 2.56 and 2.59c). There was little change in the mean number of thrusts after 15 months of age, the number fluctuating around 8 thrusts per mount (Fig. 2.55).

The frequency distribution of the number of thrusts by adult males was approximately normal with a mode of 7; the

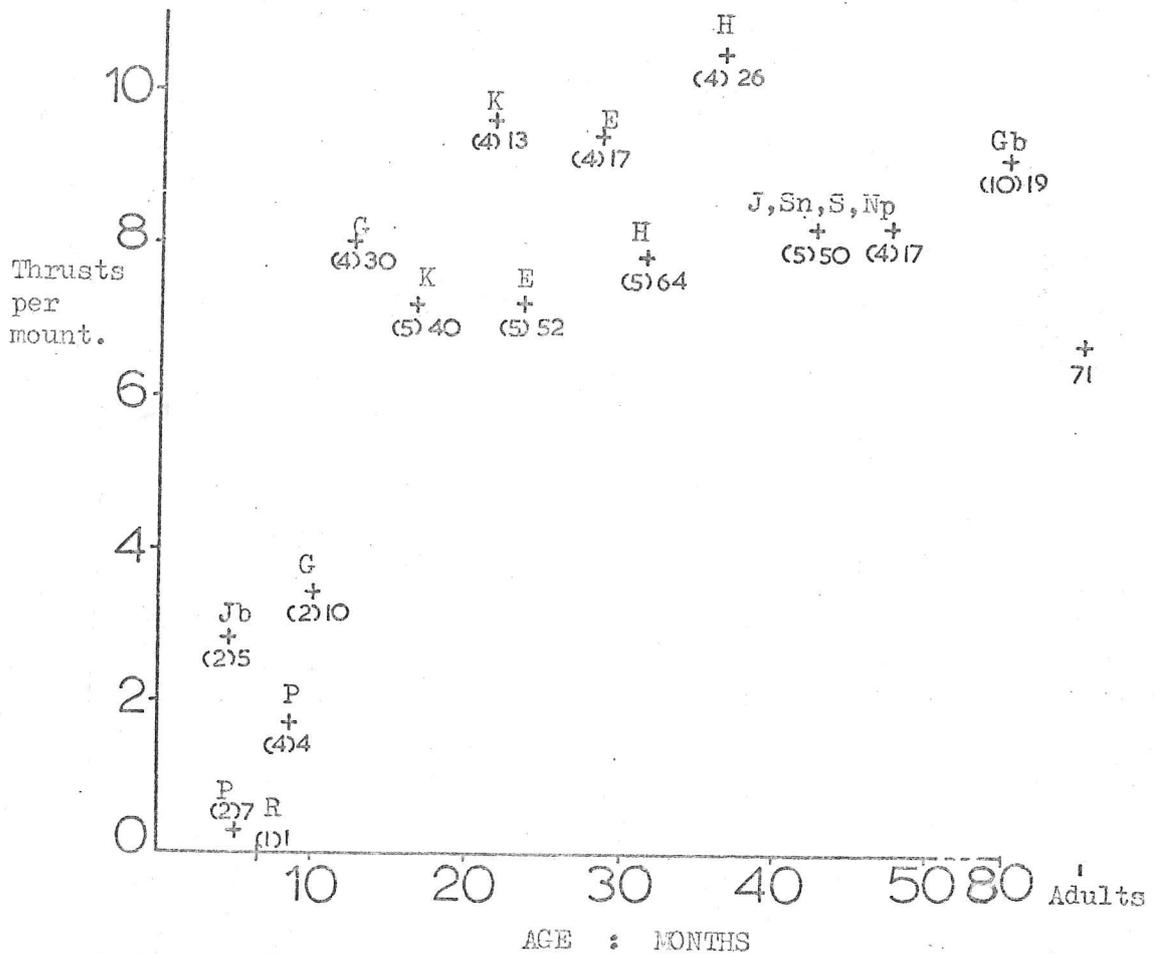


Fig. 2.55. Age changes in the mean number of thrusts per mount. Data refer to interactions between males and adult females only. Letters indicate the names of the males to which each point refers. Two points were obtained for most males by taking the earlier and later halves of the recording period separately. The length, in months, of the recording period from which each point is derived is indicated by the numbers in brackets. Other numbers indicate 'n', i.e. the number of mounts observed. For two of the points, data for four males (J, Sn, S, Np), all of a similar age, were pooled.

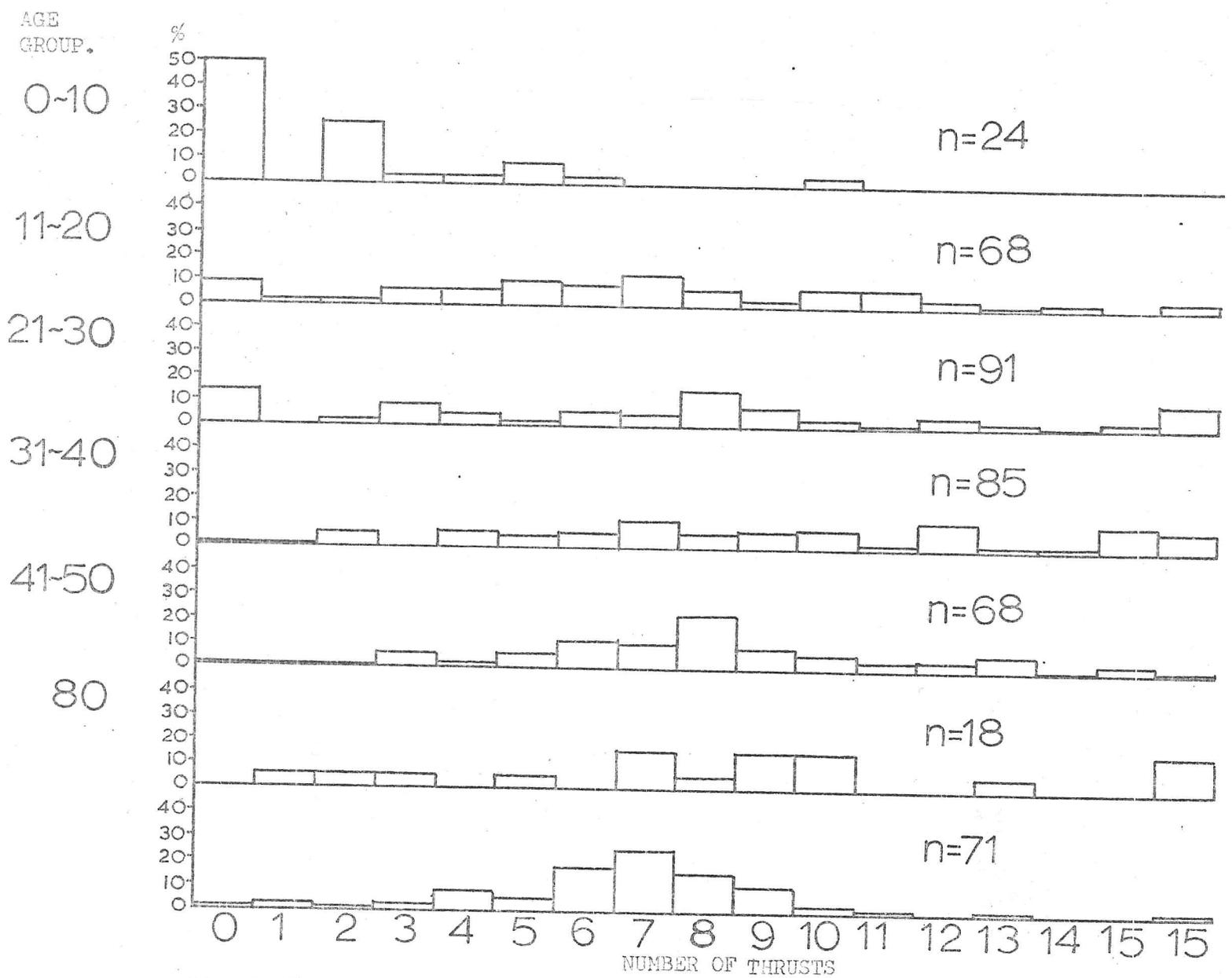


Fig. 2.56. The frequency distribution of the number of thrusts per mount in different age groups.

number of thrusts per mount showed less variability than in juveniles and there were fewer mounts with a large number of thrusts than in juveniles (Fig. 2.56). However, there was no clear trend towards less variability with age amongst the juveniles. The difference between the two groups may have been due to the adult male's greater access to oestrous females (the sexual swellings of oestrous females were probably a more effective stimulus and may have influenced the number of thrusts by causing ejaculation to occur sooner).

Intromission (Fig. 2.57)

Intromission was not achieved until after ten months of age when there was a sudden increase in the incidence of intromission to about 65 percent of mounts. From about 15 months onwards the percentage of mounts in which intromission occurred fluctuated between 50 and 94 percent. The figure for adult males was 88 percent.

One reason why intromission did not occur before 10 months was that 71 percent of mounts before ten months of age were disoriented (Fig. 2.59, a). In these early mounts infants seemed to orient themselves as if they were boarding the mother to ride, climbing up one leg of the partner, and thrusts, if they occurred, were often directed to the back, the side of the rump or leg. Sexual patterns were sometimes interrupted by grooming or by manipulating and sniffing the female's sexual swelling. The following field anecdote concerning a nine month old male infant mounting a young oestrous female illustrates these two points.

'George clings to the side of Lydia's hindquarters and makes two thrusts, penis erect. As he does so he grooms

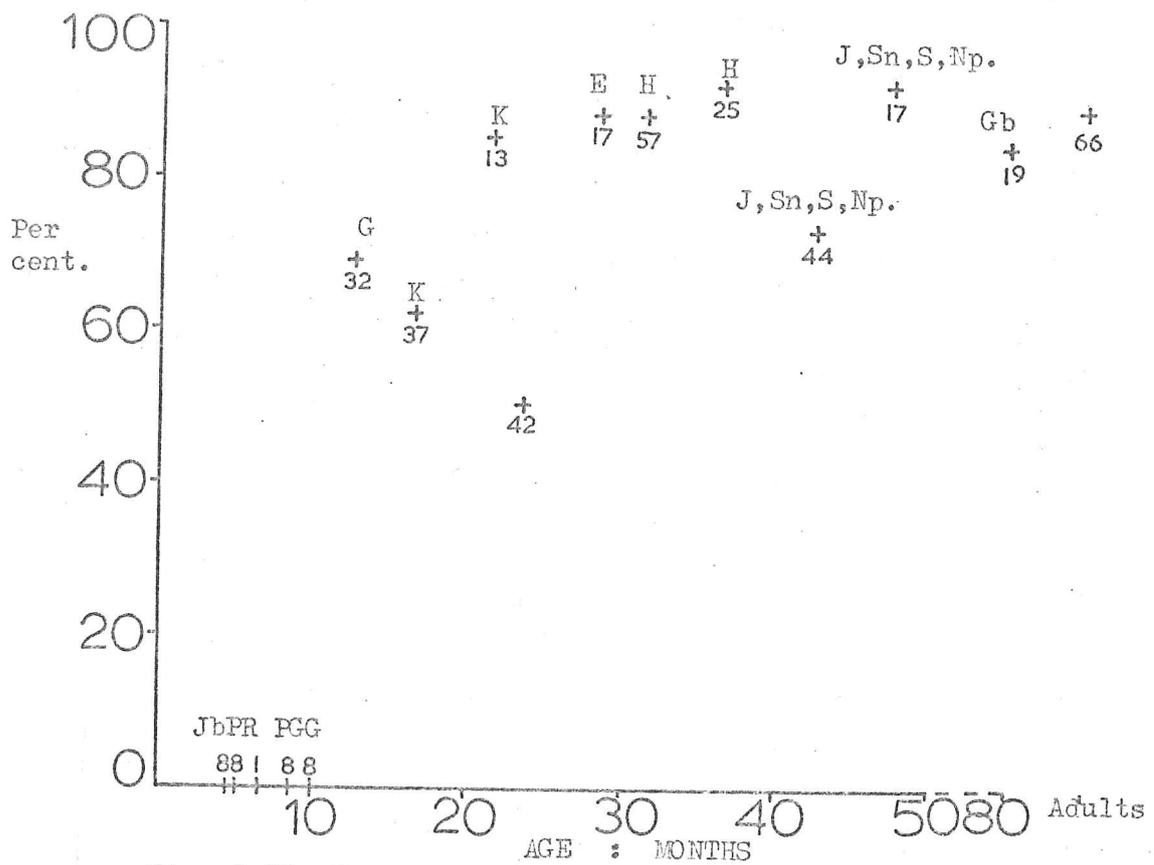


Fig. 2.57. The percentage of mounts in which intromission occurred. Numbers beside points indicate 'n', i.e. the number of mounts observed for which it was possible to see whether or not intromission occurred. Recording period and other legends as for Fig. 2.55.

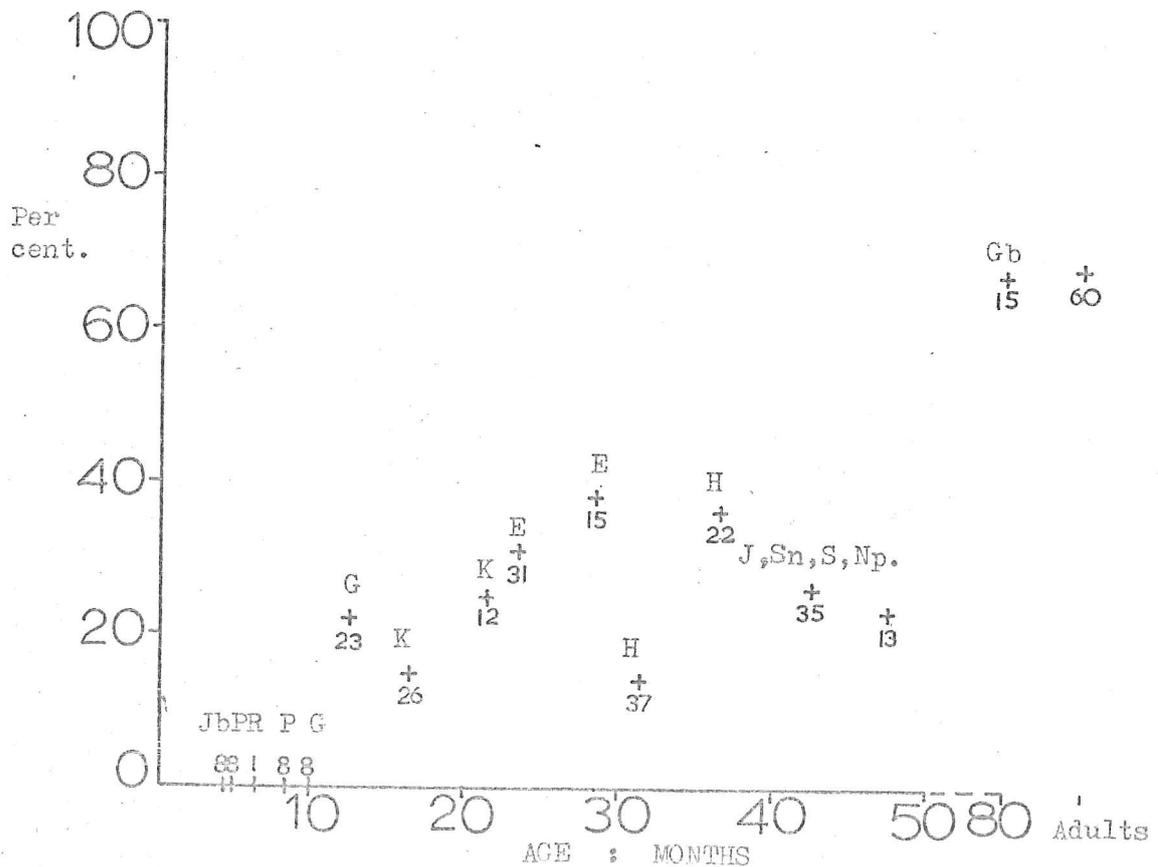


Fig. 2.58. The percent of mounts in which there was a pause at the end of the mount (orgasm). Explanations as for Figs. 2.55 and 2.57.

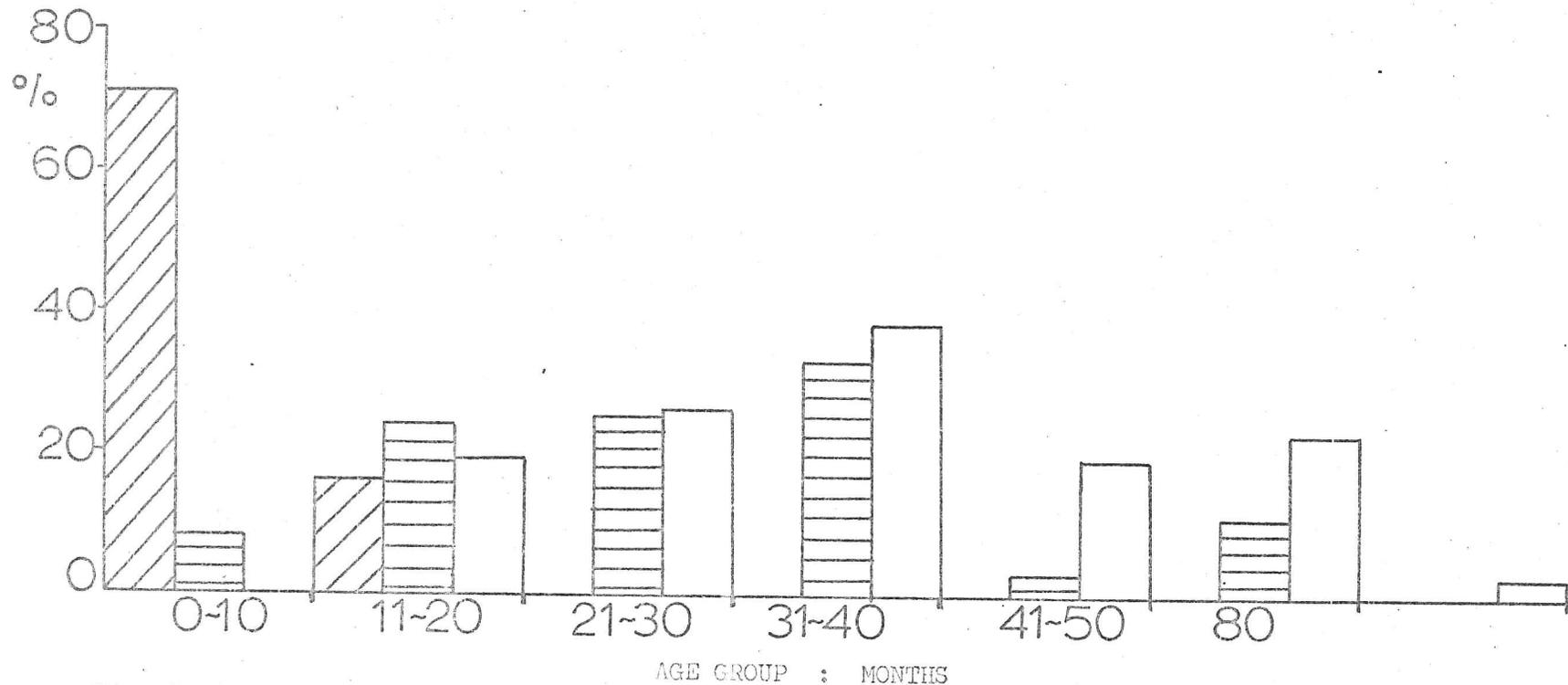


Fig. 2.59. Age changes in three characteristics of mounting behaviour by males of adult females. Left hand blocks (cross-hatched). The percent of mounts in which the mount was disoriented ie. genitalia of partners not in approximate apposition. Middle blocks (horizontal bars). The percent of mounts in which the male lay flat along the female's back whilst thrusting. Right hand blocks (no shading). The percent of mounts in which there were less than ten thrusts (data from Fig. 2.56.)

her with hands and mouth. He then moves to the other side of her rump and thrusts again. He then sits astride her back facing backwards and thrusts some more, afterwards grooming around the top of her swelling still with penis erect.'

Even when juvenile males were oriented properly they sometimes lay flat along the female's back while continuing to thrust, instead of supporting the upper part of their bodies with their arms. This was a particularly common feature of long mounts, and was probably a sign of fatigue; it was not seen in adult males (Fig. 2.59, b and c).

Orgasm (Fig. 2.8)

Orgasm was first observed between 10 and 15 months of age and thereafter it occurred in approximately 25% of mounts and stayed at this level until the sub-adult stage (80 months). In the one sub-adult watched and in adult males orgasm occurred in 68% of mounts. The higher incidence of orgasm in these older animals may have been partly due to their greater access to oestrous females.

3. Discussion

It is clear that the biggest developments in the integration of male sexual behaviour patterns took place between 10 and 15 months of age. At this stage animals seemed to adopt rather suddenly the appropriate orientation to the female when mounting; thrusting increased greatly and intromission and orgasm were first achieved. This is also the age at which male sexual behaviour (and aggressive play) was most frequent (Figs. 2.53 and 2.54). Thus the data are in harmony with the conclusion that

juvenile male incipient sexual behaviour is important in bringing about the integration of male sexual behaviour patterns.

There is little previous information concerning the development of sexual motor patterns in baboons. Athoney (1968) suggests that both mounting behaviour and embracing are derived from the grasping reflex of the infant, but he presents no quantitative evidence about the way the motor patterns develop to support his hypothesis.

Zuckerman (1932) states of male baboons that "all the manifestations of adult sexual life have developed ... when the baboon is about 9 months old", which is in approximate agreement with my data, which show that the full mounting pattern with foot clasping, thrusting and intromission did not appear until after 10 months of age.

Bolwig (1959) comes to similar conclusions about chacma baboons (Papio ursinus). Thrusting movements with an erect penis began at $5\frac{1}{2}$ months and 'copulation' was observed at 9 months. Chacma baboons, unlike olive baboons, make a series of mounts before ejaculation (Hall and DeVore, 1965: the same is true for Hamadryas baboons and rhesus monkeys, Kummer, 1963; Carpenter, 1942, b). Hall (1962, b) found that the mean number of thrusts per mount for all classes of chacma males was 9.78. This compares with my figure of 6.7 for adult males and about 8.0 for juveniles (Fig. 2.56). It would appear that not only do chacma baboons need to mount more than once to achieve ejaculation but they also tend to thrust more often per mount.

Better information about the development of sexual

behaviour comes from studies of rhesus monkeys (Macaca mulatta) in which the mounting pattern is very similar (with the exception of the number of mounts needed to reach ejaculation) to that in baboons. Harlow (1962) found that male rhesus monkeys up to a year old showed inappropriate sexual posturing, but during the year the proportion of mounts in which the correct orientation to the partner was achieved steadily increased, reaching about 80% at 9 months of age. At one year, males were showing most of the characteristics of adult male mounts, though not the complete pattern with ejaculation. These conclusions are similar to my own; between 11 and 20 months of age male baboons showed the correct orientation in 84% of mounts towards adult females and all the characteristics of adult male mounts appeared by 13 months of age. Rhesus monkeys reared alone in wire cages during the first year of life (but in visual and auditory contact with other monkeys) subsequently hardly ever showed normal sexual behaviour patterns. Mounts remained disoriented even with normal and experienced female partners. Thus there is very good evidence that in male rhesus monkeys social experience during the first year is vital for the development of normal sexual behaviour. There is however no direct evidence that it is specifically the experience of mounting which is important; experience of other types of social interaction may be adequate. In that the development of baboon sexual behaviour patterns is so similar to that in rhesus monkeys it seems likely that the same social deprivation experiments with baboons would give similar results.

There is evidence that the process of development of sexual behaviour in some other primate species resembles that in rhesus monkeys and baboons. Hanby (1972) describes the gradual development of mounting behaviour in Japanese monkeys (Macaca fuscata). Mounts by young males often occurred whilst boarding the mother to ride and were frequently disoriented but by 2 months of age some males oriented themselves to the rear of the partner. By 4 months foot claspings was attempted, and claspings steadily became more common, as did thrusting. By $1\frac{1}{2}$ years of age males closely approached the frequencies and proportions of adult males in mount postures and thrusting.

Goodall (1968) describes the development of sexual behaviour in two free-living male chimpanzees. In their earliest attempts at mounting, at 9 months of age, they did not achieve intromission, and thrusting was erratic. In addition to mounting oestrous females, sexual patterns appeared in play with peers, and by one year of age their "sexual behaviour was almost fully developed".

The development of sexual behaviour in chimpanzees was studied experimentally by Nissen (1954). Chimps separated from each other just before puberty were paired with older, experienced animals of the opposite sex well after puberty, but although components of sexual behaviour appeared, the complete pattern did not occur.

In monkeys as well as chimps important changes seem to occur around puberty as well as during the first year. My data show that there was a great increase in the incidence of pausing following a mount (orgasm) between 50 and 80

months of age (i.e. after puberty which is at about 60 months) and mounts with many thrusts became less common. Presumably ejaculation occurred much more regularly after puberty, though juveniles occasionally ejaculated from about $2\frac{1}{2}$ years old. Harlow (1962) states that mounts by rhesus monkeys are characterised by incompleteness between 2 and 4 years old and Japanese monkeys did not ejaculate until $4\frac{1}{2}$ years (Hanby, 1972).

Similar conclusions about the importance of both early and late social experience have been obtained for mammals other than primates. Social experience at an early age (before 25 days old) affects the later performance of sexual behaviour in guinea-pigs (Young, 1961), ^{but} in cats, experience of sexual behaviour in the hormonal conditions pertaining at puberty is necessary for the development of the complete sexual pattern (Rosenblatt and Aronson, 1958, a).

Imitation of other troop members as well as direct experience of sexual behaviour may also be important in the development of sexual behaviour patterns.

Rowell (1967, b) describes the behaviour of young wild baboon males which "often danced round a copulating pair making repeated coughs and touching them" and males less than a year old, after watching a mount, sometimes approached the same female and mounted her themselves. Rowell had the impression that imitation learning was taking place. The same behaviour occurred in the Gombe troop. Copulating pairs were often harassed by smaller males who were quick to take the opportunity to threaten a larger male whilst he was temporarily incapacitated during a mount,

and small infants did occasionally follow up with a mount themselves, but it is difficult to assess the importance of imitation from such observations, and experimentation is required. It is however known that imitation is important in Japanese monkeys in the acquisition of new feeding patterns (Tsumori, 1967) and in chimpanzees in learning to 'fish' for termites (Van Lawick-Goodall, 1968). Baboons did imitate one another in play (see below) and the possible role of imitation in the development of primate sexual behaviour should not be overlooked.

In conclusion, it seems likely that in baboons as in several other primate and non-primate species, social experience and probably more specifically experience of attempts at mounting at particular stages of development, is essential for the integration and orientation of the components of sexual behaviour into a functional whole. Imitation learning may also play a part.

C. Relationships in sexual behaviour

In this section I shall discuss data concerning (a) the sex of partners, and (b) relationships between individuals in sexual behaviour, to see if the data can throw any further light on the function of immature sexual behaviour.

(a) The sex of partners, with special reference to male-male mounting (Fig. 2.60)

As males became older, the percentage of mounts in which the partner was a male decreased from about 60% in animals less than 5 months old to below 10% in animals more than 25 months old ($r_s = -0.93$; $p < 0.01$; $N = 9$). This

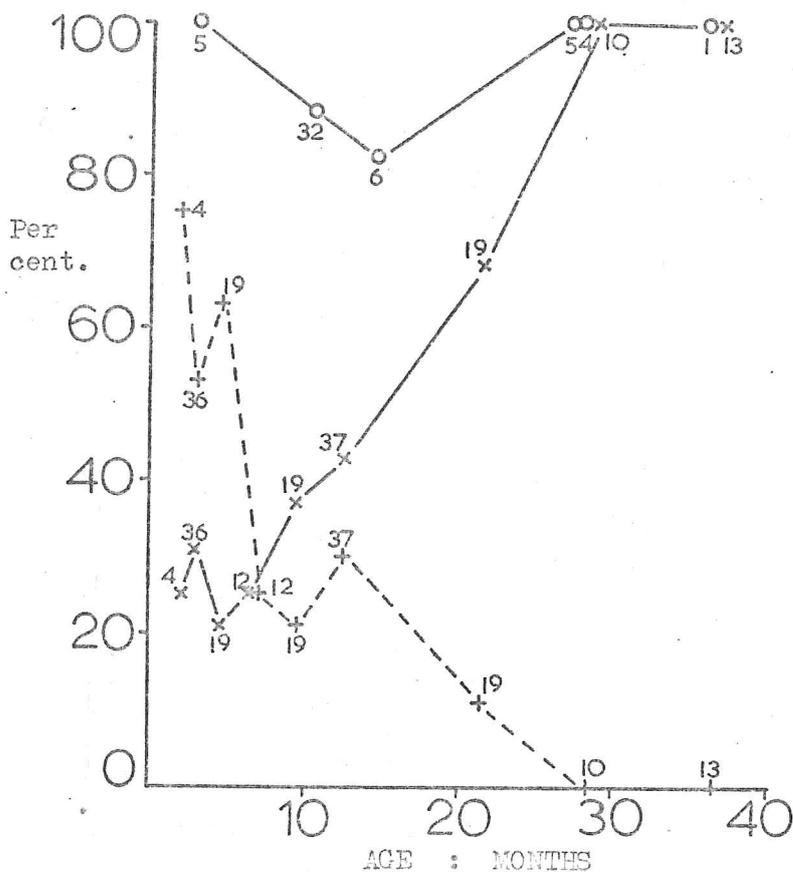


Fig. 2.60. Age changes in mounting partners.

x---x The percent of mounts by juvenile males in which the partner was an adult female.

+---+ The percent of mounts by juvenile males in which the partner was a male.

o---o The percent of mounts on juvenile females which were by males.

Numbers beside points represent 'n'. Each point refers to a different individual. Recording period for each animal is the same as for Fig. 2.53, and the mean age during the recording period is plotted.

was largely because juvenile males increasingly mounted adult females (Fig. 2.60; $r_s = 0.89$; $p < 0.01$; $N = 9$) and was not due to any consistent change in the extent to which juvenile females were mounted (no fig.). Most of the increase in the choice of adult females as partners occurred after 10 months of age, which is the age at which animals became correctly oriented and achieved intromission and orgasm.

Although males increasingly selected adult females with age, male-male mounts persisted into adulthood (although they were absent in the two oldest animals in the small sample in Fig. 2.60). Frequently mounts between adult males were accompanied by genital handling and a submissive facial expression (the 'fear grin') and appeared to be gestures of appeasement. Mounting with genital handling first appeared in animals about 5 years old and at this age often preceded bouts of sparring play. Males became more tense about each other with age and, although mounting continued, it became less frequently followed by play and more frequently followed by aggression. However, even adult males sometimes gave a gentle (play) bite to the neck following a mount. They were not seen to do this to females. Thus it seems possible that juvenile male-male sexual behaviour is important for the development of appeasement gestures (see below).

Females showed no consistent age changes in the sex of the partner (Fig. 2.60), but at all ages, over 80 percent of mounts were by males, nearly all of these males being juveniles. Although up to 20 percent of juvenile female

mountings were by other juvenile females, mounts were never observed between adult females. However, as described in the previous section, juvenile females did not show the full male mounting pattern with foot claspings and thrusting. Those patterns called mounts amongst juvenile females may not therefore be qualitatively different from aggressive play patterns.

When juvenile females had the active role they mounted males and females about equally often.

(b) Relationships between individuals (Fig. 2.61)

Males

In only 9 out of 15 pairs of juvenile males did the partner which more often had the active role in mounting also more often have the active role in non-mutual ('mauling') aggressive play, and in only 3 out of 6 cases for which there are data did the animal which more often had the active role in mounting also more often have the active role in aggression. Thus there is no clear evidence that relationships in sexual behaviour are the same as those in aggressive play and aggression. In adult males also, in only 9 out of 15 cases was there a correlation between roles in male-male mounting and roles in aggression. Thus it is difficult to assess the significance of roles in male-male mounting from the data available.

Females

In 3 out of 5 cases for which there are data, the animal which more often had the active role in mounting also more often had the active role in non-mutual aggressive play; for mounting and aggression proper the equivalent

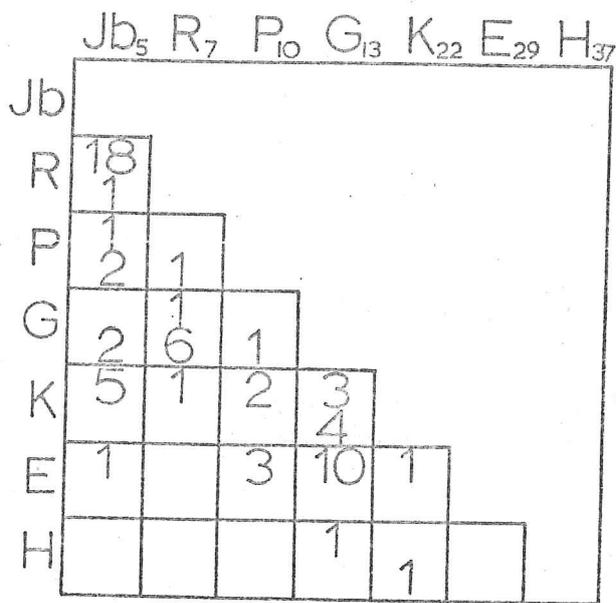


Fig. 2.61 a. Roles in mounting between individual juvenile male-male pairs. Numbers in boxes indicate the number of times each animal had the active role in mounting with every other animal. Numbers in lower halves of boxes refer to animals in the column down the left side of the figure, and numbers in upper halves of boxes to animals in the row. Numbers beside names in the row indicate the mean age of each animal during the three month recording period.

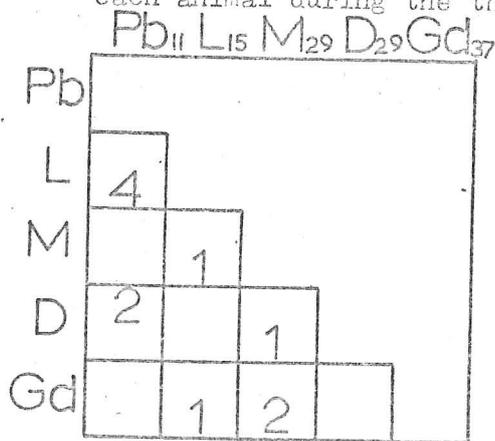


Fig. 2.61 b. Roles in mounting between individual juvenile female-female pairs. Legends as for Fig. 2.61 a.

figure is 4 out of 6 cases. Thus there is again no clear evidence that roles in sexual behaviour are the same as those in aggression. It should be remembered that no clear distinction could be made between juvenile female sexual patterns and aggressive play.

Discussion

Rowell (1967, b) found that, in wild baboons in Uganda all males (ranging in age from small juveniles to adults) mounted other males less and adult females more than would be expected on the basis of random mounting. This is in agreement with my results; in the Gombe troop 31% of the animals were adult females, and males over one year old (i.e. small juveniles to adults) mounted adult females in 40 to 100% of mounts.

In Japanese monkeys, males mounted males and females about equally up to 14 months of age and then started to show a preference for females (Hanby, 1972). Goy (cited Hanby) notes that rhesus monkey males raised in a peer group showed no clear preference for females until 4 years of age, but once puberty was reached males were able to achieve intromission with cycling females which became available at this time, and mounting with females increased greatly. This observation is in harmony with my own in that selection of females increased greatly once intromission was achieved, despite the fact that baboons and these rhesus achieved intromission at widely differing ages.

As stated above, my results indicate that roles in male-male and female-female mounting did not always reflect roles in aggression in either adult or young baboons, and

thus there was no clear evidence that relationships between pairs of individuals were determined during mounting behaviour between young animals. Role reversal occurred in both juvenile and adult male-male mounting but not in mounting between juvenile females (adult female-female mounting was not observed).

Qualitative observations suggest that roles in male-male mounting between any pair of individuals were determined by the social context; mounting behaviour had different meanings in different contexts and this might explain the lack of correlation between roles in mounting and roles in aggression.

1. Subordinate males presented to 'dominant' males (i.e. males which usually had the active role with them in aggression) and the dominant animal often responded by mounting. One would expect roles in mounting in this context to be related to roles in aggression.
2. During greeting/appeasement gestures (described above). These usually occurred between adult or adolescent males of similar status and it was often the subordinate male that mounted. In this way the subordinate animal attained a position such that the mountee could not attack him.
3. During enlisting behaviour. Observations suggest that subordinates sometimes mounted a dominant animal when they wished to enlist his support against an aggressor. Such mounting behaviour often occurred when both animals had previously been engaged in threatening a third (perhaps in consort with an oestrous female) and usually they both continued to threaten the other animal during the mount.

Similar interactions involving a mounting pair and a third animal occurred in juvenile play, and it seems possible that enlisting relationships are established partly through juvenile mounting behaviour. Such 'tripartite' relationships (though not involving mounting) have been described in Hamadryas baboons ('protected threat') by Kummer (1967) and in olive baboons at Gombe by Ransom and Ransom (1971). The Ransoms suggest that interactions between an infant and two adult males may serve as a prototype for the supportive relationships the infant will later develop with its peers.

Many authors have held that male-male mounting is an indication of dominance, i.e. that roles in mounting always reflect those in aggression. Zuckerman's (1932) view is that "mounting behaviour depends fundamentally on degrees of dominance" and Wickler (1967) reviewing the problem states that "male sexual actions imply dominance and female sexual actions submissiveness", and lists eleven species of primates in which 'dominance' mounting of males and females on lower ranking group members has been observed. Other authors however describe contexts in which male sexual actions do not imply dominance. Bertrand (1969) lists four situations other than dominance mounting in which stump-tail macaque males mounted other animals, namely; permission granting, enlistment, excitement and greeting mounts. In the latter, dominant males sometimes invited a subordinate to mount them. Hanby (1972) also found that in Japanese monkeys the relation between mounting and rank varied with the social situation in which the mount occurred. Kaufman (1967) calculated that only 75% of mountings were in the

same direction as the agonistic status relationships observed in male rhesus monkeys.

In order to fully understand the extent to which relationships are established during juvenile mounting behaviour it would be necessary to record the social context in which each mount occurs as well as the roles of the partners in the interaction.

The chapter on non-social play is
first, in order to fully appreciate the
importance of the development and integration
of the child. It is necessary to know how individual
children differ in their concept of social play.

CHAPTER TWO

B. NON-SOCIAL PLAY

B. NON-SOCIAL PLAY

The chapter on non-social play is included because I felt that, in order to fully appreciate the importance of social play in the development and integration of behaviour patterns it was necessary to know how behaviour patterns might also develop outside the context of social play.

Non-social play can be divided under two headings: the manipulation of objects, and locomotory and acrobatic play.

1. Manipulation of objects

Objects were said to be manipulated if they were picked up or grasped by the hand (other than for the purpose of locomotion) or mouthed, but were not subsequently eaten. Manipulations of self or other animals, such as grooming were excluded from this analysis as were the licking of stones on the beach and resin on tree trunks for salt. Thus manipulations involved behaviour patterns which had no immediate biological function.

Manipulations were recorded on the mother-infant check sheet and classified according to whether the hands or mouth (or both) were used, and a brief description of the object was made.

Results

The data presented are for three male and one female infant which were watched at such ages that there were usually two plots for each month in the figures.

The two infants for which I have data over the first weeks of life started to show an interest in objects such as grass stems at about ten days old, but at this age they were not able to grasp them efficiently and simply hit

them or bent them over, or mouthed them without using the hands. At about 15 days infants began to grasp objects properly, and around 20 days of age first exhibited eye-hand-mouth coordination. These figures imply a somewhat slower rate of development than those previously given for baboons (summarised by Hinde, 1971).

The percentage of minutes watched in which manipulations occurred rose to a peak of 25 percent at $2\frac{1}{2}$ months of age (Fig. 2.62) and thereafter declined to less than 5 percent at $5\frac{1}{2}$ months. Between $5\frac{1}{2}$ and $11\frac{1}{2}$ months manipulations remained at a low frequency of about 4 percent of minutes watched. Although the data go no further than 11 months of age, qualitative observations indicated that sporadic manipulation of objects continued up to at least 18 months.

Infants first swallowed solid objects in their third month and the percentage of minutes watched in which eating took place showed a regular increase up to $5\frac{1}{2}$ months. Thereafter the amount of eating levelled off and remained at about 40 percent of minutes watched until there was another increase at $11\frac{1}{2}$ months (Fig. 2.62).

The early peak in manipulations, followed by a decline as eating increased suggests that the manipulations might be incipient feeding behaviour, and that a progressively greater proportion of objects handled and mouthed are eaten as animals get older.

In order to test this hypothesis I calculated the proportion of objects manipulated which were put in the mouth (but not eaten) and the proportion of objects manipu-

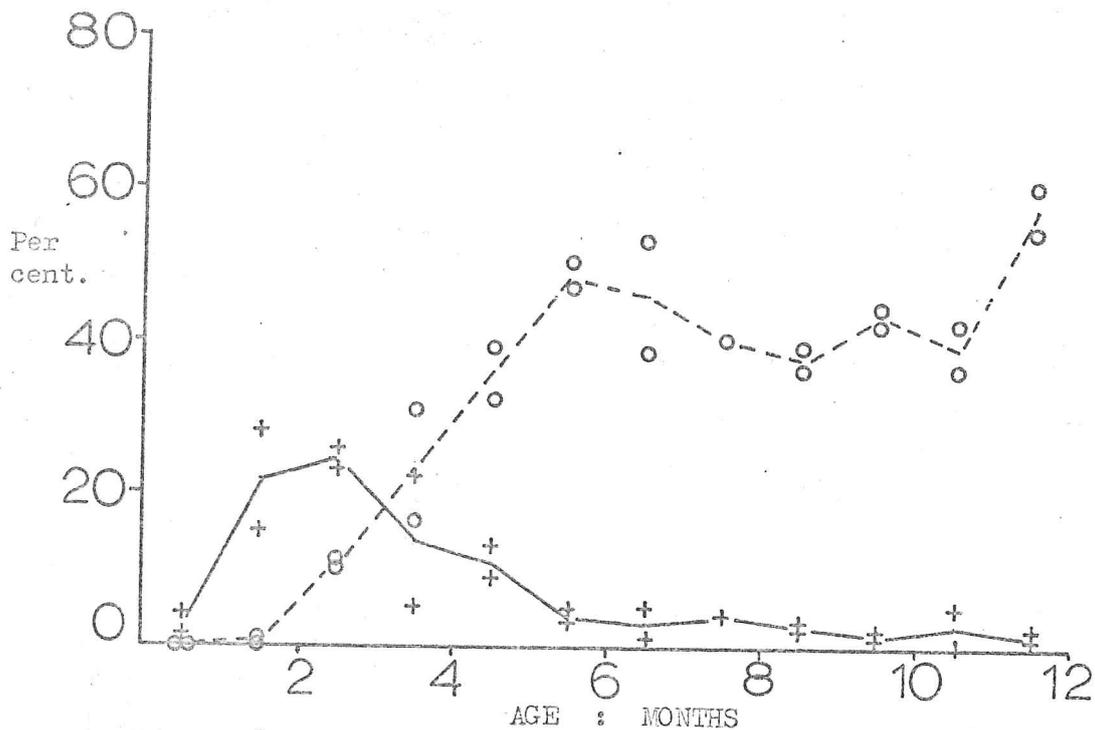
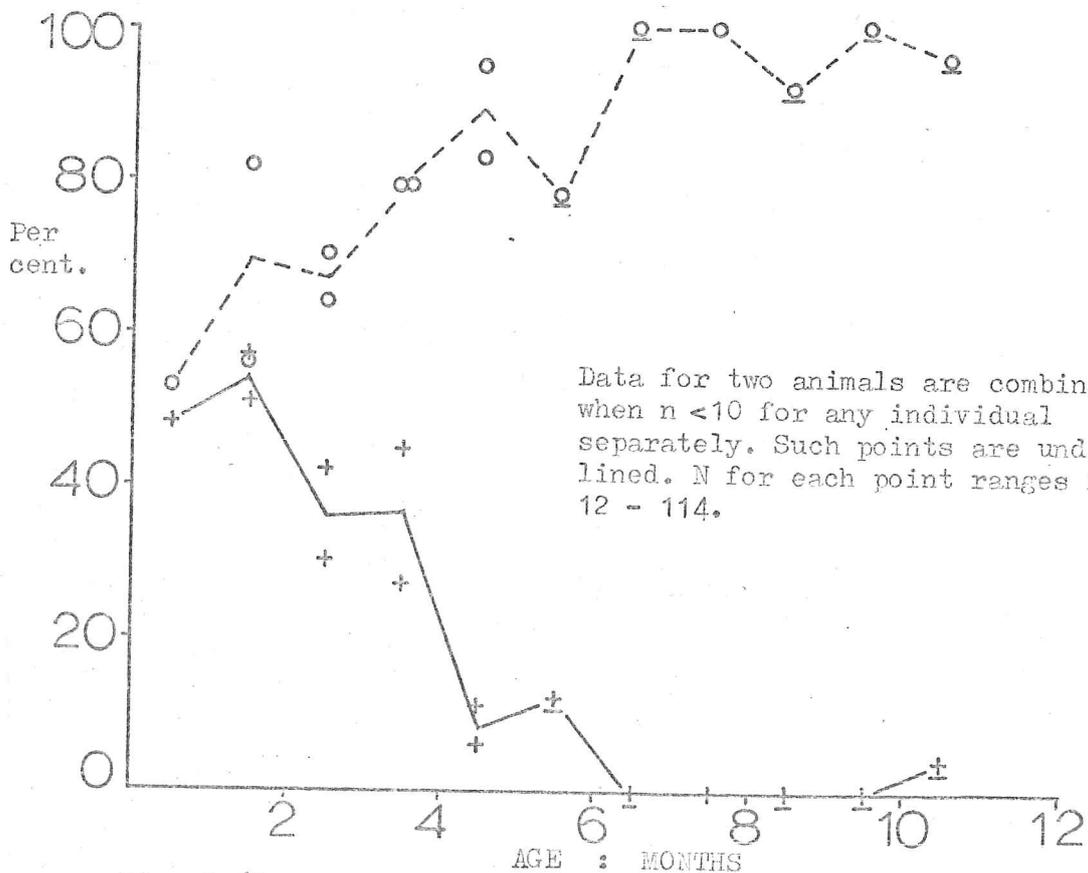


Fig. 2.62. Age changes in the manipulation of objects and feeding.
 +—+ The percent of minutes watched in which objects were manipulated (but not subsequently eaten).
 o--o The percent of minutes watched in which objects were eaten.
 See text for further explanation.



Data for two animals are combined when $n < 10$ for any individual separately. Such points are underlined. N for each point ranges from 12 - 114.

Fig. 2.63. Age changes in the manipulation of objects and oral manipulations.
 +—+ The percent of objects manipulated which were classed as edible.
 o--o The percent of objects manipulated which involved using the mouth.

lated which appeared to be edible. [Sticks, woody stems and branches, stones, dead leaves, dead grass stems etc., were classed as inedible in addition to some green plants known not to be eaten by baboons, such as palm fronds. All other objects; leaves, fruits, grasses, insects, etc., were classed as edible, though some of these, unknown to me, may have been inedible to baboons. Thus the figures given for the percentage of objects which were edible are maximum ones.]

The proportion of objects manipulated which were put into the mouth increased from 53% at 2 weeks of age to 100 percent at 6½ months (Fig. 2.63); thereafter the figure fluctuated between 90 and 100 percent ($r_s = 0.85$; $p < 0.01$; $N = 11$). (By contrast DeVore (1963) has stated that infant baboons do not begin to taste solid foods until the 5th or 6th month).

The proportion of objects manipulated which were classed as edible decreased from 45 percent at 2 weeks old to 0 percent at 7½ months and thereafter stayed very low ($r_s = 0.89$; $p < 0.01$; $N = 10$).

Discussion

These conclusions support the concept that object manipulations in baboons are largely developing feeding patterns. It makes sense that as infants start to eat solid food they will put a greater proportion of the objects manipulated into their mouths, and that the percentage of objects manipulated (but not eaten) which are edible will decrease. However, it is not clear why animals continued to mouth inedible objects after the age of about 6

months, by which time one might assume that they had learned to recognise most of the commoner food types. Such manipulations did not appear to be exploration of the more unusual foods. The objects manipulated were usually pieces of dead grass stem or small twigs which were often carried in the mouth for up to a minute before being dropped.

Bertrand (1969) describes very similar behaviour during the development of feeding in stumptail macaques: "Infants' first attempts to eat seemed to be teething and play processes rather than real feeding." Mouthing and sucking food began in the third to fourth week at which time they also started mouthing non-edible objects, such as fingers and cage bars, but infants continued to play with food objects after real eating had started. The development of feeding behaviour in Japanese macaques is said to be the same as in stumptails (Takeda, 1965; cited Bertrand). Menzel (1966) found that manipulation of inanimate objects other than food objects in free-ranging Japanese macaques was infrequent, and largely confined to simple mouthing and grasping. Eighty-one percent of manipulations were by animals less than one year old and mouthing and grasping of objects began at 6 weeks. These activities are probably equivalent to the manipulations by infant baboons which I have interpreted as incipient feeding behaviour.

Glickman and Sroges (1966), testing the responses of many species of zoo animals to novel objects (pieces of wood, chain and paper), found that baboons showed a high rate of response to these objects, chewing, rolling, poking and rubbing them. Such activities by captive primates

were more complex and frequent than similar activities reported for primates in the natural habitat. This conclusion is in keeping with Morris' (1964) hypothesis that opportunistic feeders (such as baboons) 'need' stimulation from novel objects and resolve their deprivation from adequate stimulation in a zoo environment by elaborating and extending the manipulation of the objects available.

Some authors (Butler, 1966; Harlow, Harlow and Meyer, 1950) have postulated a curiosity or manipulatory 'drive' to account for the persistent manipulation of objects by captive rhesus monkeys without any conventional reward, and Harlow et al., have demonstrated that monkeys given mechanical puzzles to manipulate became more efficient at puzzle solution than controls. Thus there is some evidence that the manipulation of objects by infant monkeys could be important in learning the manipulative abilities used in preparing food (such as the dehusking of seeds and fruits and stripping grass stems of the coarse outer sheath and roots, seen in baboons). It is also known that experience is necessary for red squirrels in learning to use the correct orientation in the chiseling movements needed to open hazel nuts (Eibl-Eibesfeldt, 1956) and in some finches in learning to use the correct force and orientation of their beaks to dehusk seeds (Kear, 1962).

Manipulation of objects by baboon infants may also be important in the development of perception. Gregory (1970) suggests that the interpretation of objects by sight may develop from experience of objects by touch in human children and Fantz (1965) holds that the manipulation of objects by

touch in human infants causes visual attention to be guided towards complex stimuli and thereby enhances perceptual abilities. Experience of both self-produced movement and concurrent sensory feedback is necessary for the development of visually guided behaviour in kittens and stumptailed macaques (Held and Hein, 1963; Held, 1966; Held and Bauer, 1967). Hinde (1971) summarises the data available for the development of visuo-motor coordination in seventeen primate species. In monkeys, coordinated reaching and eye-hand-mouth coordination generally appears in the first month of life. Five month old rhesus monkeys are already capable of discrimination learning, but at more complicated tests such as interproblem learning they are slower than adults, showing that their perceptual abilities are still not fully developed at this stage (Mason, Blazek and Harlow, 1958).

It seems likely that perceptual and manipulative abilities develop side-by-side during the manipulative behaviour of young primates. But some visuo-motor coordination must precede early attempts at preparing foods and this might develop particularly during the simple grasping and mouthing movements which preceded more complex manipulations in young baboons.

2. Object manipulation during social play and games

Results

The objects used during social play were usually brightly coloured or white and included pieces of cloth, old plastic containers and tins etc. Although these objects were fairly

often available they were not frequently used and I made only about 20 such observations during 17 months with the troop.

Social play with objects included both approach-withdrawal and rough-and-tumble patterns and objects were held in both the hand and the mouth. Sometimes a chase was invited by picking up an object whilst looking at the partner and then running away, and such play often developed into a game in which several animals competed for possession. However, the 'rules' were not always strictly adhered to as it was sometimes the chaser which carried the object. For example, in one particular play sequence involving 5 animals with a plastic carton, in 8 chases it was the chasee which possessed the carton and in 2 chases it was the chaser. Rough-and-tumble play with the carton also occurred, during which the animals not in possession frequently tried to snatch the carton away, and the carton changed possession 8 times altogether in the space of about 10 minutes. Between play bouts and sometimes during bouts the carton was manipulated in the hands. The animals involved were of both sexes and ranged from 12 to 30 months in age.

This type of game is in some ways analogous to that described under maternal play in which juveniles competed for possession of an infant. In both games animals competed for an object (or animal) which could be manipulated (or groomed) between play bouts.

Alternatively animals were sometimes seen to compete for a particular place or vantage point ('King of the castle')

(Plate XVI); a game which perhaps implies a similar level of cognitive functioning but which did not include object manipulation. Such games were also rather infrequent but there did appear to be favourite play places. These included a fork about 4 feet up in a large fig tree with a slippery trunk and some old tree stumps on the beach. Another game commonly observed was 'follow the leader' in which animals repeated the same movements as the one before them. A favourite site for this game was a branch overhanging a steep bank. Animals would jump from the bank and swing down to the bottom holding on to the branch, then scramble up the bank again as the next animal followed.

Discussion

The games described here have all been described previously in baboons and in other primates. Bertrand (1969) tabulates the games which have been recorded by various authors in 21 primate species. 'Follow the leader' and 'king of the castle' have been seen in most Old World monkeys and apes, but not in prosimians. However, Bertrand does not mention games in which there is competition for possession of an object or infant. Such games are apparently absent in stumptail macaques and are perhaps absent in many other primate species (though the fact that they are not mentioned does not necessarily indicate that they never occur). Bolwig (1959) however describes 'possessive' behaviour in chacma baboons concerning both inanimate objects and infants. Object oriented play also occasionally occurs in free-living rhesus monkeys (Southwick et al., 1965). Goodall (1968) found that social play

involving inanimate objects was common amongst free-living chimpanzees; chases occurred in which one animal tried to grab leaves or fruit carried by the other.

Games have also been reported in some sociable non-primate species (see Thorpe, 1966).

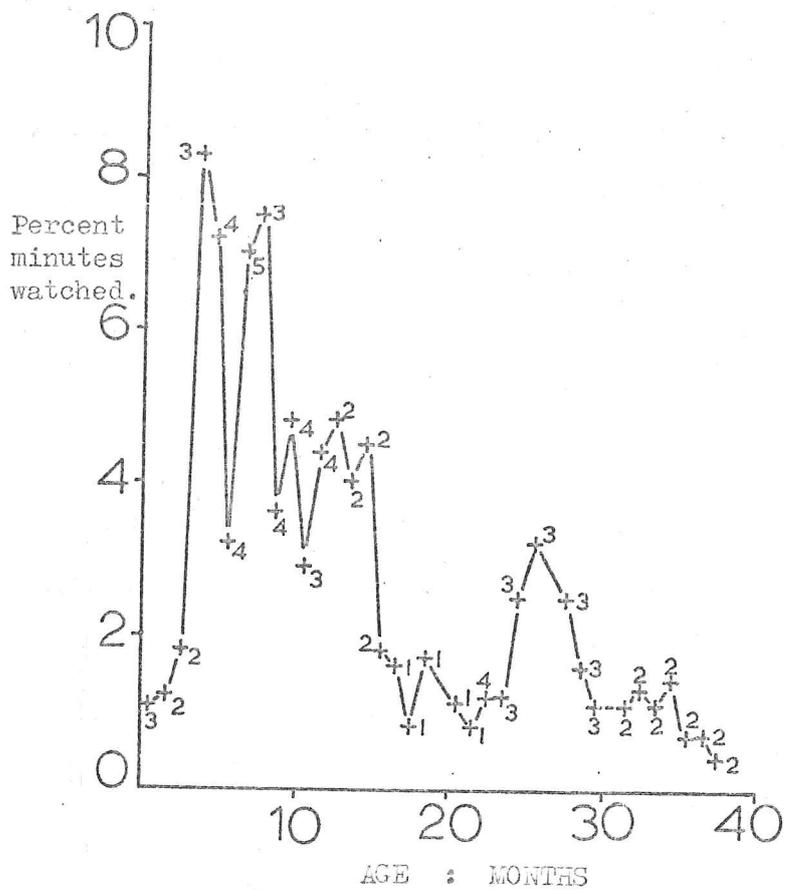
The question that these observations pose is 'in what way, if any, are games important in behavioural development?' One can only guess at the answers. The function of games in which baboons competed for possession of an infant have been discussed previously. The imitation which occurs in follow the leader games may be important in learning locomotory motor patterns. Moreover, the excitement produced during the game may induce animals to attempt extra long jumps and drops which they would not otherwise attempt, and so practice the movements they might need in an emergency (such as an attack from a predator or an adult male).

3. Locomotor and Acrobatic Play

Results

Young baboons showed many of the apparently 'purposeless' locomotory activities which have been called play in other mammalian species (e.g. Beach, 1945). Bouts of running (other than in social play) both on the ground and in trees were common and appeared to be more frequent in young than in adult animals. I also noticed that infants often wandered away from their mothers, climbed into a bush or tree and engaged in solitary acrobatic play, hanging upside down and jumping from branch to branch.

Time did not allow me to record running and jumping,



AGE : MONTHS

Fig. 2.64. Age changes in the percent of minutes watched in which animals were seen hanging from branches. Each point represents data pooled for 1-5 animals (the number of animals is indicated by numbers beside points). Each animal was watched for between 100- and 480 minutes each month.

but I did record hanging from branches. The data include all occasions on which an animal was suspended beneath a branch by any number of limbs with the exception of those instances during which animals were engaged in rough-and-tumble play. Hanging was rare amongst adult animals.

Infants had the ability to hang upside down almost from birth as exemplified by their ability to cling to their mothers' bellies, but hanging from branches was largely prohibited during the first 2 months by the infants' poor climbing ability. The only occasions when hanging was seen at this age was when infants were kidnapped by adult males and left stranded amongst the branches, and they gave many distress calls when this happened. In the third or fourth month infants became strong enough to regularly climb onto their mother's backs and into low bushes, and the frequency of hanging reached a peak of 7 - 8 percent of minutes watched between 4 and 8 months of age (Fig. 2.64). This peak roughly coincides with the first peak in male social play (Fig. 2.1). Between 8 and 15 months the frequency of hanging was somewhat lower, fluctuating around 4 percent; this may have been because animals more often engaged in rough-and-tumble play whilst hanging. After 15 months the frequency dropped suddenly to less than 2 percent apart from a small secondary peak between 25 and 28 months.

Discussion

Little is known about the age changes in the frequency of locomotor and acrobatic play in other primate species. In rhesus monkeys age changes in the frequency of non-social play follow an approximately similar course to those in

social play (Hinde and Spencer-Booth, 1968). Locomotor and acrobatic play seem to be universal amongst young primates; "patterns of swinging, jumping, spinning and somersaulting are common to them all" and "gymnastic play ... seems to differ only in the capacity of each species to make use of the available features of the environment" (Loizos, 1967). Bertrand (1969) observes that play dangling and play wrestling whilst hanging from the feet exist in most species of primates ranging from galagos to chimpanzees.

Although no experimental evidence is available for primates it seems reasonable to assume that locomotor and acrobatic play is important in the development of the coordination of movement in assessing the changing physical abilities of the body and in becoming familiar with environment (Loizos, 1967). Brownlee (1954) argues however that locomotor play in domestic cattle continues long after coordination of movement and familiarisation with the environment has been established and holds that the function of such play in cattle is 'tissue trophic'; it serves to exercise and thereby maintain tone and adequate vascularisation of the play muscles. Thorpe (1963) suggests that the skeletal and muscular structure of many mammalian forms is such as would rapidly force the young animal to adopt the characteristic gait after even a relatively small amount of practice. No experience of movement seems to be necessary for the development of some locomotor patterns, for example pigeon flight (Grohmann, 1938). In baboons it was the case that most locomotor and acrobatic play occurred after running and climbing had apparently been

perfected, but it seems probable that undetectable modifications in the amplitude and timing of movements did continue as a consequence of the sensory feedback during such play, and that it was important in the fine readjustment of movements as animals became larger, rather than in the development of gross locomotor patterns.

SUMMARY OF CONCLUSIONS

The mother-infant relationship

1. Most infants were largely independent of their mothers by the time they were 16 months old. In general, the infant had a progressively greater role in maintaining the relationship with age, and changes in the mother's behaviour were chiefly responsible in promoting the infant's independence.
2. During a period of intense rejections of the infant by the mother, the amount of social play in males decreased.

Play behaviour

3. It was found that aggressive behaviour could be classified into aggressive play and aggression proper on the basis of the presence or absence of certain gestures of intense threat.
4. There were marked age changes and sex differences in the amount of social play and in the relative frequency of the different movement patterns. Males tended to play more than females and were rougher and more often active in play than females. The amount of play that occurred suggested that social play could have an important function in behavioural development in free-living baboons.
5. The sex differences in the relative frequency of different movement patterns in rough-and-tumble play showed some parallels to the sex differences in the relative frequency of the same movement patterns in aggression, suggesting that aggression and play shared certain causal

factors.

6. In males, the relative frequency with which different movement patterns occurred in aggressive play became with age somewhat more like the relative frequency with which the same movement patterns occurred in adult aggression. However, it was not thought that play was necessary for the development of the use of the movement patterns in such proportions.

7. Maternal and paternal play were perhaps important in the development of some aspects of maternal and paternal behaviour.

8. No meaningful distinction could be made between sexual play and sexual behaviour proper. The age changes and sex differences in the frequency of mounting followed a very similar pattern to the age changes and sex differences in the amount of aggressive play. Incipient sexual behaviour in young baboons appeared to have an important function in the development of male sexual patterns, the greatest changes taking place between 10 and 15 months of age. This was also the age at which male sexual behaviour reached a peak.

9. Manipulatory play appeared to be particularly concerned with the development of feeding patterns, and acrobatic play may have had a role in the development of the coordination of movement.

10. The factors which affected the choice of a play partner included the sex, age, 'maternal club' and sibling relations of the partner. Play initiation and termination and active and passive roles in play were also largely determined by

age and sex.

11. Interactions between individuals in play were characterised by a high frequency of reversal of active and passive roles. In this respect they resembled relationships in adult male-male aggression (but not those in juvenile or adult female aggression). It was conjectured that the relationships established between females in play may have persisted into adulthood. The relationships between males in play however did not, though experience at role reversal in play may have been important to males in learning the modes of interaction of adult male aggression.

12. Relationships in sexual behaviour were not correlated with those in aggressive play or aggression proper, either in young animals or adults. This was probably because the sexual behaviour observed occurred in several different social contexts.

13. Social play involving siblings or animals from the same maternal club or involving objects may have had a function in the practice of more complex types of social interaction involving more than two animals.

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