The development of behaviour, particularly play, in young baboons

Thesis

How to cite:

Rowland, Charles Garnet (1983). The development of behaviour, particularly play, in young baboons. PhD thesis The Open University.

CHARLES GARNET ROWLAND BSc.

UNRESTRICTED

THE DEVELOPMENT OF BEHAVIOUR, PARTICULARLY PLAY, IN YOUNG BABOONS

Thesis submitted in part fulfilment of the degree of Doctor of Philosophy in the Department of Biology, Open University, 1983.

Date of submission: Feb. 1983

Date of award: 19-10-1983

No part of this thesis has previously been submitted for a degree or other qualification in any university or other institution.

CONTENTS PAGE NO.

Acknowledgements

I would like to thank several people for the parts they have played in enabling me to complete this project. I am grateful to: Mr. Jimmy Chipperfield for permission to work in the parks and to the staff of the Woburn Wild Animal Kingdom and Blair Drummond Safari Park for their friendship and co-operation: Professor Aubrey Manning for granting me the use of the University of Edinburgh, Zoology Department Library: the University of Bristol for the use of library facilities: the Open University Student Computing Service for teaching me BASIC: Ms. Val Morrison for help with data presentation and statistics: Mr. Mike Huggins for advice on programming and statistics: Dr. Mervyn Davies for permission to use the computer and reprographic facilities of Saint Brendan's Sixth Form College, Bristol, and Mr. John Dougal for his practical help in those areas: Mrs. Alma Foster and Mrs. Jean Webber who typed the text and tables. I am most grateful for the guidance given so patiently by my supervisor, Dr. Neil Chalmers. Finally, I thank my wife Charlotte for her constant support and encouragement.

Abstract

Baboons were observed in two British safari parks for 15 and 3 months. Quantitative data, on the frequencies of play and non-play motor patterns and on temporal associations between motor patterns, are used to provide a description of behaviour development and to investigate the validity and possible heterogeneity of the play category.

Infant development was comparable with that reported elsewhere for caged and wild macaques and baboons. Mothers tended to be restrictive, possibly because of stressful conditions in safari parks.

As infants became more independent they increasingly manipulated objects away from their mothers. Object manipulation was mostly nutritional but a measure of extended contact with objects is argued to be an index of investigation or manipulatory practice. There is no strong evidence to suggest this was a form of play.

Mobile activity was greatest while infants still associated closely with their mothers who were probably satisfying most of their nutritional needs.

Locomotor patterns appeared in play once they were established in the general repertoire; a result contrary to the practice hypothesis of play's function. Measures of play locomotor pattern frequency increased markedly at about 6 months. Playful behaviour may have become more beneficial. At that age the black natal colouration was finally lost; and without the social immunity which it might have afforded, infants more frequently performed potentially disruptive behaviours playfully. The development of play wrestling showed a change from a predominantly clinging to a predominantly manipulative form. This is discussed with reference to exercise regimes, age class of play partners and developing manipulative skills. The composition of play varied according to the difference between partners' ages.

Developmental and temporal clusters of motor patterns demonstrate that play, as defined in this study, was a heterogeneous but genuine phenomenon.

Toxonomic names

The following are the toxonomic names of species which are referred to by their common names in the text.

chimpanzee	*Pan troglodytes*
chacma baboon	*Papio ursinus*
hamadryas baboon	*Papio hamadryas*
olive baboon	*Papio anubis*
yellow baboon	*Papio cynocephalus*
colobus	*Colobus guereza*
howling monkey	*Alouatta villosa*
common langur	*Presbytis entellus*
bonnet macaque	*Macaca radiata*
pigtail macaque	*Macaca nemestrina*
rhesus macaque	*Macaca mulatta*
stumptail macaque	*Macaca arctoides*
common marmoset	*Calithrix jacchus*
squirrel monkey	*Saimiri sciureus*
vervet	*Cercopithecus aethiops*
African ground squirrel	*Xerrus erythropus*
Columbian ground squirrel	*Spermophilus columbianus columbianus*
mouse	*Mus musculus*
rat	*Rattus norvegicus*
black bear	*Ursus americanus*
domestic cat	*Felis catus*
domestic dog	*Canis familiaris*
coyote	*Canis latrans*
wolf	*Canis lupus*
red fox	*Vulpes vulpes fulva*
lion	*Panthera leo*

mongoose (meerkat)	*Suricata suricata*
polecat (ferret)	*Mustela putorius*
common seal	*Phoca vitulina vitulina*
grey seal	*Halichoerus grypus*
elephant seal	*Mirounga angustirostris*
sea lion	*Eumetopias jubata*
American buffalo	*Bison bison*
domestic cattle	*Bos taurus*
black tailed deer	*Odocoileous hemoinus columbianus*
reindeer	*Rangifer tarandus*
domestic goat	*Capra hircus*
ibex	*Capra ibex sibirica*
domestic sheep	*Ovis aries*
horse	*Equus caballus*
zebra	*Equus burchelli*

Chapter 1. Introduction and review of problems and issues in play research

1. Introduction

This study describes some aspects of the development of behaviour in baboons living in the relative freedom of two British safari parks. It was begun in 1971 and relates to three areas of research which had received increasing attention during the previous three decades: play and exploration in mammals, development of behaviour (particularly that between infants and their mothers) in captive primates and field studies of social behaviour and behaviour development in free-living primates.

In 1945 Beach reviewed the attempts which had been made to explain the causes and functions of play. He maintained that there were too few facts available with which to test the many theories. There was a need for greater objectivity, and he called for more quantitative research. Twenty-six years later Muller-Schwarze (1971) regretted that very little progress had been made and repeated Beach's plea for data. The present study was a response to that plea.

Most theories of function suggest that play by young animals has effects on their later adult behaviour. If play is to be seen as a developmental phenomenon, then data on development are required to elucidate it. This study compares development trends of motor patterns in both play and non-play and sets them in the context of developmental changes in other behaviours. No attempt was made to form a complete ethogram for young baboons but a wide range of behaviours was selected for study, including postures, position in relation to mother, movements while on mother, locomotion, social play and manipulation of objects. The aim was to provide a more detailed description of motor pattern development than was currently available for free-living baboons in the hope that a view of play would emerge which would shed light on its role in behaviour development.

There had been some quantitative descriptions of motor pattern development in infant rhesus monkeys by, for example, Hines (1942), Mowbray and Cadell (1962) and Mason, Harlow and Rueping (1959). These analyses, carried out in artificial experimental conditions, were at the level of limb and body movements and did not include broader behavioural categories such as play.

Broad categories were observed by Hinde and co-workers (1964, 1967) in their developmental studies of infant rhesus in caged social groups. They measured the increasing independence of infants from their mothers and the concurrent increase of social behaviours, including play, towards other group members. While they acknowledged that infants performed several different motor patterns during social play, such as "galloping" and "leaping", they analyzed its development only in terms of two categories: "approach-withdrawal" and "rough-and'tumble". Kaufman (1966) studied a group of free-living rhesus and obtained data on behaviour development in several contexts. In most respects it was a detailed study, showing the ages of first appearance of motor patterns in, for instance, locomotion, object manipulation and social contact with mother and others; but social play was treated as a single category. There was no description of behaviour development within play. Rowell, Din and Omar (1968) carried out a study of captive baboons similar to that of Hinde _et al_. on rhesus. Although they described changes in the interactions of infant and mother in some detail, play development was shown only in terms of the proportion of time spent playing. Their definition of play covered all infant-infant interactions and therefore was too general to contribute to the detailed understanding of baboon play. The field study of baboon social behaviour by Hall and De Vore (1965) gave quantitative data on social dynamics but social development was described qualitatively. They distinguished developmental stages, from new-born to adult, and listed the significant changes in behaviour, including play, at each stage. When the present study was begun there were no long-term quantitative data on motor pattern development in free-living baboons which included motor patterns used in play.

Hall and De Vore discussed the difficulties of studying behaviour development in the field and said: "The interactions of social learning, of play and exploration, of sensori-motor coordinations and of reflex systems are such that they can be described only tentatively from field data"

(Hall and De Vore, 1965). My purpose in this study was to provide a not-so-tentative description of motor pattern development, in terms of frequency changes, under conditions approximating to a natural habitat.

2. The problem of defining play

It was necessary in this study to have an operational definition of play with clear criteria so that motor patterns in play and non-play could be recorded unambiguously and consistently throughout the period of data collection.

A paradox confronts all students of animal play. Observers may sense that an animal's behaviour is playful yet find it difficult to identify the behavioural cues which create that impression (Fagen, 1981; Hinde, 1974; Lorenz, 1956). This is because play is fundamentally a human concept built on our shared experience. We know when we are playing ourselves, and can recognize play in others because we are privileged with a subjective understanding of other people's intentions. If we infer from a complex of behavioural cues, of which we may not be aware, that a person does not intend his behaviour to be taken seriously or that he does not intend it to have a serious effect, we might judge that behaviour to be playful. We do not have the same privilege with animals yet we do feel capable of making the same judgement; that certain behaviour is playful. The judgement has to be based on two types of criteria. Firstly, the manner of behaving might be reminiscent of some feature of human play. Secondly, since it is not possible to know an animal's intentions, a judgement must be made of whether the behaviour has a serious effect and contributes to the animal's survival or reproductive success. The implication of the second criterion is that play has no survival value. This is another paradox. Can it reasonably be assumed that such a ubiquitous and frequent behaviour is not adaptive? This question will be discussed later. If the criterion is to remain within the Darwinian evolutionary paradigm, then it must be modified to: does not contribute to survival or reproductive success in an immediately obvious way.

Several authors have drawn on our common experience when claiming that animals do play. For example, Beach (1945) wrote: "...animals of many species do exhibit various types of behaviour which, if they were observed in humans, would undoubtedly be called play". Lancaster (1971) reminded her readers, in support of her claim that infant care by immature primates is a form of play, that: "...when we see similar maternal behaviour patterns displayed towards a doll by a juvenile female of the human species we do not hesitate to call it play". Play is defined by consensus; but an objective study requires objective operational criteria. These are best arrived at after examining the range of human and animal activities which have been regarded as play.

It is appropriate to consider human play first because it is the model for animal play. Play is not restricted to the behaviour of children although it is characteristic of them rather than of adults. At one extreme are movements with no discernible object or goal, for instance, skipping or clapping hands, and referred to as "pure assimilation" by Piaget (1951). At the other extreme are games of various complexity, from tag to chess, which have goals and rules but which have no obvious survival value (Eifermann, 1972; Miller, 1973; Opie and Opie, 1969; Piaget, 1965). Between these extremes are such activities as exploration and make-believe with objects (Greif, 1974; Hutt, 1966), chasing and wrestling with peers (Blurton Jones, 1967) and make-believe role playing such as "mothers and fathers" (Greif, 1974; Garvey, 1976). Within this diversity run the themes of pretending, of lacking serious intent and of enjoying an activity for its own sake.

The animal behaviours described as play in the literature are diverse, like their human model (see Table 1 for references).

Most accounts are of play between two or more social partners. The type described most frequently, perhaps because it gives the strongest impression of lacking serious intent, is aggressive play. The superficially aggressive interactions have been called play fighting, chasing,

Table 1. References in the literature to play in three very different contexts: solitary, with objects and with a social partner

animal group	reference	type of play		
		solitary locomotion	with objects	with a social partner
6 different orders	Wilson and Kleiman 1974	*		*
rats	Poole and Fish 1975	*		*
mice	Poole and Fish 1975	*		
polecats	Poole 1966	*		*
	Poole 1978			*
	Weiss-Burger 1981		*	
ferrets	Lazar and Beckhorn 1974			*
African ground squirrels	Ewer 1966	*		
Columbian ground squirrels	Steiner 1971			*
domestic cats	Barrett and Bateson 1978			*
	Bateson, Martin and Young 1981			
	Biben 1979	*	*	*
	West 1974		*	*
lions	Schaller 1972		*	*
	Schenkel 1966			*
mongoose	Wemmer and Flemming 1974			*
Canids	Bekoff 1974			*
black bears	Henry and Herrero 1974			*
sea lions	Farentinos 1971		*	*
	Gentry 1974			*
seals	Wilson 1974	*		*
domestic goats	Chepko 1971	*		*
ibex	Byers 1980			*
black tailed deer	Muller-Schwarze 1968	*		*
reindeer	Espmark 1971	*		*

Table 1 continued

Animal group	reference	type of play		
		solitary locomotion	with objects	with a social partner
domestic cattle	Brownlee 1954	*	*	*
American buffalo	Lumia 1972			*
rhesus macaques	Altmann 1962			*
	Bertrand 1969	*		*
	Harlow and Harlow 1965	*		*
	Harlow 1969		*	*
	Mears and Harlow 1975	*		
	Meier and Devanney 1974	*	*	*
	Redican and Mitchell 1974			*
	Symons 1974			*
stumptail macaques	Rhine 1973			*
bonnet macaques	Simmonds 1965			*
howling monkeys	Carpenter 1934		*	*
langurs	Jay 1965			*
vervets	Fedigan 1972, Lancaster 1971			*
	Rose 1977			*
colobus	Rose 1977			*
marmosets	Chalmers and Locke-Haydon 1981			*
	Stevenson and Poole 1982			*
	Voland 1977			*
squirrel monkeys	Baldwin and Baldwin 1969	*		*
	Baldwin and Baldwin 1974			*
	Latta, Hopf and Ploog 1967			*
hamadryas baboons	Leresche 1976			*
chacma baboons	Hall 1962	*		*
yellow baboons	Cheney 1978			*
olive baboons	Chalmers 1980a and b			*
	Hall and DeVore 1965			*
	Owens 1975a and b			*
Chimpanzees	Angus 1971	*		
	Bierens de Haan 1952	*		
	Van Lawick Goodall 1968	*	*	*
	Loizos 1969			*
	Mason 1967		*	*
	Merrick 1977			*
	Schiller 1952		*	
	Welker 1956		*	

approach-withdrawal, rough and tumble and wrestling. Sometimes behaviours which would be considered sexual or to do with infant care when seen in an adult have been regarded as playful when seen in immature animals. There is also non-social or solitary play involving acrobatics and vigorous locomotion or the prolonged manipulation of objects. Bouts of play can be quite short and simple or long and repetitive, even taking the form of complex scenes or games.

Animals are judged to be playing when they behave as if they have no serious intention or as if they are enjoying themselves. But these are not objective criteria and perhaps ought not to feature in an operational definition. Nevertheless, they do form part of the paradigm which researchers have of play and are useful as a "coarse filter" for identifying candidate behaviours which the researcher can reject or accept as play on the basis of more objective criteria.

The criteria used in ethology for classifying behaviour are based on structure (appearance), cause and function (Hinde, 1970). At the present stage of knowledge, cause and function provide unsound criteria for defining play. The factors which cause play are poorly understood and can only be used in a negative way. For example, behaviour occurring when an animal is highly aroused is not considered to be play (Baldwin and Baldwin, 1977; Mason, 1967; Poole, 1966; Simonds, 1974; Welker, 1961).

The function of play has been the subject of a great deal of speculation and while there may be some experimental and observational evidence to support certain hypotheses (e.g. Einon, Morgan and Kibbler, 1978; Byers, 1980; Owens, 1975a; Harlow and Harlow, 1965, 1966; Fagen and George, 1977; Symons, 1974) no theory is so well established as to provide an acceptable defining criterion. The one most frequently used - lack of function - is the basis of the logic which makes play: that which is "not serious" or "not in earnest". If this is the only criterion employed, then play is turned into a sink category limited only by our current ignorance (Beach, 1945; Berlyne, 1960). The structure of behaviour provides the most objective and useful operational criteria; especially in a field study, where the researcher has no control over causal factors and only imperfect means of assessing the consequences of behaviour. Structural criteria include motor patterns, postures and expressions, and take into consideration the economy with which motor patterns are executed and the organization of behaviour sequences.

Attempts to define animal play have resulted in lists of structural, functional and causal features from which criteria can be chosen. Beach listed five:

> an emotional element of pleasure;
>
> characteristic of immature rather than mature animals;
>
> species specific appearance;
>
> frequency, variation and continuation into maturity increase with the phylogenetic level;
>
> no immediate biological result.

Only the latter could contribute to an operational definition. Meyer-Holzapfel's (1956) list was more useful:

> lack of immediate biological consequence;
>
> motor pattern sequences are different from those in a serious context and may even be random;
>
> partners exchange dominance roles;
>
> movements normally associated with different motivations can be combined in the same bout;
>
> sequences can be repeated again and again without coming to an end point;
>
> facial expressions and gestures appear to express a state of pleasure.

Loizos (1966) added:

> fragmentation: sequences are broken up by irrelevant actions;
>
> repetition within a sequence: for instance, repeated intention movements;
>
> exaggerated and uneconomical movement.

She particularly emphasized the importance of exaggeration in communicating playfulness to human observers.

Other authors, for example Altmann (1962), Muller-Schwarze (1971), Poole (1966) and Steiner (1971), have described self-handicapping and inhibition by the larger partner in play fighting. This gives the impression that the behaviour is not in earnest.

Operational criteria should be immediately apparent, rather than apparent only in retrospect, and objective rather than subjective. On that basis, randomness and pleasure can be discarded as criteria. Self-handicapping seems to imply a subjective judgement, but it can be objective if the true capability of the animal is known. I have already argued that lack of immediate biological consequence could be used as part of a definition. The remaining features are structural and so should lend themselves to objective decision making.

Play signals

If an observer uses predominantly structural criteria and identifies play by its appearance he is responding to the movements as if they were signals. Humans, and presumably conspecifics, infer from these signals something about the significance of the accompanying activity - that it is not likely to have serious consequences. This is metacommunication (Altmann, 1962; Bateson, 1955). Metacommunication signals cause a recipient to respond differently from how it would otherwise respond to the activity of the sender. The value of such signals can be appreciated when the motor patterns are those which at other times are associated with aggression. An approach in one context might communicate the beginning of an aggressively motivated attack and stimulate the approached animal to respond aggressively or withdraw. An approach accompanied by play signals may be less readily interpreted as a threat and the partner may be less likely to respond defensively. Loizos (1969) investigated, in chimpanzees, the effect of facial expressions, vocalizations and other signals on the tendency of social partners to disperse. She found that if the behaviours were accompanied by, for instance, hair erection, the recipient responded by fleeing. If, however, the signal was the "play-face"then the recipient responded in such a way as to continue the interaction. Chalmers (1980a) showed that wild olive baboons were more likely to change behaviour in response to a change in the behaviour of a social partner, and thereby maintain the interaction, if one of the partners was performing a "play marker" such as the play-face. Furthermore, vigorous encounters with play markers lasted longer than encounters without play markers.

It is not obvious whether such signals would serve any useful function when accompanying less potentially disruptive social activities such as infant-care or infantile sex, or non-social activities such as locomotion or object manipulation. The play-face has been seen in chimpanzees; for instance, when manipulating leaves (McGrew, cited in Smith, 1981) and when splashing alone in water (Angus, 1971).

But olive baboons make no play signals to accompany sexual and parental play (Owens, 1975a); and Poole (1978) pointed out that polecats did not have "open mouth" or "bouncing gait" when playing with inanimate objects.

The play-face or relaxed open mouth expression is the signal most frequently described (Van Hooff, 1967). Several orders of mammals show this expression prior to and during playful, or at least amicable, interactions (Van Hooff, 1962). In canids the mouth is open with lips back and the angles pulled up (Fox, 1970). Black bears have an expression with puckered lips (Henry and Herrero, 1974). In primates the mouth is opened wide with the corners relaxed, pulled neither forward nor backward, and the lips remaining over the teeth (Van Hooff, 1963, 1967).

Some play signals appear to be intention movements, showing ambivalence between approach and withdrawal, such as lunging and bobbing (Wilson and Kleiman, 1974; Bekoff, 1974). Loizos (1966) drew attention to the exaggerated way that animals move during play. Bekoff (1974) described the exaggerated approach of canids as a loose, bouncing gait with side-to-side movements of the head and shoulders. A similar bouncing gait in lions was described by Schaller (1972). Grey foxes show violent head and body shaking (Fox, 1970), common seals jerk their heads (Wilson, 1974), reindeer run friskily (Espmark, 1971) and primates have gambolling gaits (Altmann, 1962; Simonds, 1974). Although West (1974) did not say that play movements in cats are exaggerated, she did say that they are carried out at a typical intensity which enhances signal value.

A few attempts have been made to analyze the components of the exaggeration. Wilson and Kleiman (1974) found that in a wide variety of species locomotion and body rotation are exaggerated in both speed and amplitude and suggested that locomotor-rotational play signals are ubiquitous among the mammals. Sade's (1973) investigation into the principal anatomical planes occupied by display movements of free-ranging rhesus macaques showed that in play there is a greater emphasis on transverse rotational movements. Head and shoulder rotation and limb abduction give play activities such as running and wrestling an exaggerated, twisting appearance. This compares directly with the locomotor rotational movements described by Wilson and Kleiman. There is also a relaxed quality in play fighting, distinguishing it from the tense economy of serious fighting, which has prompted authors to use the terms "held back" and "inhibited" quoted earlier. Poole (1978) described play movements in polecats as "clumsy" and suggested this was brought about by reduced muscle tone. Fagen (1976) considered that difference in muscle tone might account for the difference between the economic movements of adults and the exaggerated movements of infants; but he did not distinguish between play and non-play in infants. He later points out that no myogenic studies have tested this hypothesis (Fagen, 1981).

Motor patterns which occur only in play might be especially effective signals; for example, common seals resting the head over the partner's back or chest (Wilson, 1974) and primates looking between their legs (Altmann, 1962; Voland, 1977) or pulling the partner's tail (Voland, 1977). If such movements appear before a bout of social play they might be interpreted as invitations to play. If they happen during a bout they might serve to reinforce the message of playfulness and so keep the action going. Symons (1974) suggested that the same signals might serve both functions and this is supported by Wilson's (1974) observation that grey seals repeat the invitation signal of head-over-body throughout the bout, otherwise the bout stops. Loizos (1966) suggested that these signals would be powerful and unambiguous since, from her own observations, chimpanzees seldom interpret play fighting as serious aggression. Leresche (1976) looked for specific and unambiguous signals in the play of hamadryas baboons at the points where the action changed. She found none and concluded that the action itself conveys sufficiently powerful signals. Muller-Schwarze (1971) commented on the reciprocity of social play: once a bout begins the action provides stimuli which elicit further action. Presumably this gives some play the appearance of lacking an end point. Sometimes the non-specific stimulus of an animal playing is sufficient to induce others to play also (Bertrand, 1969; Ewer, 1966).

Play as a behaviour category

Is play best thought of as a single category of behaviour? Should it be sub-divided? Or should it be considered a sub-division of a wider category? The answers hinge on how play is defined. In the classification of behaviour there are no absolutes. An animal's behaviour repertoire could theoretically be divided into any number of groups, but only some of them would be useful for advancing our understanding (Hinde, 1970). Grouping animal behaviours on the basis of their similarity to a human construct - play - is useful in that it defines an area of study but may not necessarily help us to understand the behaviours within that group. It is not obvious whether those behaviours are in any other sense the same phenomena as those in human play or indeed the same as each other. Three major aims of ethology are to understand cause, function and ontogeny of behaviour. These aims could be furthered with regard to play if the constituent motor patterns were grouped by causal, functional or developmental criteria in order to test the validity of play as a phenomenon, to identify subgroups within play or to show play as a subgroup itself within some wider category.

The paradigm of play adopted recently by Fagen (1981) and Smith (1981) is formed by a mixture of causal, functional and structural criteria: a group of behaviours satisfying no immediate homeostatic need (functional), performed in the absence of higher priority behaviour (causal), performed in a relaxed manner and frequently accompanied by certain signals (structural). By this, play is limited to social, non-agonistic wrestling and chasing, solitary locomotion, acrobatics and object manipulation. The range of behaviours would be different if one criterion were applied at a time. If only the functional criteria were applied, then all non-homeostatic (or apparently so) behaviours would be classed together and would include "idle" manipulation of objects, exploration, infant-care by immatures, rough-and-tumble, approach-withdrawal, solitary acrobatics and any self-manipulation which was not comfort behaviour or autogrooming. Classification by structure only would provide a class consisting of approach-withdrawal, rough-and-tumble, solitary acrobatics and all poorly coordinated infant behaviour. As Fagen (1981) has pointed out, different combinations of criteria would bring together different behaviours. In each case the common paradigm is reduced to a sub-category. How useful then is that paradigm and how useful are the wider categories?

Berlyne (1969) advocated that expediency should dictate the limits. The word "play" was probably not useful with its implications of unity and should be discarded. Wider and narrower categories might be used depending on the particular problem under investigation. Lazar and Beckhorn (1974) have argued that play might be a useful concept when investigating the function of behaviour but not if the aim is to analyze behaviour ontogeny. They pointed out that play is always defined against the standard of adult behaviour which is seen to have implications for reproductive success. Therefore the concept of play is only relevant in studies of adaptation. If the goal is simply to describe ontogenetic processes then each motor pattern should be studied in its own right as part of an ontogenetic sequence. They considered that "playful" and "play-like" might be useful descriptive terms, but talking of play and non-play motor patterns cannot contribute to an understanding of development. The same stance had been taken by Fox and Clarke (1971) when they described the development of agonistic motor patterns in coyotes. They showed how each motor pattern, after its original maturation, passes through developmental stages of stimulus generalization, specialization with ultimate integration into complex sequences. There was no need to distinguish play from non-play motor patterns. Play was simply one behavioural context in which the motor patterns were used. Smith (1981) took issue with Lazar and Beckhorn's approach and cited several accounts of play motor patterns being significantly distinct in appearance and development from the equivalent non-play motor patterns. He concluded that play is a distinctive behavioural category requiring an explanation. But the view is accommodated within Lazar and Beckhorn's thesis. Smith's aim was to examine the function of play and therefore he legitimately considered it to be a real phenomenon. Lazar and Beckhorn's aim was to describe the development of certain motor patterns. Play was not a useful concept. Fagen (1981) argues that play should be considered a real phenomenon. He has built a complex theoretical framework on the premise that it is not a spurious category.

A few studies have shown heterogeneity within play by discovering more than one developmental or temporally associated grouping of behaviours. Play has been sub-divided using developmental data by Chalmers (1980) and Barrett and Bateson (1978). Barrett and Bateson recorded the development trends of seven behaviours in domestic kittens. There was little correlation between them, suggesting they were the results of "several independent systems". Chalmers found that in olive baboons the acrobatic and energetic locomotor behaviours such as running, leaping and climbing followed development trends which were similar to one another but different from those of behaviours involving hands and mouth. Both groups contained playful and non-playful behaviours, according to the usual definitions. The set of behaviours traditionally considered playful was not only shown to be heterogeneous in development but also, it was suggested, the traditional concept of play was too limiting.

Blurton Jones (1972) used factor analysis to show up three categories in the behaviour of nursery school children. They were "rough-and-tumble/work", "aggression" and "friendly social behaviour". The group "rough-and-tumble/work" contained those behaviours which are usually considered playful, such as chasing, wrestling, manipulating objects and painting (work) as well as laughing and the play-faceexpression. It is significant that within this group the energetic social interactions and the object manipulation formed two subgroups whose intercorrelations were high but negative. That is, in an observation session the children tended to be either wrestling and running or working.

It was an important study because it showedthat playful behaviours could be identified and subtlely sub-divided into meaningfulgroups using objective, empirical data rather than by subjective impressions of appearance or a priori notions of cause or function.

In the present study the strategy adopted to investigate the question of homogeneity or heterogeneity is as follows. A narrow definition of play is set up, mainly on criteria of appearance, so that the behaviours come within the scope of all published definitions. Frequency changes of the constituent motor patterns are examined to discover whether they develop as an intercorrelated unit or fall into different groups according to developmental trends. Development trends of motor patterns outside the narrow definition of play are compared with those of motor patterns within play to find out whether developmental groups extend beyond the limits imposed by the operational definition. Cluster analysis is used for identifying behaviours which tend to occur close together in time. Behavioural groups are thus defined in three separate ways: using operational criteria such as the definitions of play and non-play, by correlated development and by temporal association. They are compared to find to what extent they correspond with one another.

The operational definition of play used in this study

Criteria were chosen which were as objective as possible while recognizing that there must be a subjective element in any definition of play. Ambiguity was minimized by excluding infant-care, sexual behaviour, solitary locomotion and object manipulation.

Lancaster (1971) counted infant-care by juvenile female rhesus monkeys as play only on the assumption that play has the function of providing immature animals with practice of adult behaviour. Owens (1975a) included sexual behaviour in young baboons as play not because of its appearance but because it sometimes occurred in bouts of activity with other, less controversial,play behaviours such as rough-and-tumble. Smith (1981) dismisses these as "dubious" play because they lack a structural component in their definitions. For the same reason Fagen (1981) does not consider them in his analysis of play.

The "comical" way an infant baboon runs and jumps might appear playful by human standards but that appearance could result from the degree of coordination of which its motor system is capable at that age. If so, then a distinction between play and non-play would serve little purpose. An analysis of motor coordination was beyond the scope of the study, so in the interests of rigorous definition all solitary locomotion was considered to be non-play. This even included acrobatic twisting and leaping because it was not possible to define an acrobatic threshold above which the pattern was playful and below which it was at an appropriate level of coordination.

In some studies manipulation and mouthing of non-nutritional objects has been regarded as play. This implies that food objects are not played with. Object manipulation was recorded in this study but no distinction was made between food and non-food, neither was an attempt made to distinguish a playful kind of manipulation. That would have relied too heavily on a subjective judgement. An investigation is made into the possible association between object manipulation and play on the basis of correlated development and temporal association.

The narrow definition limited play to social interactions. The response of the focal animal's partner was used as a test of playfulness in the focal animal. If the partner responded to the focal animal's potentially disruptive behaviour in a way which seemed compatible with that behaviour being play, then it was considered to be so - provided it contained one of the following structural features:

> a play-soliciting signal such as an approach with locomotor-rotational movements, lunging, bobbing or slapping and ducking away;
>
> the relaxed open-mouthed expression (play-face);
>
> movements with a relaxed but exaggerated quality.

Other aspects of play such as dominance role reversal, repetitive games and the absence of signs of intense threat or distress could not become apparent until the behaviour had continued for a while. They were therefore used for confirming a decision made on the other criteria.

3. Cause, function and development

The issues of cause, function and development have been mentioned several times and so it is appropriate to consider them now in more detail.

Cause

Behaviour is caused by internal and external factors. Internal factors might include neural or hormonal activity, homeostatic imbalance or, less tangibly, motivational state. External factors are the stimuli to which, and the contexts in which, animals respond.

One of the earliest causal explanations was that play is driven by surplus energy and is thus a channel through which the surplus is expended (Spencer, 1873). But Groos (1898) offered exceptions: as when a young animal, apparently exhausted by play, can be induced to play even more. Loizos (1966) has argued that the theory is unfounded, pointing out that high levels of energy have never been demonstrated to be a sufficient condition for play. Beach (1945) suggested that superabundant energy is an illusion produced by the greater general activity of young animals compared with adults. He also criticized the circular logic relating "surplus" energy and play - it must be surplus because the animal is playing rather than doing something important!

Some authors have attempted to explain play's motivation on the basis of its appearance. It is empirically true that play contains behaviour patterns which are also used in other functional contexts (e.g. chasing, fleeing, biting); that in play the sequences usually lack that component which would make them functional - the consummatory component (e.g. attack, escape or infliction of a wound) and that in play sequences which would otherwise be more likely to occur at different times may alternate frequently within one bout of activity (e.g. approach-withdrawal). These phenomena have been seen to represent a shift in the control of those behaviour patterns from their functional motivational source to a different motivation (e.g. Eibl-Eibesfeldt, 1963, 1975; Ewer, 1968; Lorenz, 1956; Meyer-Holzapfel, 1956; Muller-Schwarze, 1968). However, there have been different representations of this secondary motivation. Ewer and Lorenz are among those who have perceived a directness or intent in the animals they have watched, as if the animals were actively seeking play. From this they have inferred the existence of a specific play drive to which the behaviours become subordinated. Eibl-Eibesfeldt (1975) believes that the special motivation for play comes from a learning drive combined with motivation for motor activity. Meyer-Holzapfel and Muller-Schwarze have proposed that play is the result of an urge to be active in any way, which is itself the manifestation of a general activity drive.

These authors have used the concept of drive as if it were a real entity located in some physical structure or process within the nervous system, but their evidence for it is the behaviour itself. Invoking a drive simply restates the problem in a different way. Motivational models of this kind were criticized by Hinde (1959). They seek to explain complex, real phenomena, but use hypothetical and ill-defined constructs such as unitary drives and hierarchically arranged control centres. In the end they explain nothing and succeed only in oversimplifying the problem.

Nonetheless, there must be internal processes which cause playful behaviour. It may not be possible to comment with any authority on their organization but it might be possible to determine whether they operate in similar ways to those which control more obviously homeostatic behaviours such as in feeding or temperature regulation. Recent models of motivation for those kinds of behaviour are built on the premise that deprivation causes a deficit or imbalance which is corrected by an appropriate amount of an appropriate behaviour (Toates, 1980). The notion that play is not an obviously homeostatic behaviour seems logically to preclude the possibility of a homeostatic deficit. However, some experiments in which animals have been deprived of play seem to demonstrate rebound effects, that is, increased levels in certain measures of behaviour after deprivation. The results reported by Chepko (1971, goats), Oakley and Reynolds (1976, macaques) and Smith and Hagan (1980, human children) suggest the possibility of specific play motivation, but the conclusions are by no means clearcut. Chepko pointed out several weaknesses in the design of her study such as small samples and failure to take account of the effects of weather. What is more important, she did not measure any non-playful locomotions. This leaves open the possibility that all mobile activity increased after deprivation, which weakens the argument for separate control of play. Bekoff (1976) reported that in a follow-up study Chepko failed to obtain any statistically significant post-deprivation rebound effects. Oakley and Reynolds showed play rebound in one but not the other of the macaque species. Smith and Hagan demonstrated post-deprivation increase in "vigorous physical activities", the majority of which, they claimed, would probably be described by most observers as playful - "...but this was not required in the scoring procedure". The dependent variable was not necessarily play but vigorous activity; a wider and, in this case, more useful category - following the argument of Berlyne (1969). Muller-Schwarze (1968) concluded against specific play motivation. He found that, in deer, while there was some change in activity level after deprivation it was not specifically play that was affected. These few studies, with their shortcomings and ambiguities, leave the question of play deprivation effects unanswered and the problem of play's motivation unsolved.

It would be naive to think that there are stimuli sufficient to elicit play which are common to all the contexts in which play occurs. It is more likely that the causal system or systems operate in a wide range of stimulus conditions, not all of which need be present. Fagen (1981) points out that while the control systems of other more obviously homeostatic and reproductive behaviours may not be so flexible, the difference may be a matter of degree: "The system controlling play, like that controlling feeding or mating, seizes the best available resource patch (in terms of benefits and costs). In the case of play that resource patch may be a conspecific, an inanimate object, a living or dead prey item or even a suitably furnished space in the environment".

There have been very few analyses of specific stimuli which elicit play. It is a truism to say that play-soliciting signals are among the eliciting stimuli for social play but it is equally true, although less obvious, that the whole complex of signals which accompany play in one animal can stimulate another animal to participate (this was discussed earlier). Egan (1976) investigated the physical characteristics of objects which elicited predatory play in cats. She found that the most effective ones were those which made the object resemble live prey such as possession of fur, small size and movement. On the other hand, Poole (1966) suggested that aggressive play in polecats was elicited by stimulus complexes which were inadequate for eliciting true aggression such as a young polecat or an inappropriate object like a food bowl. Perhaps this difference is a suitable criterion for putting feline predatory prey in a separate category from aggressive play. In predatory play the animal might simply be making a mistake!

There have been some analyses of stimulus and contextual characteristics which elicit interaction with non-nutritional objects from primates. For example, Welker (1956) found that captive chimpanzees responded most to objects which provided conspicuous and complex stimuli: large size, bright colour, movement and complex shape, preferably curved. Welker (1956, chimpanzees) and Mason (1961, caged rhesus) have both demonstrated the importance of novelty in eliciting and maintaining a response, and further, that the nature of this response depends on the degree of novelty. Extreme novelty elicits fear and avoidance, moderate novelty promotes contact and familiar objects are usually ignored. Menzel's (1965) observations of the response of wild Japanese macaques to novel plastic toys show that there is no simple relationship between stimulus and response. The monkeys noticed, but did not contact, the objects when they were presented in one particular place yet they picked up and scattered identical objects when they were discovered in another place. These studies did not differentiate between explorative interaction and playful interaction. The distinction between the two will be discussed in a later section. Several authors have discussed the significance of novelty. Novelty is a function of the stimulus situation and the animal's previous experience. It has been suggested that the relationship between novelty and play or exploration is mediated through an intervening variable; conceptualized as a physiological state such as arousal (Baldwin and Baldwin, 1977), or as a psychological state such as "subjective uncertainty" (Weisler and McCall, 1976). The optimal internal state for play has been suggested by some authors to be one of moderate arousal, not so great as to be stressful (Baldwin and Baldwin, 1977; Mason, 1967; Schenkel, 1966; Symons, 1974; Welker, 1961). Hutt's (1966) experiments with human infants showed that a novel object is first investigated and then, when the child has become more familiar with it, is played with. Arousal theories have been used to account for this switching between exploration and play. Weisler and McCall (1976) suggested that exploration occurs when the degree of subjective uncertainty is moderately high, play occurs when it is somewhat lower. Baldwin and Baldwin (1977) set up a theory of reinforcement by sensory stimulation. Arousal is an intervening variable whose level is increased or decreased by, respectively, higher or lower levels of sensory stimulation and by greater or lesser degrees of novelty. Moderate arousal is positively reinforcing but high and low levels are negatively reinforcing. The sense organs are stimulated in both exploration and play,but more so in play. Thus, in a very novel and therefore arousing situation the animal explores rather than plays because play would be over-arousing and negatively reinforcing. Exploration will result in habituation of the arousal system as well as reduced novelty, to the extent that it becomes negatively reinforcing. Now play will be positively reinforcing because it will produce moderate arousal. The sequence, first explore, then play, is generated by the changes in reinforcement. Baldwin and Baldwin also use this model to explain long-term changes during development in the frequency and form of exploration and play. Habituation, which comes from age and experience, results in changes in the stimuli and actions which generate optimum arousal. Thus different amounts of different types of play are characteristic of different ages.

A weakness of models based on the concept of arousal is that arousal itself is a hypothetical construct (Bekoff, 1976) subject to the same criticisms that are levelled against drive concepts (Hinde, 1959, 1970). An arousal model of play cannot predict when an animal will play because it requires information on the optimum level of arousal; a quantity which can only be recognized to exist once play is happening. What is more, the presence of stimulus conditions which supposedly generate arousal can only be detected by the presence of the overt behaviour. Attempts to relate stimulus, arousal level and behaviour are therefore circular.

Bekoff (1976) reviewed theories of play and concluded a section on motivation in a tone of exasperation: "It is obvious that theorizing about play is getting us nowhere...". One presumes this is not a condemnation of theorizing but simply a recognition that internal processes have been postulated on the basis of insubstantial data. Theorists have tended to offer explanations which are generalized to a wide range of species, when data of the right sort are available only for a few species. They usually make the unsupported assumption that playful behaviour represents the same phenomenon in all species. Even within one species there is usually an assumption that all the observable forms of play (solo, social, object) share important causal factors and that there is a close enough link between play and exploration to warrant a simple model of causation.

One aim of the present study was to investigate the question of common causation between social play, locomotion and object manipulation. As stated in a previous section, it was hoped that groups of behaviour would be identified by development trends and by temporal clusters. It should never be argued that the behaviours within such a group necessarily share causal factors; but it is certainly the case that group members are strong candidates for common causation (Hinde, 1970).

Functions

Fagen (1981) prefaces his book with a question: why should animals spend time and energy and risk injury in performing apparently useless behaviour? Classical Darwinian evolutionary theory would suggest that such ubiquitous behaviour was not useless but had survival value. The question is not new, having been asked directly or tacitly by most authors who have written about play. It is at the heart of the play enigma.

Many theories of funtion have been proposed, mostly based on anecdotal or qualitative descriptions of play. Quantitative data with which to test them were scarce until the 1970's when several studies were published in response to the pleas for data referred to earlier. However, the data did little to prove or disprove any particular theories.

Fagen (1981) claims that this was because none of those theories had been formulated rigorously enough or on sound enough biological principles. He considers that it is the lack of adequate theory rather than the lack of data which has held up progress in play research. Fagen's theoretical framework acknowledges more than one function and its predictive value comes from the premise that the probability of play occurring in a particular context depends on a mathematical relationship between short-term cost and long-term benefits. It is likely to be the theoretical base of much future research.

Two themes appear in the theories of function: development and discovery. They are not mutually exclusive and the theories differ mostly in emphasis.

a. Theories emphasizing development

Developmental theories fall into four groups. One proposes that play provides a situation in which motor patterns are practised. Another considers that vigorous exercising of physiological systems aids general development. Another concentrates on the developing nervous system, saying that the particular stimulus patterns received during play are necessary for developing coordination and nerve connectivity. Another regards play as a socializing activity whereby young animals develop skills which will enable them to live successfully as adults in a social group. Socialization theories also rely on the possibility of discovery and learning through social play.

i. Development of motor patterns

The main thesis of Groos (1898) was that when a young animal performs in play behaviours which become functional only in mature animals, it is practicing the necessary movements. He was considering particularly play-fighting. Morgan (1900, cited in Beach, 1945), arguing from a theoretical position which emphasized the instinctive nature of behaviour, looked on practice in play as a means of refining an instinct by learning in a context where errors could be made without fatal results. Again, aggressive play provided the main example. More recent proponents of this practice theory have included Eibl-Eibesfeldt (1963) and Jay-Dolhinow and Bishop (1970). Smith (1981) speaks of socially competitive skills, without resorting to the concept of instinct. Such skills, which by definition are potentially dangerous, may be practiced in a safe context created by play.

A common experimental technique for investigating the significance of early social experience on behaviour development has been to isolate very young animals from social influences; but it is difficult to interpret the results. If a behaviour appears after isolation it might be tempting to conclude that the isolation conditions did not interfere with its development. However, it should be borne in mind that the relevant dependent variable might not be the presence or absence of the behaviour but, rather, the way in which the behaviour is performed. This might require subtle measurement of the precision or efficiency of movements; and a negative result could always be questioned on the grounds that measurement was not subtle enough. Studies which show behavioural deficit following isolation should be interpreted with particular caution (Hinde, 1971; Marler and Hamilton, 1966). Isolation prevents all kinds of social interactions and not just one aspect such as play. There may be little justification for attributing a result specifically to lack of play. Furthermore, isolation when young might induce behavioural abnormalities and levels of anxiety which interfere with an adult's behaviour patterns, even though it might be potentially capable of performing them. Finally, it could be argued that isolation is an ineffective method of depriving an animal of play if one considers that solitary play and play with objects might be equivalent to social play. This raises once more the problem of how play should be defined. Experimenters must be prepared to define their terms very precisely and then draw conclusions strictly within the limits of those definitions. If a behaviour is performed after a period of social isolation, it would be wrong to conclude that play is insignificant in the development; only that social play might be.

Such evidence as there is from isolation studies does not support the hypothesis that social play is a necessary prerequisite for the development of adult behaviour. Rats, which normally perform elements of mating in their play, were still able to mate as adults after spending their infancy in social isolation (Beach, 1942). Harper (1968) obtained a similar result with guinea pigs. Beach (1968) reared beagles in isolation and then compared them on measures of proficiency in sexual behaviour with socially reared controls. Both isolates and controls showed similar tendencies to behave sexually, although the isolates made more errors to begin with. Some isolates were just as proficient as the controls at mounting and intromission. Social contact was therefore not absolutely necessary in order that effective adult sexual behaviour should develop. The errors of orientation shown by the isolates may have resulted from the lack of opportunity to practice but, equally, other aspects of isolation might have been responsible. Rasa (1973) compared prey-catching behaviour of isolation-reared mongooses with pair-reared controls. The pair-reared subjects were able to deliver killing bites to the necks of mice at an earlier age (9½ weeks) than the isolates, who continued to aim their bites to all parts of the back until 13 weeks. It is tempting to conclude that the pair-reared animals had been able to practice their bites during social play, but Rasa warned against this. She attributed the behavioural differences to different levels of excitement in the test situation. The paired animals were more excited by the competition and mongooses are more likely to bite this way when excited.

The only isolation experiments to include tests of intraspecific aggression have been those of Harlow with rhesus macaques. It is surprising that there have not been more since the preponderance of aggressive patterns in social play would suggest that these were the most likely motor patterns to be practiced. Harlow (1969) has shown that whereas rhesus reared in total isolation were deficient in sexual and defensive behaviours, those reared without mothers but with regular access to peers developed normal responses. This at least suggests that access to peers has a beneficial effect on the later use of certain motor patterns but does not prove that play is responsible. If social play does have a role in motor pattern development, then it is likely to be concerned with the "fine tuning" or control of orientation and coordination of motor patterns which will develop anyway.

If deprivation experiments are to yield unambiguous results then they must be designed to allow infants to participate in all normal interactions with conspecifics and inanimate objects other than playful interactions. This would require long-term manipulation of the conditions which control play: a difficult task in view of the poor understanding of play's causes. However, insight into possible techniques is given by the short-term deprivation experiment of Muller-Schwarze (1968) and Oakley and Reynolds (1976) which were referred to earlier. They were able to distract young animals from play by offering them small amounts of food. Baldwin and Baldwin (1977) suggested that the amount of play is dependent on the amount of leisure time available. Oakley and Reynolds provisioned their macaques at a low level which required constant foraging, thereby allowing a minimum of leisure. Another promising approach is that of Bajpai (1980) who has achieved social isolation without physical deprivation by rearing rhesus infants in a forest area with no other monkeys and no contact with one another.

It may never be possible to achieve specific social play deprivation without interfering with other social behaviour but Einon, Morgan and Kibbler (1978) have gone some way towards it. They succeeded in denying young rats the opportunity to interact with a partner while allowing contact between them. The partners were drugged with amphetamine or chlorpromazine and although they were awake and mobile, they did not respond to the social solicitations of the experimental animals. Isolation-reared rats are slower to habituate in an open field test situation and slower to reverse a learned response than socially-reared controls (Morgan, Einon and Nicholas, 1975; Einon, Morgan and Kibbler, 1978). If isolates are allowed brief periods of socialization with normal partners their performance on these tests is intermediate between that of total isolates and normally-reared rats. Isolates who are allowed some contact with drugged partners perform on the tests more like the total isolates than like partial isolates. Two points are to be made. Firstly, social isolation had a very subtle effect on behaviour. It reduced flexibility: the rate of switching between behaviours. Secondly, interaction rather than mere contact with a partner seems necessary in order to promote behavioural flexibility. Once again, this does not prove that social play affects behaviour development but the implication is stronger than in any other deprivation study. Moreover, the subtlety of the socialization effect supports the view that, if anything, social play refines rather than establishes behaviour patterns.

Some situations which occur in the wild might be considered natural deprivation experiments. For instance, Baldwin and Baldwin (1973a, 1974) reported groups of squirrel monkeys in which the infants showed no social play because their time was occupied with foraging. They have also reported that small groups provide only a small number of possible play partners for an infant, who, as a result, will play less frequently than infants in a larger group (Baldwin and Baldwin, 1971). The effect of such restriction during infancy would only be seen in long-term studies where the resultant behaviour of adults is compared with that of adults in whose infancy there had been more opportunity to play.

Another approach to investigating the association between play and adult activity has been to compare in detail the motor patterns used in each context. Steiner (1971) described similar fighting motor patterns in the play and aggression of Columbian ground squirrels, with hits being aimed at the same places. He was in favour of the practice theory, proposing that aggressive patterns are improved in a context of limited possible damage. Bekoff (1976) looked for aspects in the play of young coyotes which correlated with successful prey-killing. Success was unrelated to the total amount of play, the frequency of agonistic patterns or of prey-killing actions. Only the frequency of pouncing and striking at play objects or partners was significant. It may be that the more practice of pouncing and striking there was in play the better they were performed later. But an alternative explanation might be that among the coyotes there were those individuals who pounced and struck frequently and efficiently, whatever the context, and those who did not. Black bears use similar biting and clawing movements in aggression and play (Henry and Herrero, 1974) but the orientation is more varied in play. Aggressive blows are confined to the side of the face and neck, but in play, while most blows are aimed here and possibly serve as practice, a large proportion go to other body parts.

In some cases important features of adult motor sequences are missing from, or appear infrequently in, play when other parts of the sequence may be present. In such cases the play can hardly provide practice for the missing or depleted actions. For instance, in the play-fighting of polecats biting occupies only two percent of the time as opposed to forty percent in true fighting (Poole, 1978). Rats have been reported to have no sex play or prey-catching play (Poole and Fish, 1975) yet these types of behaviour are present in adults.

Aggressive displays are absent from the social play of black bears (Henry and Herrero, 1974), polecats (Poole, 1966, and Poole and Fish, 1975), rhesus macaques (Symons, 1974) and olive baboons (Chalmers, 1980a). There is a danger of circular reasoning here. We may not be justified in concluding that play does not offer practice of aggressive displays, for should the animals have shown such displays the observer might not have categorized the behaviour as playful. Owens (1975) and Cheney (1978) both incorporated lack of threat display or loud vocalization into their definitions of play.

Play frequently contains motor patterns which are either absent from or present to a lesser degree in non-play contexts. Presumably they are not being practiced for another functional setting. For example, in the sex play of squirrel monkeys both males and females use the sex behaviour of either sex (Latta, Hopf and Ploog, 1967). Young howling monkeys spend a lot of time play-wrestling but no aggressive contact-fighting is seen in adults (Carpenter, 1934). Richard (1970) supports this observation to the extent of saying that adult fighting is extremely rare, but she does describe one fight between adult males which involved competitive pushing. Each attempted to push the other off the branch. Owens (1975b) reported that in female olive baboons aggressive encounters contain no mutual contact such as sparring or wrestling, yet both of these patterns appear in female play. On the other hand, the play-fighting of male baboons becomes more like aggressive fighting as they get older. It is conceivable that play-fighting has a different function for each sex.

If play provides opportunities for practice then one would expect to see improvements during or between sessions. Few authors have commented on this but Poole (1966), for example, has stated that in polecats the form of play motor patterns does not change with experience. Play is stereotyped with motor patterns appearing in their complete, perfect form at their first performance. His example of the neck-bite being precisely aimed and quite distinct from, and not arising out of, indiscriminate biting was questioned by Lazar and Beckhorn (1974). They argued that all biting is precise in that the bites land just where they land and deny that neck-biting is a special case. In their view neck-biting develops out of general biting of partners' bodies. They considered that the concept of play hinders our understanding of behaviour development because it focuses attention on adult forms occurring in infant behaviour which by definition are recognizable and complete. Fox and Clarke (1971) traced the development in infant coyotes of several motor patterns associated with aggression. Far from improving in play, they developed to sufficient proficiency to be used as a truely aggressive fight before any recognizable play was observed.

The evidence suggests that functional behaviour can and does develop outside of play. However, it is clear that adult patterns do occur in play and it is reasonable to assume that whenever an action is performed there will be some practice effect which improves later performance and so confers selective advantage (Hutt, 1966). Loizos (1967) recognized this and referred to the lack of evidence that the playful performance of motor patterns rather than their serious performance is required to bring about improvement. She said: "...it is not necessary to play in order to practice: there is no reason why the animal should not just practice". But such a statement ignores the problem of what is meant by play. If play implies only fragmentation, reordering and combining various behaviour types then her statement is reasonable. If, however, it implies exaggerated locomotor rotational movements and the play-face then it becomes less reasonable. It might be quite necessary for two young animals to transmit such play signals in order to maintain contact and continue an interaction involving aggressive or otherwise potentially dangerous or disruptive motor patterns in safety. Smith (1981) concluded that play functions to provide a safe context in which socially competitive behaviour can be performed. Indeed, Loizos made the point in a later paper (1969) that certain of the characteristic features of play, particularly role reversal, might be mechanisms which allow potentially disruptive interactions to continue. Similarly, the restrained nature of play-fighting, particularly of biting, seems a necessary requirement for continued practice by promoting, in Altmann's (1962) terms, stable and fair games. The paradox is that because play is restrained, reordered and possibly ritualized, it does not provide an accurate simulation of a "real" situation.

This discussion has concentrated on behaviours which seem more relevant to adult life than to that of infants (e.g. fighting and prey-catching). It has concentrated on pre-practice in play. But what of motor patterns which are functional at all ages, such as locomotion? Is it not possible that play provides a special opportunity for the development of, say, running, jumping and climbing? Fagen and George (1977) found that horses gallop, turn and kick more in play than in non-play. Rose (1977a) found that olive baboons run very little except in play and that most leaping and jumping and half of all climbing occur in play. Van Lawick-Goodall (1968) claimed that infant chimpanzees were more proficient at swinging and leaping by the end of repeated swings and leaps compared with the beginning. By her definition the swings and leaps constituted locomotor play. But are these low level categories of behaviour (running, jumping, etc.) subject to development themselves or do they merely create the playful context in which higher categories of behaviour (fighting, prey-catching, etc.) are modified? One aim of the present study was to investigate the possibility that locomotor patterns are practiced in social play.

Improvement of motor pattern performance at this level is seldom seen as a practice phenomenon but more often as an example of physical training improving coordination and strength.

ii. Physical training

Performing an action in play might not benefit that action specifically. It may be that any action in play increases the body's strength and agility so that there is an overall improvement in the way it behaves. This point of view has been taken by a number of authors, either as a sufficient explanation of play's function or as a supplement to a more specific theory. Groos (1898) allowed that play stimulated the development of muscles and bone while exercising "instinctive" motor patterns. Brownlee (1954) suggested that the muscle blocks stimulated during play were those which would not otherwise receive much stimulation until they were used in the mature animal for escape, fighting, prey-catching and reproduction. If a growing animal did not use these muscles they might not develop fully. Rasa (1971) has described the aggressive play of elephant seals as practice which leads to "corporate agility". Beach (1945), Farentinos (1971), Hinde (1971), Jay Dolhinow and Bishop (1970), Loizos (1966), Muller-Schwarze (1971), Poirier and Smith (1974), Simonds (1974) and West (1974) are among those who have mentioned the possible training effect of play on muscles, skeleton and cardio-vascular systems.

Fagen's (1975, 1976 , 1981) far-reaching theoretical framework has as one of its main themes that the vigorous exercising of physiological systems in play brings the body towards an optimum level of functioning, and, as a result, growing animals take an efficient body with them into maturity. This enables them to cope better with environmental stresses and gives them a greater chance of survival and reproductive success. The probability of play evolving in a species or of being performed by a particular age/sex class or even of being performed by an individual in a particular situation depends, according to Fagen, on the balance of short-term costs and long-term benefits. The value of this theory lies in its predictive strength. A complete review of it is beyond the scope of this thesis, but three of its predictions are pertinent to the present study and will be mentioned here.

The form of play:

The motor patterns used should be those which produce a training effect most efficiently. An effective play exercising regime would both develop particular muscles and increase stamina. This would be achieved in play bouts combining wrestling with chasing: static overload exercise in wrestling benefits particular muscles and prolonged chasing increases stamina. Indeed, such play bouts are among those most commonly described in the literature. What is more, an efficient training regime should be interrupted and repetitive; again two observed features of play.

Following Brownlee's (1954) suggestion that play exercises those muscles which would otherwise not be used, Fagen regards the "capers, jinks and gambols" and intermittent running and leaping of play to be examples of emergency behaviour whose other functional contexts are in predator avoidance, fighting and responses to accidents such as falling.

Play partners:

An animal can maximize the benefits from exercise if it chooses as a play partner another animal which is likely to "play back" with sufficient intensity to provide an effective exercise regime yet not so intensely as to be a danger. This prediction seems to be borne out in the few studies in which animals have had a reasonably wide choice of partners. They tend to choose partners of approximately equal weight, strength and vigour as themselves. Their partners tend to be of like age and sex, or, if of different sexes, the female tends to be the older. Very wide age differences are avoided, at least by the younger party (e.g. in primates, Altmann, 1962; Cheney, 1978; Fady, 1969; Hall, 1962; Jay, 1965; Owens, 1975a; Simonds, 1974; Voland, 1977; polecats, Poole, 1966; ibex, Byers, 1980). It is interesting to note that in interspecific play between colobus and vervets (Rose, 1977) infant colobus tended to play with juvenile vervets. Since colobus is the larger species this was in fact a size match.

Fagen's is a sociobiological theory which looks at the benefits from play in terms of the inclusive fitness to be derived. From the viewpoint of kin selection the theory predicts that siblings will be preferred partners. This is upheld in the few studies to have tested it (in macaques: Fady, 1969; baboons: Cheney, 1978; Owens, 1975a; ibex: Byers, 1980). Mothers should play with their offspring but there are few references to this in wild groups (sea lions: Farentinos, 1971; seals: Wilson, 1974; chimpanzees: Van Lawick-Goodall, 1968).

Life-history strategies :

Exercise has a greater effect on a young, growing body than on an adult (references in Fagen, 1981), so play should be more frequent in the young. Between birth and the juvenile period the balance of costs and benefits changes. Before an infant has developed thermoregulation the energy costs of muscle activity outweigh the benefits of exercise. When it becomes endothermic and has also developed the ability to walk an infant should start to play. Maximum play should occur when there is a maximum difference between cost and benefit - when young enough to benefit substantially from exercise yet not so young as to lose heat too rapidly nor so old and heavy as to expend too much energy. Time playing is time lost from feeding. It also represents time in a position vulnerable to predators. Thus maximum play should occur at an age when food and protection are provided by the mother and the infant is strong enough to be very active. This should be just prior to weaning. Play should decrease during the period of weaning and maternal rejection but maybe increase once more when the young animal's foraging efficiency is great enough to support the energy demands of play. Thus play might have a unimodal or bimodal time course (Fagen, 1980). There have been too few long-term studies to adequately test this hypothesis but there is some evidence of a decrease in measures of play when parent-offspring conflict is high because of weaning (olive baboons, Nash, 1978; Owens, 1975a; sheep, Sachs and Harris, 1978). On the other hand, experimental studies with cats appear to contradict this. Early weaning has been simulated by separating kittens from their mothers (Bateson and Young, 1981) and by interrupting lactation with bromocriptine injections (Bateson, Martin and Young, 1981). The effect in each case was an increase in the frequency of play, especially play directed to objects. The mothers' behaviour also changed. They effectively helped the kittens take solid food. Kittens did not suffer from lack of energy input and this might have confounded Fagen's prediction.

iii. Neural development

When animals behave in an exaggerated, fragmented, playful way it is likely that their nervous systems receive patterns of stimuli which are different from those received at other times. For instance, proprioceptive inputs are likely to be different. It might be that such patterns are beneficial to a developing nervous system (Bekoff, 1976).

Post-natal development of the central nervous system has been shown in a number of mammals (review by Bekoff and Fox, 1972). Maturational changes have been reported in such parameters as cell density, synaptic connectivity, dendritic branching, myelination and enzyme activity. Bekoff and Fox took the view that the course of neural ontogeny results from an interplay of genetic and environmental influences. Neural structures are set up under direction from the genes but adequate environmental stimulation is required for proper development. The effects of rearing conditions on neural development have been investigated by a number of authors. Stimulus enriched environments tend to promote the development of greater complexity in the central nervous systems of rats - in terms of connectivity or dendritic branching - than impoverished environments (Globius, Rosenzweig, Bennett and Diamond, 1973; Schapiro and Vukovich, 1970; Holloway, 1966). It was not clear from these studies which stimulus modalities provided the effective inputs for neural change, but there is strong evidence that direct contact and manipulation of the environment and of social partners is necessary, rather than the perception of complexity at a distance (Ferchmin, Bennett and Rosenzweig, 1975; Ferchmin and Eterovic, 1977).

During play young animals move through the environment altering their behaviour in response to environmental changes, which might have been brought about by themselves. It is conceivable that qualities of interaction unique to play can generate the optimal stimuli for a developing nervous system. A greater knowledge of play's characteristics is needed before those qualities can be identified and their role in neural development understood.

iv. Play and socialization

Of all the behaviours categorized as play that between two or more conspecifics - social play - is perhaps the most easily recognized and most commonly described. It stands in contrast to agonistic fighting which is the other social behaviour involving extended and vigorous close contact and locomotion. At the end of an aggressive bout the participants are usually at a greater distance from one another than they were at the beginning, whereas a play bout usually ends with the participants remaining close. This difference has been used as part of an operational distinction between aggression and play (e.g. Bekoff, 1972). Play appears to be socially cohesive and the possible importance of social play in maintaining the integrity of groups or of keeping young animals within a home area, whilst still allowing them to have bouts of extended locomotion, has been noted by, for example, Poirier (1970), West (1974), Wilson (1974) and Wilson and Kleiman (1974).

The fact that some young animals spend a high proportion of their time in such cohesive, apparently amicable interactions has led many authors to conclude that social play provides an opportunity for them to learn such things as the properties and characteristics of their social companions, to develop bonds of affection, to learn the subtleties of communication and to practice the competitive aspects of social life: that is, social play has been seen as a means by which to develop those skills and attitudes which will enable animals to live adaptively with other mature members of a social group (reviews by Poirier and Smith, 1974; Dolhinow and Bishop, 1974; Bekoff, 1972; Jolly, 1972; Loizos, 1967; Simonds, 1974; and Smith, 1981). Different authors have emphasized different aspects of play's possible socializing role. A summary of these is given in Table 2.

Jolly (1972) has taken the socialization theory for granted, saying that despite a lack of systematic proof it is an obvious conclusion that play with peers determines in some way an animal's behaviour as an adult. Meier and Devanney (1974) have formed the opposite conclusion,that play need not have a socializing role, from the evidence that rhesus infants are able to take part in successful social relationships with their mothers during the ontogeny of social play. This point of view assumes that infant-mother and infant-peer social interactions are equivalent in terms of communication, tolerance and bond development. But it seems unlikely to extend to the very specific social skills involved in developing dominance relationships or learning sex or parental behaviour.

If play does have a socializing influence it is unlikely to be the only such influence in a young animal's life. It is pertinent to refer once more to Baldwin and Baldwin's (1973, 1974) observations that social play between infants is not a universal feature of all free-living groups, even of the same species, and so may not be a necessary requirement for adaptive socialization. But we must remain cautious here, until long-term studies have investigated the social success of adults who were themselves non-playing infants.

b. Theories emphasizing discovery

Development of social skills requires that the properties of social companions be discovered. A young animal must also discover how best to behave so as to benefit from a social situation. It has been suggested that play with group members is a context in which an animal learns how it and others behave in certain circumstances (e.g. Farentinos, 1971; Fedigan, 1972; Poirier and Smith, 1974; Rhine, 1973). Loizos (1967) has even likened the process to imprinting. Such learning may not be confined

Table 2

POSSIBLE ROLE OF PLAY IN SOCIALIZATION	REFERENCES
Promotes group cohesion.	Bekoff 1974, Horwich 1972, Poirier 1970, West 1974, Wilson 1974, Wilson and Kleiman 1974.
Encourages the copying of other individuals and so promotes co-ordination of group activities (allelomimetic).	Bekoff 1972, Horwich 1972, Scott 1968.
Enables young to become familiar with other group members.	Carpenter 1934, Etkin 1964, Farentinos 1971, Fedigan 1972, Horwich 1972, Loizos 1967, Simonds 1974, Wilson 1974, Wilson and Kleiman 1974.
Promotes the formation of bonds of affinity and affection.	Harlow and Harlow 1965, 1966, Jay 1963, Poirier and Smith 1974, Schaller 1972, Simonds 1974, West 1974, Wilson 1974.
Young develop tolerence of others and learn to inhibit their own aggression.	Bekoff 1972, Jay 1965, Wilson and Kleiman 1974.
Young learn to anticipate the behaviour of others.	Fedigan 1972.
Young learn the relationships and affinities between others.	Fedigan 1972.
Social experimenting - discovering the physical and psychological attributes of others.	Carpenter 1934, Gentry 1974, Jay 1965, Rhine 1973, Simonds 1974, Simpson 1976.
Communication - learning the subtleties of sending and interpreting social messages.	Bekoff 1972, Baldwin 1974, Jay 1965, Jolly 1972, Mason 1960, 1961, 1965, Miller, Caul and Mirsky 1967, Mitchell 1972, Poirier and Smith 1974, Suomi 1973.
Learning future parental roles.	Baldwin 1969, Simonds 1974, Lancaster 1971.
Learning future sexual roles.	Baldwin 1969, Greiff 1976, Kagen and Beach 1953, Mason 1965, Simonds 1974.
Establishing dominance relationships.	Altmann 1962, Baldwin 1969, Bekoff 1972, Carpenter 1934, Harlow and Harlow 1965, Jay 1965, Poirier and Smith 1974.
Developing socially competitive skills.	Smith 1981.

to social events. Through play information might be gained about inanimate objects and their relationships with the environment and the playing animal (e.g. Welker, 1961). The literature also contains reminders that we should not consider play to be the only possible way for information to be gained, animals presumably learn through their total experience (e.g. Bekoff, 1972; Loizos, 1966; 1967; Thorpe, 1963).

When an animal manipulates or reacts to objects in ways which do not seem to confer immediate advantage (they are not eaten, removed as obstacles, formed into a nest or used as a tool) or when it moves around orientating the sense organs towards different features of the environment, it could either be said that the animal is exploring or that it is playing. The distinction has not always been made clear in the literature. By definition, an animal seeks information when it explores, and during play it may well gain some information - as well it might when it performs any type of behaviour. Seeking information has not been used as part of any definition of play yet Lorenz (1956), for example, considered exploration and play to be identical phenomena. Sometimes the differences in form and possible function have been seen only as matters of degree within a continuum (e.g. Baldwin and Baldwin, 1977; Fagen, 1974; Poirier and Smith, 1974; Weisler and McCall, 1976; Welker, 1956a,b). Sometimes those degrees of difference have been seen as significant (e.g. Hutt, 1966).

On what grounds can play and exploration be considered the same? Welker (1961) proposed that they both function to maintain a flow of stimuli into the animal and so keep it alert and in contact with the changing environment. Poirier and Smith (1974) equated them on the assumption that they both result in passive learning (i.e. learning without an obvious reward). Welker (1961) asked whether chimpanzees would learn the properties of play objects and so gain insights into the solution of a problem which called for the objects being used as tools. He found that any such insights were not used profitably until some time after the play bout. The playful activity seemed to inhibit problem solving in the short-term. Hutt (1966) found that children who played with a novel object very soon after meeting it for the first time sometimes failed to discover all of its properties. Weiss-Burger's (1981) study of polecats suggests that play only facilitates the learning of tasks requiring the same sensory and motor processes as the play behaviour itself. Barnett (1958, 1963) suggested that play might have a general, positive effect on learning ability: deutero learning or "learning how to learn", but the above investigations indicate a negative relationship between play and discovery at least in the short-term. Muller-Schwarze (1968) commented on the apparent similarities of play and exploration in young blacktailed deer. They are both intermittent and can occur together in the same bout of activity. He asked whether they are similarly motivated. If so, then he expected significant positive or negative correlation between their frequencies. He defined several exploratory behaviours which included orientation of the sense organs towards objects or partners and manipulations such as digging and pulling. Play included vigorous locomotion and sexual and aggressive patterns. He found no significant correlation between measures of play intensity and exploratory frequency and concluded that they do not arise from the same motivation. However, this finding should be viewed in the light of Miller's (1957) and Hinde's (1959) observations that we need not expect to find a correlation between different outputs from the same motivational system. Hutt's (1966) experiments with nursery school children demonstrated important differences between exploration and play both in their form and the order in which they occurred in response to a novel object. Typically, the subject first explored the object in an economical, directed manner (specific exploration), gathering information to discover what the object was like and what it could do. Secondly, the subject played with, on or around the object (diversive exploration), perhaps discovering what he or she could do with it. This is consistent with Barnett's (1958) finding that neonatal rats explored the environment around their nest for 17 days, beginning as soon as their eyes were open, and then repeatedly re-explored the area during play. Fagen (1981) offers a functional explanation for this temporal relationship. His theory predicts that play will occur in a supporting, benign environment as a strategy for generating testing situations. The animal's decision to play depends on its knowing when it is in such an environment and whether the environment is likely to stay benign long enough for an investment of energy in play to be worthwhile. Therefore in a novel situation play is preceded and possibly interrupted by periods of exploration.

The question must be asked: are there any features of play which would make it especially suitable as a context for discovery and learning? It has already been argued that the use of play signals enables animals to continue interacting and to maximize the chance of social learning. But several authors support the view that other features of play make it more suitable for information gathering than non-play behaviour (e.g. Fagen, 1974; Fedigan, 1972; Van Lawick-Goodall, 1968; Leyhausen, 1965; Poirier and Smith, 1974; Simpson, 1976; Washburn and Hamburg, 1965; Welker, 1961). These features include repetition, exaggeration, fragmentation and recombination. Play has frequently been thought of as a means of subjecting objects, situations or social partners to random or unusual stimuli which cause them to react in ways which yield extra information which had remained undiscovered during a more systematic examination (e.g. Fagen, 1974; Fedigan, 1972; Leyhausen, 1965; Van Lawick-Goodall, 1968; Simpson, 1976). Hutt (1966) suggested that during play new features or situations are thrown up which can then be investigated.

It is appropriate here to refer back to the motor pattern practice theory of play. One way of formulating it, which emphasizes discovery, is to say that in play situations are created in which those motor patterns can be tried out. For instance, domestic cats cause small objects to move when they hit at them in play. They can then perform some elements of prey-catching such as pouncing and biting (Egan, 1976).

When an animal uses newly acquired motor patterns in the context of play, it might not answer for itself the question: "how is the behaviour performed?", as the practice theory proposes, but rather: "what happens when the behaviour is performed in this situation?" In play, behaviours are combined which would not otherwise be performed together. This has been seen as an opportunity to learn new patterns of activity (Eibl-Eibesfeldt, 1963) and to discover the effects of a more flexible behaviour repertoire (e.g. Bruner, Jolly and Sylva, 1976; Fagen, 1974; Fedigan, 1972). Thorpe (1963) saw this flexibility arising from the "...freeing of appetitive behaviour from the primary needs..." and suggested that it widens the potential perception and mastery of the environment. Simpson (1976) has drawn parallels between the play of young animals and human scientific investigation. The analogy extends to the notion that play constitutes controlled experiments. Perhaps, through play animals can categorize the world and calibrate their own movements; testing speed, strength and accuracy according to how the environment responds. A growing, developing animal will presumably require constant recalibration. Fagen (1981) uses the metaphor of debugging a computer programme to describe the process of learning from mistakes. The quality described as exuberant, spirited or energetic could be a means of exposing the environment or the playing animal itself to unusual stresses so that mistakes become more likely. An example is given by Van Lawick-Goodall (1968). An infant chimpanzee fell from a tree when a thin branch broke because she jumped on it during exuberant and uncautious locomotor play. After that experience she tested small branches before trusting them with her weight. In cautious, peaceful, non-play locomotion through trees the same branch would have borne her weight. The extra forces exerted during play resulted in the infant learning something about thin branches.

This anecdote raises once more the problem of how play should be defined, and in particular whether the concepts of locomotor play and object play are at all useful. It might have been more realistic simply to have said that the infant chimpanzee was uncautious rather than to have invoked playfulness. Both are suitable adjectives but "uncautious" relates more to the observed effect. Play, exploration and accidents do not follow a simple sequence of (in the terms of classical ethology) orientation, appetitive behaviour and consummatory act. This might distinguish them from other more obviously homeostatic behaviours but it makes them difficult to distinguish from one another. Hutt (1966) considered this problem and saw that it was compounded by our eagerness to categorize the behaviour of the young as playful. There is more novelty in the environment of an infant than of an adult (also Welker, 1956a,b). Infants are therefore likely to spend more of their time investigating. The behaviour of human infants (and Hutt generalized to other species) is often repetitive - a characteristic of play. Thus frequent exploratory behaviour performed in an apparently playful way by infants, who we expect to play a great deal, has led to the two types of behaviour being linked more closely than is really justified. During ontogeny exploration might decrease and a clearer dichotomy might appear between playful and exploratory behaviours. Yet, Hutt says, we transfer the assumption that they are equivalent from the infant to the older animal and ignore the distinctions.

The narrow operational definition of play in the present study excludes object manipulation. An attempt is made during the analysis to find links between behaviour towards objects and behaviour towards play partners.

Development of play

There have been few longitudinal studies describing age changes in play. More quantitative data are needed on changes in such parameters as total time, motor pattern frequency and form and choice of partners, with ages sampled at small enough intervals to detect slight variations in rate of development and precise times of peaks and troughs.

Some quantitative studies have measured frequency changes between more or less broad age ranges (e.g. Barrett and Bateson, 1978, cats;

Voland, 1977, marmosets). When the present study was begun there had been few investigations of motor pattern frequency changes through small increments of time (e.g. Harlow and Harlow, 1965; Hinde and Spencer-Booth, 1967 for captive rhesus) but recently there have been more (e.g. Chalmers, 1980; Cheney, 1978; Nash, 1978; Owens, 1975a,b for baboons; Meier and Devanney, 1974 for rhesus; Barrett and Bateson, 1978 for cats). The studies of Chalmers, Cheney, Nash and Owens are of particular value because they are of wild populations.

Trends in play development

There is not enough information with which to make detailed comparisons between taxa but it is possible to identify some very general trends in play development.

i. Increasing complexity

The full play repertoire is not seen at the first appearance of play; elements appear at different ages. For instance, in reindeer (Espmark, 1971) and blacktailed deer (Muller-Schwarze, 1971) the first play patterns are solitary running and jumping which are later performed in peer groups, either as parallel locomotion or as social chases. Social contact patterns, such as butting and striking with the forelegs, appear next and, in blacktailed deer at least, mounting is one of the last patterns to develop. The final repertoire comprises playful escape, fighting and sexual behaviour. The first play patterns in rats (Muller-Schwarze, 1971) are solitary running and exploration, to which are added attacks on peers and then chasing. Polecats (Poole, 1966) begin with contact play with littermates, such as neck-biting and rolling, which is later combined with non-contact locomotor patterns such as "dancing", chasing and jumping. The trend of increasing complexity is also seen in primates. Weisler and McCall (1976) compiled a developmental sequence from several accounts of human play. The earliest form is pure investigation of objects by very young infants. This leads to imaginative manipulation play. Social play begins as solitary actions in the company of others, progressing through parallel and imitative play to playful interactions between pairs or within groups. Harlow and Harlow (1963, 1965) identified stages in the development of social play in captive rhesus monkeys progressing from simple to complex and solitary to social. The first "exploration" stage involves body contact with, and manual and oral manipulation of, stationary objects and later moving objects and peers. The reactivity of moveable objects and peers leadsto the stage of "interactive play". Here, rough-and-tumble peer contact play and approach-withdrawal non-contact play develop first as separate activities and then become integrated into sequences. In the final "aggressive" stage the rough-and-tumble become intensified, appearing more and more like serious fighting. Harlow and Harlow maintained that rough-and-tumble and approach-withdrawal appear at the same age and show parallel age changes in frequency. This point was contradicted by Hinde and Spencer-Booth (1967) who showed that rough-and-tumble in captive rhesus makesup a greater proportion of social play than approach-withdrawal and increases in frequency relative to approach-withdrawal through the first year. Kaufman (1966) showed that in wild rhesus social play with little or no contact was typically seen for the first time in weeks 3 to 4 whereas play with frequent contact typically appeared later, in weeks 6 to 7. For rhesus monkeys, then, the picture is confusing but two studies on play development in wild olive baboons show some agreement (Chalmers, 1980[a,b] and Owens, 1975a). Owens described rough-and-tumble patterns occurring first, but approach-withdrawal eventually becomes the more frequent pattern. Chalmers (1980) showed indirectly that mouth-and-wrestle (equivalent to rough-and-tumble) develops before locomotion becomes frequent in play. The development of social play in semi-wild, "monkey jungle"squirrel monkeys (Baldwin , 1969) begins with exploratory interactions, followed by contact play and finally non-contact locomotor play. In langurs (Poirier and Smith, 1974) the sequence is: exploration, then chasing, then wrestling, then integrated chasing and wrestling. Social play is a very complex type of behaviour. Even when it has been divided into the simplest of categories - contact versus non-contact -

no consistent pattern of development has been demonstrated across the primates, or even, in the case of rhesus, within a species. We are not in a position to explain inter-study differences in terms of environmental or social conditions. More quantitative data must be obtained, which is one of the aims of the present study.

ii. Play becomes more like the serious adult equivalent

As a young animal becomes older there is an increase in the frequency of play bouts in which the play-fighting becomes more and more intense, sometimes resulting in one partner being hurt (e.g. Blacktailed deer, Muller-Schwarze, 1971; Columbian ground squirrels, Steiner, 1971; lions, Schenkel, 1966; polecats, Poole, 1966; domestic dogs, Fuller, Easler and Banks, 1950; howling monkeys, Carpenter, 1934; rhesus monkeys, Altmann, 1962; Harlow and Harlow, 1965; vervets, Fedigan, 1972). Baldwin (1969) described the proportion of playful threats in the play-fighting of male squirrel monkeys increasing with age. With wild olive baboons (Owens, 1975a) the proportions of certain motor patterns in male play-fighting become similar to those in true aggression. Clinging and mouthing decrease while sparring (contact at arms' length) increases. Females, however, show no such convergence of play and aggressive patterns. There is very little contact in female aggression but the level of contact in play-fighting remains the same.

iii. Ages of peak frequency

The frequency of play bouts increases to a peak during infancy and then decreases towards adulthood (e.g. blacktailed deer, Muller-Schwarze, 1971; polecats, Poole, 1966; domestic cats, West, 1974; captive rhesus, Harlow and Harlow, 1965; Hinde and Spencer-Booth, 1967; wild baboons, Cheney, 1978; Nash, 1978; Owens, 1975a). Some studies have shown there to be two peaks during the ontogeny of play. Sachs and Harris (1978) reported this for domestic lambs. Hinde and Spencer-Booth (1966) found, in captive rhesus, slight evidence for a second peak at about one year when the young animals were fairly independent. Cheney (1978) found a second peak at about one year in chacma baboons and Nash (1978) observed one at about ten months in anubis baboons. Fagen's theory of energy budgeting, discussed earlier, suggests that it is the trough between two peaks which must be explained rather than the peaks themselves. It predicts that the trough is caused by weaning.

Studies of age changes in play are most valuable when the changes are shown alongside the development of other behaviours. Unfortunately there have been few quantitative studies of this kind. Age changes in play frequency have been compared with the ages at which social changes occur. For instance, Bekoff (1974) found that captive wolves and beagles reached the age of peak play frequency before they formed dominance relationships, whereas coyotes and red foxes settle dominance relationships through aggressive interactions before play becomes frequent. Fox and Clarke (1971) also found this in coyotes. Play may have a socializing role in wolves and beagles, which are the more highly social canids. Changes in measures of play in cats have been shown to broadly coincide with changes in the family environment. They begin to play less with littermates and more with objects at about four months, when they are almost adult size, independent from their mothers and capable of finding their own food (West, 1974). Until then, West suggested, social play had been a cohesive force keeping the litter within the home area. Its decline comes at an age when young cats would be expected to start independent lives. Bateson _et al._ (1981) found that play actually increased immediately after early weaning. They suggested that early weaning might be a signal to the kitten that there is little food in the environment and that they should "...accomplish as much play as possible..." before they become independent. In primates play development has been described against the background of the changing mother-infant relationship. Hinde and Spencer-Booth (1967) considered that increasing frequency and vigour of play in captive rhesus infants becomes more and more of a nuisance to mothers and may be one of the factors stimulating maternal rejection. Nash (1978) found that play in wild infant olive baboons decreased at the age of maximum rejection and suggested it was because they spent more of their time trying to stay near their mothers and so had less time for play. However, Cheney (1978) found no correlation in wild chacma baboons between the decline in play frequency and the incidence of infant tantrums brought on by maternal rejection. Nash's results are consistent with the prediction from Fagen's energy budgeting theory, but Cheney's are not.

Only in Chalmers' (1980a and b) study of wild olive baboons have data been presented comparing the development of motor patterns in both playful and non-playful contexts. His findings will be referred to in results chapters where comparisons will be made between his investigation and the present study.

4. A formal statement of the aims of this study

The principal aim was to describe how the frequency of play and of the motor patterns used in play and non-play changed with age. It was also hoped to investigate the effect of the relative ages of play partners on the form of play.

The context in which motor patterns first appeared and in which they first became frequent would be identified by comparing development trends in play and non-play. Furthermore, the observed changes would be viewed in relation to other changing aspects of the life of young baboons (e.g. mother-infant relationship and colour change). These observations might contribute to an understanding of the role of play in behaviour development.

The possible heterogeneity of play would be investigated in the following ways:

1. by looking for correlations between the development trends of locomotor patterns, wrestling and object manipulation and so identifying developmental groups;
2. by looking for temporally associated clusters of behaviour;

3. by looking for correlations between behaviours such that individuals who score highly on measures of one also score highly on the others;
4. by asking whether the behavioural groups so defined correspond.

Chapter 2. Procedures

1. History, study areas, material and methods

History of the present study

The data analysed here were collected between February 1972 and November 1973 in the safari parks at Woburn, Bedfordshire and Blair Drummond, Perthshire. The Woburn phase lasted thirteen months, finishing in March 1973 when the baboons were removed from the park as part of a change in management policy. The same company ran the park at Blair Drummond, which retained its baboon colony, and the study was continued there in September 1973. That phase lasted ten weeks. By the end of November severe cold and damp were affecting the behaviour of the baboons and so no more data were collected.

Study areas: the safari parks

Woburn:

The monkey enclosure had an area of approximately four hectares. About three quarters of it were taken up by a mature oak and beech wood. The trees were well spaced and between them the ground was fairly level, although there were some bumps and depressions. There were tussocks of grass and vehicle ruts but overall it was reasonably flat. The other quarter was flat and grassy with occasional mature oaks. At different times during the period of study zebra and bears shared the enclosure with the baboons.

Blair Drummond:

The enclosure was approximately five hectares. It was very flat and grassy, without a definite wooded area but with scattered, large, mature sycamore trees. Two young elephants, four zebras and some eland were present throughout the study period.

Both parks had sheds with bedding straw which the baboons and other animals used during the day and night.

Both colonies were fed twice per day on a similar diet of vegetables and fruit (whatever was available), supplemented with vitamin and mineral enriched livestock pellets. The food was unloaded from a vehicle in an accustomed spot with little attempt to scatter it.

Although this may have provided an adequate diet, the baboons still spent a large proportion of their time foraging for roots, young shoots, leaves, buds, bark and so on. On two occasions at Woburn I saw adult males eating meat - a bird and a rat.

The parks were open to the public who were able to drive through the monkey enclosures on metalled roads. Visitors were present at all times during the study.

a. Advantages of safari parks

There were several benefits to be gained by doing this research in safari parks rather than embarking on an African field trip from the U.K.

Low cost:

There was an obvious saving.

Accessibility:

Travel and search times were minimal. I knew where to find the animals each day and there were no problems involved getting there. The metalled roads in the enclosures meant that no special vehicle was necessary; private cars were adequate.

Efficiency:

Some data were guaranteed on most visits.

Constant populations:

I knew what troop I would find at a site and I knew that its numbers would remain fairly constant. There were no predators, few escapes and very few deaths. Injury seldom led to death because wounded animals always received veterinary attention.

Personal safety:

The management imposed certain rules which, while restricting my access to the animals, ensured my safety. Keepers were always at hand in case of trouble.

There were obvious advantages over using conventional zoos or laboratory cages. The safari park enclosures were big and were reasonable approximations to a natural environment.

b. Restrictions and limitations

All observations had to be made from inside a vehicle with the windows closed. The condition was imposed, for safety, by the management, but it limited the flexibility of observation. It was possible to use check sheets and tape recorder for recording the occurrence of motor patterns but this was easy only when the subject animal was fairly near and in full view. Once it moved some distance from the road or among trees, data collection had to stop. All of the baboons in both parks spent a lot of time in the branches of the trees, especially during spring and summer when buds and leaves provided food. On occasions when a behaviour sequence involved locomotion such as chasing and climbing, and the subject repeatedly disappeared behind foliage or tree trunks, the data record was frequently interrupted.

The wooden sheds and huts were the sites of many play bouts. Young baboons would run in and out, climb on the walls, run on and jump from the roofs or swing on the doors. As a result they were out of sight for much of the time and data collection was often quite slow.

A great many cars went through the enclosures each day. They were always an attraction for the baboons, who would spend long periods on or near them. The occupants often offered food, which no doubt added to the attractiveness of cars. In an attempt to make this study more comparable with studies of wild baboons, I recorded behaviour only when it was apparently unaffected by human interference. That is, I did not record behaviour performed on or close to cars.

At feeding times food was simply dumped from a trailor in one or two piles. Competition for such a concentrated food source precipitated more frequent fights and chases than before feeding, particularly between adult males. Injuries were common, often serious enough to warrant treatment by the keepers. Mothers became conspicuously more restrictive with their infants, and for this reason data collection was stopped during, and for one hour after, feeding.

The baboons

Both parks had mostly olive baboons *(Papio anubis)* with some yellow baboons *(Papio cynocephalus)*, Chacma baboons *(Papio ursinus)* and Hamadryas *(Papio hamadryas)*.

The ages of all those born in captivity before the study began were calculated from the records kept by the parks' staff. All births during the study were noted. Baboons whose ages were not known were classed as juvenile, sub-adult or adult, according to the guidelines of Hall and DeVore (1965).

At the end of the time at Woburn there were 57 baboons:

16 adult males ------- approximately 9 anubis, 4 cynocephalus, 3 ursinus

9 adult females ----- approximately 7 anubis, 2 cynocephalus

28 sub-adults of both sexes (mostly male) -------- approximately 15 anubis, 6 cynocephalus, 6 chacma, 1 hamadryas female

4 infants born in the safari park ------ 1 anubis male, 2 anubis females, 1 cynocephalus male

3 infants were born and died during the study ------------ 2 anubis males, 1 anubis female

The ratio of adult males:females was 1.78:1

At Blair Drummond there were 30 baboons:

11 adult males ----- 7 anubis, 2 cynocephalus, 2 ursinus

7 adult females ----- 6 anubis, 1 cynocephalus

3 sub-adult males --- 1 anubis, 1 ursinus, 1 hamadryas

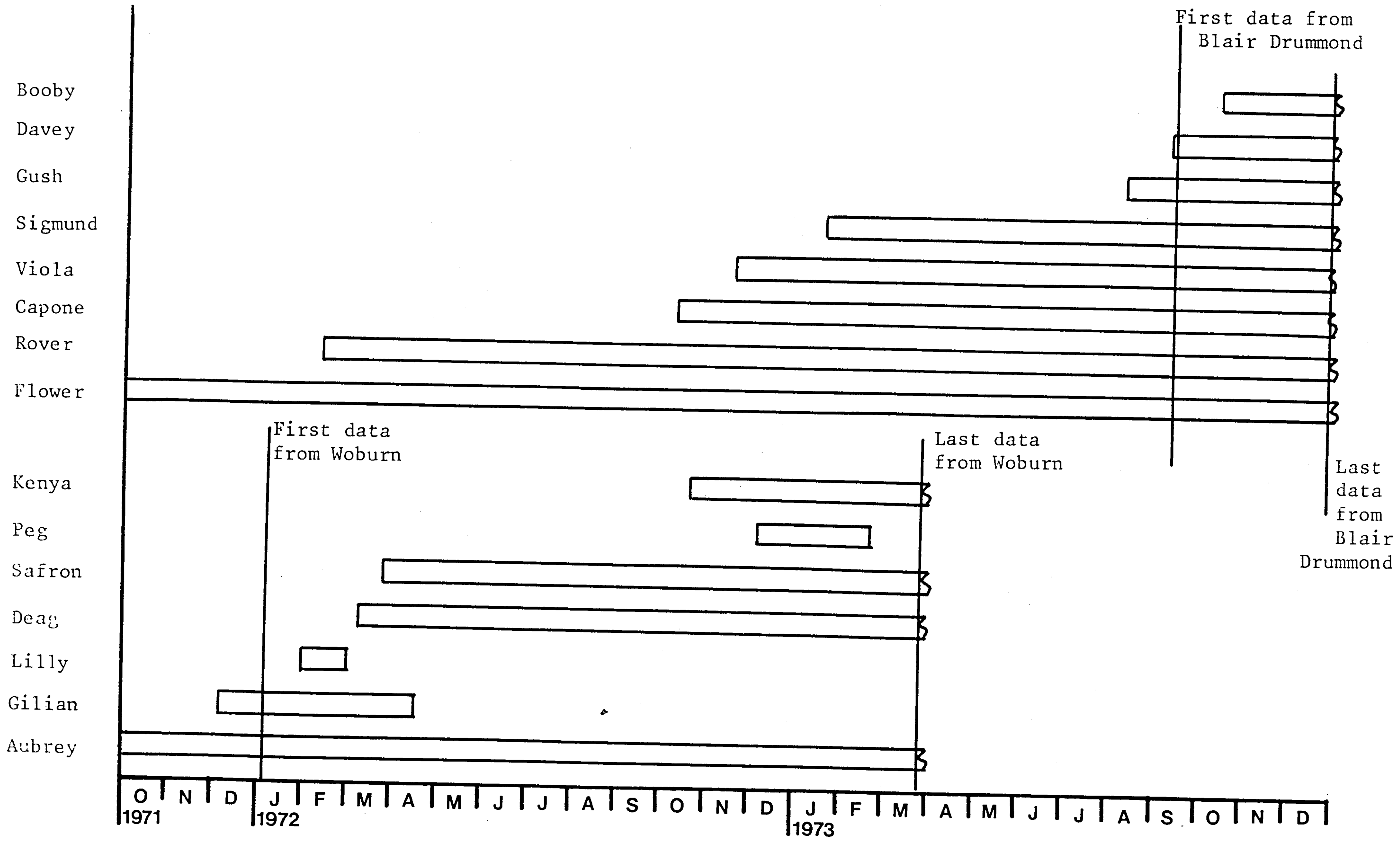
2 juvenile females -- anubis

7 infants ----------- 4 anubis males, 2 anubis females, 1 cynocephalus male

The ratio of adult males: females was 1.57:1

Table 3 shows the history of births and infant deaths in both parks.

Table 3. History of births and deaths of young baboons at Woburn and Blair Drummond



In both parks there were more males than females, which contrasts with the situation reported for wild groups. Altmann and Altmann (1970) gave the adult male:female ratio (an average from various authors) to be 0.8:1. Rose (1977) and Chalmers (1980) gave the ratio for the same group (counted at different times) to be 0.4:1.

Observation methods

In each observation session subjects were chosen opportunistically. Each subject was watched for as long as possible, until it moved out of sight or so far away that its motor patterns were no longer discernible, or until it found itself in one of the situations, described above, in which no data were recorded. Another animal would then be watched. Choice was always a matter of expediency. It depended on which animal was in a suitable position. An attempt was made, during each week, to obtain some data on each young baboon present. This was achieved with more success at Woburn than at Blair Drummond[1]. At Blair Drummond the baboons were frequently out of observation range for much of the day, and in the cold, damp autumnal weather spent more time sheltering inside the sheds.

Check sheets were divided into observation intervals of 30 seconds and the timing was signalled by an electronic buzzer. Sometimes the action was slow enough to be recorded onto a check sheet directly, but more often a tape recorder was used and information transcribed later.

---

[1] Let one infant observed during one week (in which any data were collected) count as one infant-week.
The actual number of infant-weeks can be expressed as a proportion of the maximum possible infant-weeks. This is a measure of the degree to which the aim was achieved of obtaining some data on each infant in each week.

Woburn

Actual infant-weeks = 84
Maximum infant-weeks = 117
Degree of success = 0.72

Blair Drummond

Actual infant-weeks = 20
Maximum infant-weeks = 72
Degree of success = 0.28

The timing signal was fed straight onto the tape.

a. The behaviour record

Both events and states were sampled (Altmann, 1974). Events are those occurrences which can be considered to have no appreciable duration, such as the onset of a bout of behaviour. States are the continuing performance of a behaviour or the maintenance of a posture or position. Two sampling methods were used: instantaneous sampling and one-zero sampling.

i. Instantaneous sampling

When the thirty-second marker sounded a record was made of certain of the subjects' current behavioural states (e.g. on, off or in contact with mother and on or off nipple). These data were used to calculate the proportion of time spent in these states. The rationale was that the probability of being in a particular state when the marker sounded was proportional to the total time spent in that state.

ii. One-zero sampling

If a behaviour occurred once or more during a thirty-second sampling interval, it was recorded only once. If it did not occur, then no record was made. Both events and states qualified. These data were used to construct a non-absolute measure of the amount of behaviour. It was, literally, the proportion of some set of sampling intervals in which the behaviour was scored.

One-zero scores had been used to quantify behaviour in several investigations of primate development at the time of starting the study (e.g. the schools of Hinde at Cambridge and Harlow at Wisconsin). I followed the lead of these research teams.

It has not always been clear what dimension of behaviour authors have considered themselves to be measuring with the one-zero technique: frequency or time? Hinde et al. (1964, 1967, 1968) used the term "number of half-minute intervals in which behaviour occurred" when labelling the ordinates of graphs; but in the texts they sometimes referred to "frequency" in connection with motor patterns such as wrestling or grooming, and "proportion of time" with positions such as proximity to mother.

Harlow (1961) used "mean score per session" on his ordinates but referred to "frequency of response" in the text. Harlow and Zimmermann (1959), however, used one-zero scores as measures of "time in contact with mother". Hansen (1966) and Mitchell (1968) did not extrapolate to behavioural frequencies or times from one-zero scores but used the term "frequency" with reference only to those scores. Mitchell (1968) acknowledged that the scores reflected something of both frequency and duration.

Altmann (1974) has drawn attention to the fact that they are not an absolute measure of the true frequency of behaviour (i.e. the rate at which bouts begin), nor the absolute or proportional time occupied by a behaviour. If the word "frequency" is to be used it can only refer to the frequency of sampling intervals containing the behaviour. She has advocated abandoning one-zero sampling because the data seem not to correspond in a simple way with either true frequency or true time. She also dismissed the notion that it should be retained for its convenience, ease of use and high inter-observer reliability. She argued that the saving in effort and the increase in reliability are not worth the inevitable loss of information; and in any case instantaneous sampling is even easier yet yields a more valid measure of time.

Simpson and Simpson (1977) considered that the one-zero technique required investigation. Since a lot of information in the literature is based on this sampling method, they argued that it would be more useful to discover its inherent bias rather than abandon it. Their empirical study showed one-zero scores to over-estimate the proportion of time spent in a behaviour, but the size of the bias would depend on the particular circumstances. If the stochastic properties of the processes generating the behaviour were known (for instance, if sequences could be described as Markov chains), then, theoretically, the error factor could be calculated. Otherwise they recommended scan sampling (instantaneous sampling) for measuring proportion of time. They pointed out that true frequencies could not be measured by one-zero.

Rhine and Linville (1980) investigated the reliability and validity of one-zero sampling in an empirical study using data from primates. They found that traditional methods of quantification, including one-zero and instantaneous sampling, yielded highly intercorrelated measures when applied to the same behaviour record. From this they argued that no one method should be taken as a standard against which to compare the validity of others. Furthermore, they found evidence that one-zero scores were precise functions of both frequency and duration. If, as Altmann suggested, frequency and duration should be considered valid measures of social behaviour, then, said Rhine and Linville, on theoretical grounds so should one-zero.

The present study did not require that behaviour be measured in absolute units of frequency or duration. The measure had only to be sensitive to relative differences in behaviour between individuals and between ages in the same individual. Altmann's objections to the use of one-zero scores therefore did not apply. One type of analysis applied to the data was rank correlation over time between behaviours. Slater (1978) has concluded that one-zero scores provide suitable data for this sort of analysis.

Instantaneous sampling gave an equally valid relative measure, and would have been approved by Altmann. But too much time would have been required to gather sufficient data on all the behaviours investigated in this study if that had been the only sampling technique employed. One-zero provided a better chance of scoring rare and short duration behaviours.

Furthermore, the one-zero technique made cluster analysis of the data possible. It was a convenient method of sampling behaviours which occurred close in time. Slater (1978) has given this as a possible use of one-zero sampling.

(b) Catalogue of behaviours

Behaviours were chosen and defined according to the following rationale:

they should be unambiguously recognized at a distance;

they should be applicable to all age/sex classes (except behaviours performed on-mother);

they should be defined structurally, without recourse to speculation about function or cause.

Six categories of activity were scored: postures and positions relative to mother (including on- or off-nipple), movement while on-mother, object manipulation, wrestling and locomotion.

The posture and position data allowed general descriptions of activity which were comparable with those from several other developmental studies. Some of these scores were used as bases against which to express the one-zero frequencies of other behaviours (e.g. number of intervals with running as a percent of intervals off-nipple).

Behaviour performed while on-mother was broken down into a few very simple movement types. It was most important here that they could be scored even at a distance and when the subject was partially obscured by its mother's arms and fur.

Wrestling comprises rapidly changing sequences of movements involving the whole body. It was impossible to score the individual elements of these sequences. Casual observation revealed that there was more than one style of wrestling, and these were accommodated by two categories based mainly on distance between the partners' bodies. This was an easy distinction to make. It could be completely objective, requiring no assessment of intensity or motivation. Theoretically they could have applied to both agonistic and playful contact but it transpired that only playful wrestling was observed.

All locomotor patterns fell under one or other of the definitions used here, which meant that some definitions were quite broad. For instance, "walk" covered quadripedal, tripedal and bipedal progression. They could all have been scored in both play and non-play.

Object manipulation was split into a few very simply defined categories which covered the majority of manipulatory acts (casual observation). Some rare events, such as manipulation with hands only (not involving the mouth) were not scored at Woburn. An attempt was made to widen the scope of object manipulation analysis by adding more categories to the catalogue used at Blair Drummond. However, the short time spent there, and the rarity of complex object interactions produced too few data for subsequent analysis.

The catalogue of behaviours which were eventually used for analysis is given on pages 55a to 55f.

Catalogue of Behaviours

Behaviour	Definition	Scoring technique One-zero (1-0) Instantaneous (I)	Date of Introduction	
POSITIONS AND POSTURES				
ON MOTHER	One or more of:- 1) Entire weight of subject supported by mother. 2) At least three feet clasping mother and taking most of its weight. 3) Mother sitting and subject sitting between her legs such that a large proportion of its surface is contacting her ventral surface	I	Jan. 1972	
IN CONTACT WITH MOTHER	Any situation in which any part of the subject is touching any part of the mother - except as in ON MOTHER.	I	Feb. 1972	OFF MOTHER
OUT OF CONTACT WITH MOTHER	Any situation not covered by ON MOTHER or IN CONTACT WITH MOTHER.	I	Jan. 1972	
ON-NIPPLE	Mother's nipple is in subject's mouth	I	Feb. 1972	
OFF-NIPPLE	Mother's nipple is not in subject's mouth.	I	Feb. 1972	
STATIONARY	At least one foot and/or part of the trunk remains in contact with one part of a substrate even though the body might be moving.	I	Jan. 1972	
MOVING	Any instance which cannot come under the definition of STATIONARY.	I	Jan. 1972	
STANDING OR HANGING	One or more feet are in contact with a substrate and take the full weight of the body. Ventral surface, rump, back or sides are not in contact with the substrate.	I	Feb. 1972	
SITTING	Rump is in contact with a substrate and takes the full weight of the body Ventral surface, rump, back or sides are not in contact with the substrate.	I	Feb. 1972	
LYING	Ventral surface, side or back are in contact with a substrate and take all or part of the weight.	I	Feb. 1972	

Behaviour	Definition	Scoring technique	Date of Introduction
MANIPULATION OF OBJECTS			
REACH	Infants arm is extended towards, but does not touch, an object. This was only recorded when the subject was on mother.	1-0	Jan. 1972
TOUCH	After extending an arm the subject contacts an inanimate object with its hand, but does not bring the object nearer.	1-0	June 1972
PICK-UP	After extending an arm the subject grasps an inanimate object with its hand. The object is brought closer to the subject - rather than the subject moving nearer the object - and the object's weight is borne, at least partly, by the subject. If the object is loose and free from any substrate the entire weight is taken, but if it is moveable yet attached (e.g. a twig attached to a branch) the subject takes only part of the weight.	1-0	Jan. 1972
HOLD AND MOUTH	An object is in contact with at least one hand and the mouth simultaneously. This does not include actions which are not part of object manipulation, such as maintaining balance on a branch or drinking.	1-0	Jan. 1972
SCRATCH GROUND	Hand is drawn across the substrate by movement of the arm and/or wrist - it is not just dragged while the subject is moving.	1-0	Jan. 1972
BEHAVIOURS PERFORMED EXCLUSIVELY WHILE SUPPORTED BY, OR IN CONTACT WITH MOTHER			
MOVE HAND OR FOOT IN MOTHER'S FUR	An arm or leg is extended so that the hand or foot moves in contact with, or is brought in contact with the mother. This is not scored if the movement appears to be performed in order to maintain or gain support.	1-0	March 1972

Behaviour	Definition	Scoring technique	Date of Introduction
GRIP FUR	Hand or foot is moved from one position on or off mother's fur to a new position on her fur, and then the fur is held tightly. As a result the infant must support all or most of its weight but still remain stationary on the mother gripping fur during clambering on mother or shifting position is not counted.	1-0	Jan. 1972
SHIFT POSITION	Infant's trunk moves a small amount (less than one body length) in relation to the mother's body as a result of the infant's own movements.	1-0	Jan. 1972
ROOTING	Lateral movement of the head by which the infant's mouth is brought in contact with the mother's nipple.	1-0	Jan. 1972
LEAN OUT	Infant reaches away from its mother with the top part of its body so that its head and/or the whole or part of its trunk is out of contact with her. The infant may partially support itself on the substrate using its arms, or the mother may take its full weight.	1-0	Jan. 1972
CLAMBER ON MOTHER	The infant is supported entirely by its mother and moves over its mother's body a distance of at least its own body length under its own power.	1-0	March 1972
BEHAVIOURS PERFORMED AWAY FROM MOTHER			
CLAMBER ON OTHER	As with "clamber on mother" but on an animal other than the mother.	1-0	Jan. 1972.

Behaviour	Definition	Scoring technique	Date of Intro-duction
LOCOMOTIONS AND WRESTLING			
WALK	Quadripedal, tripedal or bipedal progression horizontally or near horizontally, with body above feet (i.e. not upside down) by moving arms and legs such that arm alternates with arm and leg alternates with leg. Three or more steps must be taken.	1-0	Jan. 1972
RUN	Quadripedal or tripedal progression horizontally or near horizontally, body above feet, such that arm moves simultaneously with arm and leg moves simultaneously with leg. Three or more steps must be taken.	1-0	Jan. 1972
JUMP	Animal pushes itself away from a substrate so that all parts of the body are clear of the substrate for a time. The animal must land higher or on the same level as it took off, or its trajectory must take it higher than its take-off point. If it is at no time higher than its take-off level and lands lower, then "jump" is scored if: 1) take-off was head first, and 2) the landing was at a reasonable horizontal distance from take-off (i.e. there is evidence of the subject having pushed-off rather than fallen).	1-0	Jan. 1972
CLIMB-UP	Progression of at least one body length up a vertical or steep surface or pile of objects.	1-0	Jan. 1972
CLIMB-DOWN	As with "climb up" but downwards.	1-0	Jan. 1972
SWING/HANG	Subject hangs under a branch or similar object supported by one or both arms or legs and not supported by the ground or any other substrate.	1-0	Jan. 1972

Behaviour	Definition	Scoring techniques	Date of Introduction
SLOTH-LIKE PROGRESSION	Progression along a branch (or similar) with the body hanging below and the entire weight taken by the hands and feet, which grip the branch. The branch should be horizontal, or at least at a fairly shallow gradient so that the limbs do not push, but pull against gravity (so that it is not confused with climb-up or climb-down).	1-0	Jan. 1972
CONTACT BETWEEN SUBJECTS			
CLOSE-CONTACT WRESTLING	Two baboons are close together with many points of contact - especially of trunk and arms. There is biting, pressing mouth against partner, kicking, pushing and pulling and the subject's body is twisted while maintaining close contact with that of the partner.	1-0	June 1972
LITTLE-CONTACT WRESTLING	Two baboons hold each other, especially by the arms, so that there are few points of contact, particularly between the trunks. There is holding, grasping, squeezing, pushing, pulling, biting, pressing mouth against the partner, and the body is twisted - but out of contact with the partner's body. There is also jumping and bouncing while holding the partner.	1-0	June 1972
POKE/TOUCH	Gentle touching and holding with very few points of contact, no body twisting and no mouthing.	1-0	June 1972

PLAY	Any locomotor pattern, when performed socially, is considered to be playful if the criteria below are met. In the text such a locomotor pattern is referred to as "play locomotor pattern" (e.g. play run, play climb-up etc.).
PLAY CRITERIA	1) The subject gives a play soliciting signal such as bobbing, ducking away or slapping and running away. 2) The subject shows the relaxed open mouth display or play-face. 3) Although there may be elements of aggression such as chasing, hitting, wrestling etc., neither partner shows intense threat, loud vocalizations or signs of distress. 4) There is an exaggerated quality which is difficult to describe but which nonetheless makes the performance of motor patterns appear different from their performance on other occasions.
NON-PLAY	Any, performed socially or non-socially, which does not qualify as play is considered to be non-playful. In the text such a locomotor pattern is referred to as "non-play locomotor pattern" (e.g. non-play run, non-play climb-up etc.).
PLAY AND NON-PLAY AS UNITARY CATEGORIES	
PLAY	A subject's play score is the total number of intervals with at least one play locomotor pattern recorded.
NON-PLAY	A subject's non-play score is the total number of intervals with at least one non-play locomotor pattern recorded N.B. Non-play is a class of MOBILE ACTIVITY (see below). It is not simply the absence of play.
MOBILE ACTIVITY	This comprises all behaviour involving a change in position of at least one body length, i.e. locomotor patterns, close contact and little contact wrestling and clambering on mother or other

2. Presentation of results

Age-blocks

Originally it was hoped that frequency changes would be shown in increments of one week, but the final pattern of data collected did not allow such resolution.

Table 4 shows how much data were gathered (in terms of 30-second observation periods) for each subject at each week of age between 0 and 89 weeks. Three points arise from this distribution of data to argue against using weekly increments: (i) for 27 of the weeks there are no data, although the sequence is complete up to 25 weeks - the period during which the greatest rate of behavioural change might be expected. The gaps occurring during the later weeks, however, would still make the determination of trends difficult; (ii) 28 of the weeks have only one subject represented. If graphs were drawn with so many points from single subjects the trends might be biased by individual differences; (iii) the amount of data gathered for each week of age varies considerably (ranging from 1151 to 14 30-second periods). On the assumption that the reliability of a frequency value will depend on the amount of data from which that value is calculated, the confidence one could attach to individual values will vary considerably.

In order to improve reliability it was decided to combine adjacent weeks into larger age blocks. Although this action would automatically reduce the precision with which age changes could be described it was considered an acceptable price to pay for increased confidence.

The studies with which the present study compares most closely are those by Owens (1975a,b) and Chalmers (1980^{a,b}). Owens used age blocks of one month and Chalmers recorded behaviour at particular ages (1,2,4,8,12, 16,20,28,36,44 and 52 weeks). In the present study age blocks were chosen so as to maximize the number of subjects and observation periods represented in each block, and also to make meaningful comparisons with Owens' and Chalmers' studies.

Table 4. The amount of data obtained for each young baboon at each week of age. The body of the table shows the number of 30-second observation intervals.

	Age in weeks	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
MALES	Lilly W	43	30	65	60														
	Safron W	85		45	119	119		265	330	443	140	126	99	276	172	200	462	80	
	Peg W		21		226														
	Aubrey W																		
	Gush B						175		30				48						
	Davey B	124			239				20										
	Sigmund B																		
	Capone B																		
	Rover B																		
FEMALES	Gilian W					30	60	30			98	60	30			211	42	42	
	Deag W	33	79	139		17	39	88		212	467	210	139	410	112	143	304	80	300
	Kenya W	866	364	142				160	99	24		112							
	Booby B			35															
	Viola B																		
	Total intervals	1151	494	426	644	166	274	543	479	679	705	508	316	686	284	554	808	202	300
	Intervals per subject	203.2	123.5	85.2	161	55.3	91.3	135.7	119.7	226.3	235	127	79	343	142	184.7	269.3	67.3	300
	Number of subjects	5	4	5	4	3	3	4	4	3	3	4	4	2	2	3	3	3	1

Table 4 continued

	Age in weeks		18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
MALES	Lilly	W																								
	Safron	W		30	308	25				180		120	175	249	20	92			130						29	
	Peg	W																								
	Aubrey	W																	96	127		44	132		54	
	Gush	B																								
	Davey	B																								
	Sigmund	B																30		280			39			
	Capone	B																								
	Rover	B																								
FEMALES	Gilian	W	285																							
	Deag	W	120	299		40		204	51					180	60	278	107	45		109			60			
	Kenya	W	418		220	300	18																			
	Booby	B																								
	Viola	B																								
	Total intervals		833	329	528	365	18	204	51	180	0	120	175	429	80	370	107	75	226	516	0	44	132	99	83	0
	Intervals per subject		274.3	164.5	264	121.7	18	204	51	180	0	120	175	214.5	40	185	107	37.5	113	172	0	44	132	495	415	0
	Number of subjects		3	2	2	3	1	1	1	1	0	1	1	2	2	2	1	2	2	3	0	1	1	2	2	0

Table 4 continued

	Age in weeks		42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
MALES	Lilly	W																								
	Safron	W									58	33	230													
	Peg	W																								
	Aubrey	W	174	42	220		299	298	120	40	20	297	84			60		186	187	188	201					
	Gush	B																								
	Davey	B																								
	Sigmund	B																								
	Capone	B								44		7														
	Rover	B																								
FEMALES	Gilian	W																								
	Deag	W										140		127												
	Kenya	W																								
	Booby	B																								
	Viola	B	12			21	145																			
	Total intervals		186	42	220	21	444	298	120	84	78	447	314	127	0	60	0	186	187	188	201	0	0	0	0	0
	Intervals per subject		93	42	220	21	222	298	120	42	39	119.2	157	127	0	60	0	186	187	188	201	0	0	0	0	0
	Number of subjects		2	1	1	1	2	1	1	2	2	4	2	1	0	1	0	1	1	1	1	0	0	0	0	0

Table 4 continued

	Age in weeks		66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
MALES	Lilly	W																								
	Safron	W																								
	Peg	W																								
	Aubrey	W	80					147			160															195
	Gush	B																								
	Davey	B																								
	Sigmund	B																								
	Capone	B																								
	Rover	B																	96	14					43	
FEMALES	Gilian	W																								
	Deag	W																								
	Kenya	W																								
	Booby	B																								
	Viola	B																								
	Total intervals		80	0	0	0	0	147	0	0	160	0	0	0	0	0	0	0	96	14	0	0	0	0	43	195
	Intervals per subject		80	0	0	0	0	147	0	0	160	0	0	0	0	0	0	0	96	14	0	0	0	0	43	195
	Number of subjects		1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1

The age blocks are: 0-2, 3-5, 6-11, 12-17, 18-23, 24-29, 30-41, 42-53, 54-65, 66-77, 78-89 weeks, and are indicated on Table 4 by vertical dotted lines. The earlier blocks are smaller than the later ones, which follow Chalmers' (1980) argument that one might expect age changes to be more rapid in the early weeks, so requiring smaller time increments to detect them. Table 5 shows the final distribution of data among the age blocks and is in the same form as Table 4. It also shows the amount of data collected for juveniles, sub-adults and adults.

Table 6 shows that variation in the amount of data from age block to age block is less than the amount of variation in the data from week to week. This allows us to be more uniformly confident in the results.

Expression of frequency

Behaviour frequencies are the number of observation intervals in which the behaviour occurred expressed as a percentage of some larger subset of intervals. The denominator used depends on the question being asked at that point in the analysis. For example, frequency of intervals with play-jump might be expressed as a percentage of total observation intervals, intervals when off-nipple, intervals in which play occurred or intervals in which any jumping occurred.

Frequency as percentage of intervals in which a subject was off-nipple :

While data were being collected it was assumed that frequencies would be expressed as percentages of total observation intervals or of intervals in which a subject was in a particular position relative to its mother. During the analysis phase it was realized that it would be more useful to express frequencies as percentages of intervals in which a subject was awake. This would allow comparison to be made with Chalmers' (1980) results in which frequencies were expressed as proportions of time awake.

No record had been made of sleeping or waking. Over large observation distances it was seldom possible to determine whether a subject was awake or asleep when it was on its mother and inactive. However, it has

Table 5. The amount of data obtained for each subject in each age block and age class

	AGE BLOCKS	0-2	3-5	6-11	12-17	18-23	24-29	30-41	42-53	54-65	66-77	78-89	JUV.	SUB ADULT	ADULT FEM.	ADULT MALE
NAMED SUBJECTS	L	138	60													
	S	130	238	1403	1190	363	724	159	321							
	P	21	226													
	A							453	1594	822	387	195				
	Gu		175	78												
	Da	124	239	20												
	Si							349								
	Ca								51							
	R											153				
	Gi		90	218	295	285										
	De	251	56	1116	1349	663	231	659	267							
	K	1372		395		956										
	B	35														
	V								178							
UNNAMED													120	53	45	103
													30	37	52	177
													60	60	80	80
													120	240	100	113
													56	138	80	180
													40		120	
													57			
TOTAL INTERVALS		2071	1084	3230	2834	2267	955	1620	2411	822	387	348	483	474	477	653
MEAN INTERVALS PER SUBJECT		295.8	154.8	538.3	994.7	566.7	477.5	405	482.2	822	387	174	69	94.8	79.5	130.6
NO. OF SUBJECTS		7	7	6	3	4	2	4	5	1	1	2	7	5	6	5

Number of 30 second observation intervals are shown for each subject

Table 6. Variation in the amount of data when organized into weeks of age compared with the variation when organized into age blocks

	NUMBER OF AGE INTERVALS FOR WHICH DATA WERE OBTAINED	TOTAL NO. OBSERVATION PERIODS IN STUDY	MEAN NO. OBSERVATION PERIODS PER AGE INTERVAL	STANDARD DEVIATION
WEEKS	63	18029	286.2	236.9
AGE BLOCKS	11	18029	1639	944.6

The standard deviations can be compared using coefficients of variation.

$$V = \frac{100S}{M}$$

V = coefficient of variation

S = standard deviation

M = mean

WEEKS: $V = 82.8\%$

AGE BLOCKS: $V = 57.6\%$

The coefficient of variation for "age blocks" is less than for "weeks", indicating that there is less variation between the amounts of data in each age block.

proved possible to obtain an estimated measure of wakefulness by making certain assumptions about the on- and off-nipple scores. It has been assumed that when asleep on their mothers infants held a nipple in the mouth, and furthermore when on-nipple but awake they were not free to perform the behaviours with which this study is concerned (except certain small movements performed on mother: shift position, rooting, moving hand in mother's fur). A measure of "intervals in which a subject was off-nipple" is the nearest that has been achieved to "intervals in which a subject was awake and free to behave".

It was not originally envisaged that intervals off-nipple would be used in this way. In fact the method of scoring was inappropriate. On- or off-nipple was sampled every 30 seconds at the beginning of each observation interval. This instantaneous sampling technique was adequate for estimating the proportion of time spent on- or off-nipple but did not yield the one-zero scores needed as measures of intervals during which subjects were off-nipple.

A further complication arose from the fact that for some intervals with a subject beginning on mother or in contact with mother it had been impossible to tell whether it was on- or off-nipple and so no nipple score could be entered. Such would have been the case, for instance, when an infant was on its mother's ventral surface and she had been facing away from me, or when the observation distance had been too great to see clearly the position of the infant's mouth.

Nonetheless, an approximate measure of intervals in which a subject was off-nipple was obtained as follows:

The check sheets contained a record of those intervals when a subject:

(1) began out of contact with mother;

(2) began on mother but then moved to either the out of contact or in contact with mother position;

(3) began in contact with mother but then moved to either the on mother or out of contact position.

Clearly the subject had to be off-nipple at some time in all of these intervals.

When a subject remained either on mother or in contact with mother throughout an interval it could be confidently identified as having been off-nipple only at the beginning because the position relative to the nipple was only scored then. But the nipple position had not always been visible, so the number of such off-nipple intervals had to be estimated. I made the assumption that the intervals beginning with the nipple position visible formed a random sample of all intervals beginning on mother or in contact with mother. The proportion of intervals entirely on mother or in contact with mother which began off-nipple would therefore be the same as the proportion of nipple-visible intervals which began off-nipple. Thus:

$$(4)\quad \text{Estimated intervals spent entirely on mother and beginning OFF-NIPPLE} = \text{Intervals entirely on mother} \times \frac{\text{Intervals beginning on mother and OFF-NIPPLE}}{\text{Intervals beginning on mother and nipple was visible}}$$

and

$$(5)\quad \text{Estimated intervals spent entirely in contact with mother and beginning OFF-NIPPLE} = \text{Intervals entirely in contact with mother} \times \frac{\text{Intervals beginning in contact and OFF-NIPPLE}}{\text{Intervals beginning in contact and nipple was visible}}$$

The final estimated off-nipple measure was the sum of the quantities from 1, 2, 3, 4 and 5 above.

There were two sources of error in these calculations, the magnitude of which cannot be estimated, but whose effects may have been in opposite directions:

(i) If a subject began an interval on-nipple but subsequently came off-nipple - that is, was actually awake and free to behave - yet did not change its position relative to the mother then that interval would not have been detected. By not contributing, such an interval would have decreased the off-nipple measure;

(ii) the assumption that a subject would have been off-nipple for the same proportion of time whether the nipple position was visible or not had no empirical basis and so remains an opinion. It is conceivable that it caused an over-estimate of off-nipple intervals because in reality the nipple position was more likely to have been invisible when an infant was still inconspicuous and probably on-nipple than when it was conspicuously active and off-nipple. The formulae in 4 and 5 above do not allow for this weighting and so may result in an inflated off-nipple measure.

It has been possible to set logical upper and lower limits to the estimated off-nipple measure by two extreme and probably unrealistic assumptions.

Upper limit:

This is set by assuming that subjects were awake, free to be active and off-nipple during every interval. Maximum off-nipple time equals the total observation time.

Lower limit:

This is set by assuming that subjects were never awake, free and off-nipple in intervals spent entirely on or in contact with mother. Minimum time off-nipple equals the sum of intervals beginning off-mother and intervals beginning on or in contact with mother with subsequent movement to another position.

In the results chapters, where frequency is expressed as a percentage of intervals off-nipple, the mean is displayed together with maximum and minimum values for that mean based on these logical limits.[1]

The expression of central tendency

The usual measures of central tendency found in behaviour studies are medians and arithmetic means. Owens (1975 a and b) and Chalmers (1980 a and b) both used medians. In the present study I have departed from this and have chosen to use weighted means.[2]

---

1. See Appendix I.

2. The method of calculating the weighted mean is shown in Appendix III.

a. The choice of weighted means

Within each age block the data sample size varies between subjects (see Table 5). For example, at age 0-2 weeks the samples vary between 1372 intervals for Kenya and 21 intervals for Peg. The reliability of those results must vary with the sample size such that we can have more confidence in Kenya's results than in those of Peg.

Some studies do not meet this problem because equal-sized samples of data are obtained on each subject. But even if it had been possible in the present study to observe each subject for the same amount of time, the problem would still remain. Time is not the only denominator used to express behaviour frequencies. Suppose two subjects of the same age had been watched for 600 30-second intervals each and that one had "run" in 100 intervals and the other in only 20. If it were necessary to express the frequency of "play running" as a percentage of "all running" then the frequency of one would be based on the denominator of 100 and the other based on 20. It was impossible in this study to arrange for all frequencies to be based on the same denominator. The measure of central tendency has to cater for this unequal confidence by being biased towards the larger sample.

If the samples had been of equal size the choice of median or mean would simply have been based on assumptions about distribution - are the data symmetrically distributed? There are never more than seven subjects in any age block and for such small numbers medians would ordinarily have been chosen because they do not require an assumption of symmetry.

One might have expected the small samples of intervals for some subjects to yield extreme results, in which case medians would have been suitable central measures because they are not affected by extremes. I counter this argument by giving evidence, later, that while there may be a slight tendency for extreme results to come from small samples they do not necessarily come from the smallest ones. The extreme results should not be assumed unreliable and need not be avoided by the measure of central tendency.

Another argument, this time against the use of medians, is that it is quite possible for the frequency of the median subject (or the two subjects immediately adjacent to the median) to be based on fewer observation intervals than others in that age block. In that case one might have less confidence in the median as a representative value than in one from another subject based on a bigger sample of intervals.

The weighted mean fulfils the requirements of this study: it does not avoid extremes and is biased towards the larger, and presumably more reliable, samples.

i. Evidence in support of weighted means: a comparison of three measures of central tendency

Figures 1-7 are a selection of results taken from later chapters and are included here so that the effects of different central tendency measures can be compared. They show age changes in frequency of seven motor patterns, positional states and activities using medians, arithmetic means and weighted means. They were selected randomly.

In general the trends appear very little affected by the choice of central measure. However, there is one instance where the expression of a trend does depend on this choice: the frequency of intervals with mobile activity expressed as a percentage of intervals in which subjects were off-nipple (Fig.2). The arithmetic means give peak frequency at 18-23 weeks but according to the medians and weighted means the peak is reached in the previous age block, 12-17 weeks. The frequency at 6-11 weeks is also in contention. The individual data for this age are given in the table below.

6-11 WEEKS

SUBJECT	S	De	K	Gil	Gu	Da
Intervals with mobile activity	578	447	127	35	31	3
Intervals off-nipple	661.0	601.6	242.2	114.7	59.5	16.2
Frequency %	87.4	74.3	52.4	30.5	52.1	18.5

MEDIAN %	ARITH. MEAN	WEIGHTED MEAN
52.25	52.5	72.0

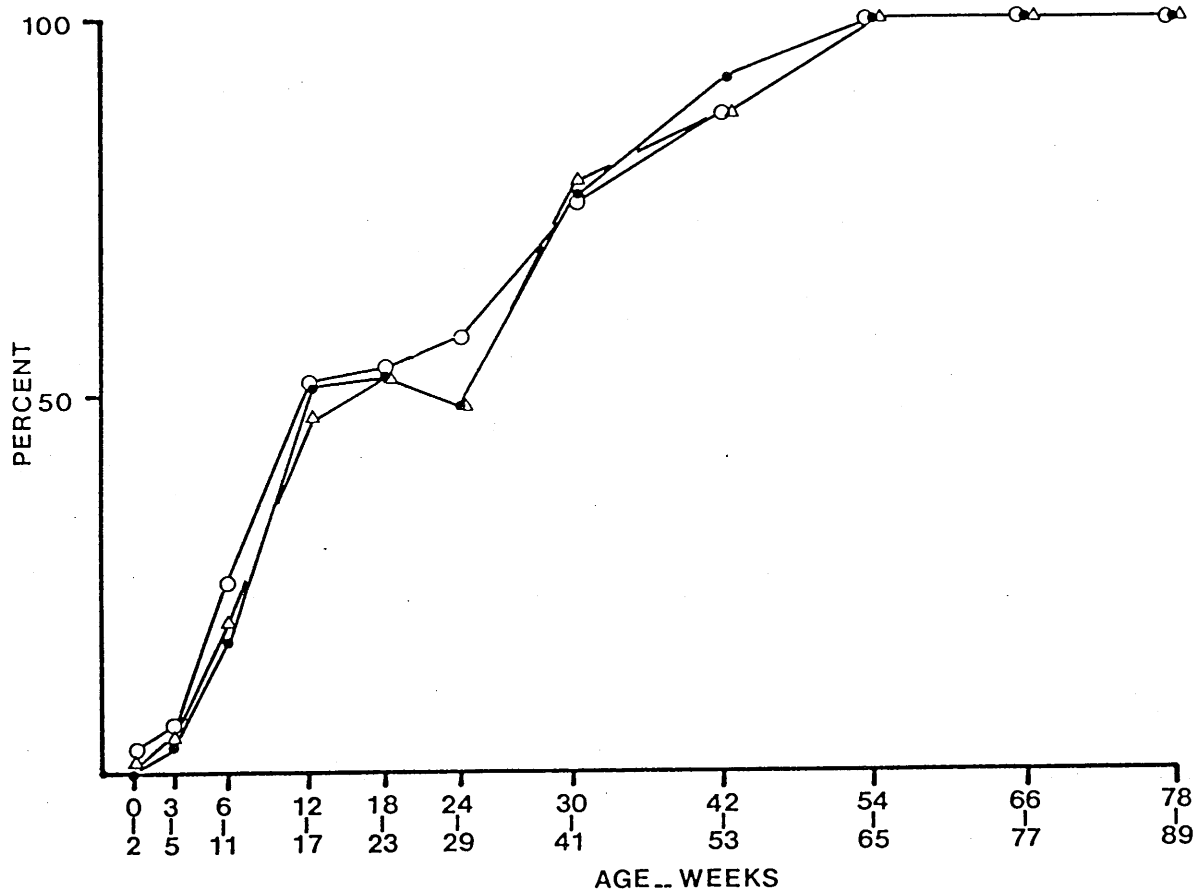


Figure 1. The percentage of total intervals in which infants were out of contact with mother. Comparison between measures of central tendency.

- ● medians
- △ arithmetic means
- ○ weighted means

See Appendix II for the number of subjects at each age.

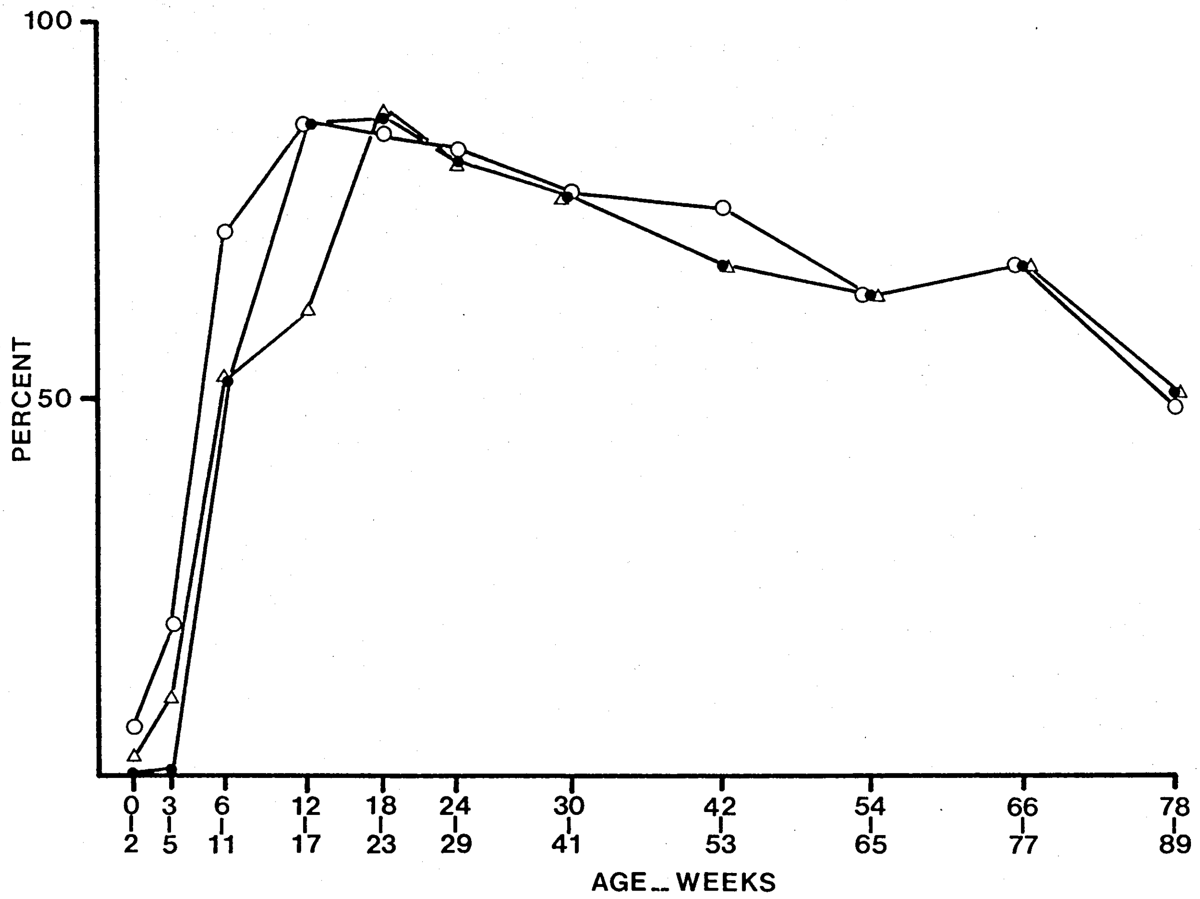


Figure 2. The percentage of off-nipple intervals with mobile activity. Comparison between measures of central tendency. Key as in Figure 1.

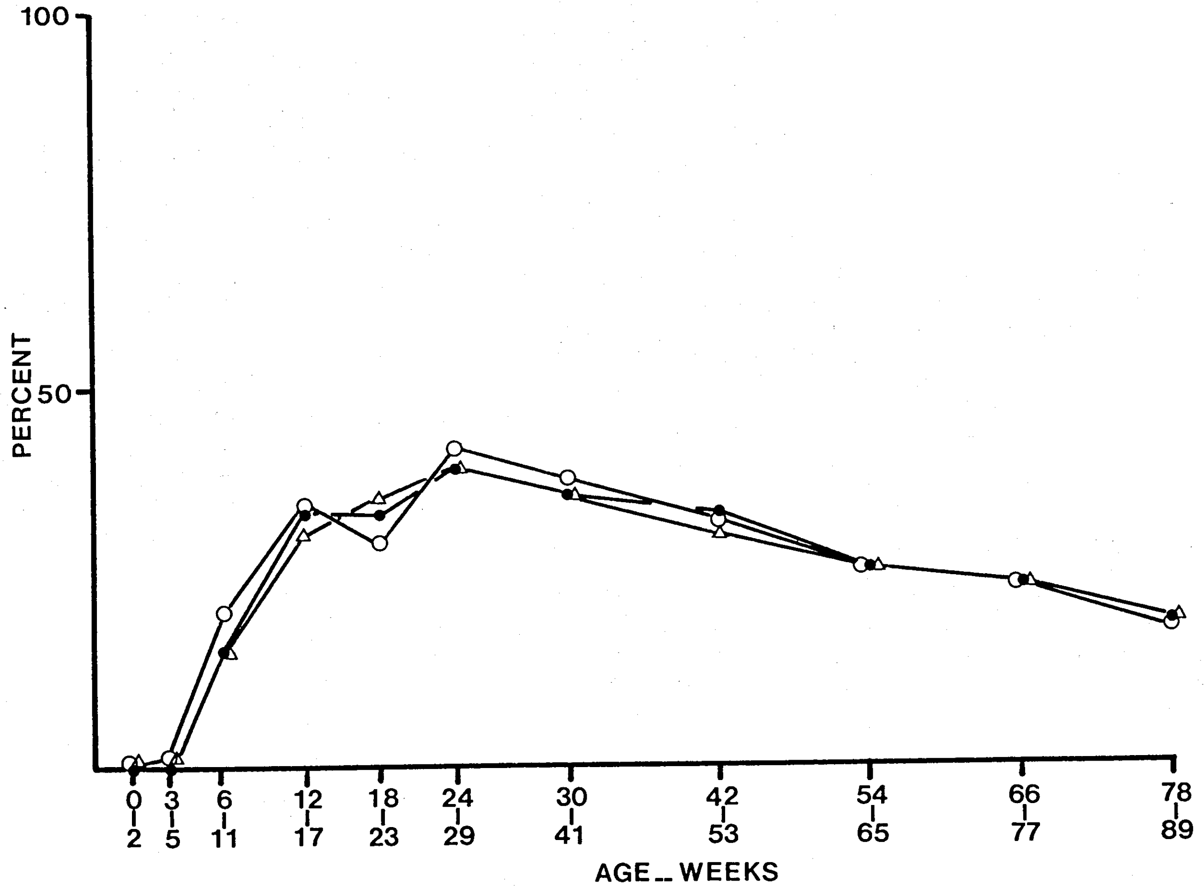


Figure 3. The percentage of off-nipple intervals with run. Comparison between measures of central tendency. Key as in Figure 1.

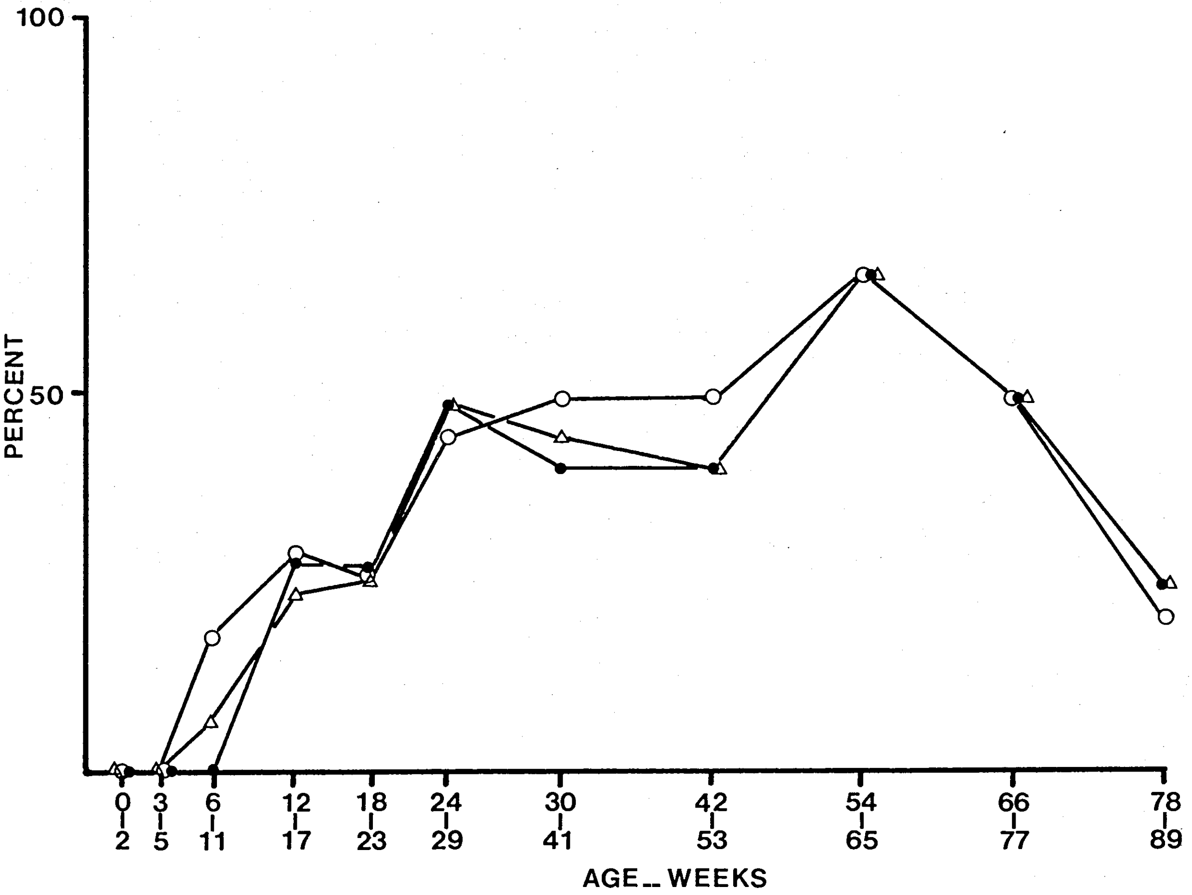


Figure 4. The percentage of intervals with run which contained play-run. Comparison between measures of central tendency. Key as in Figure 1.

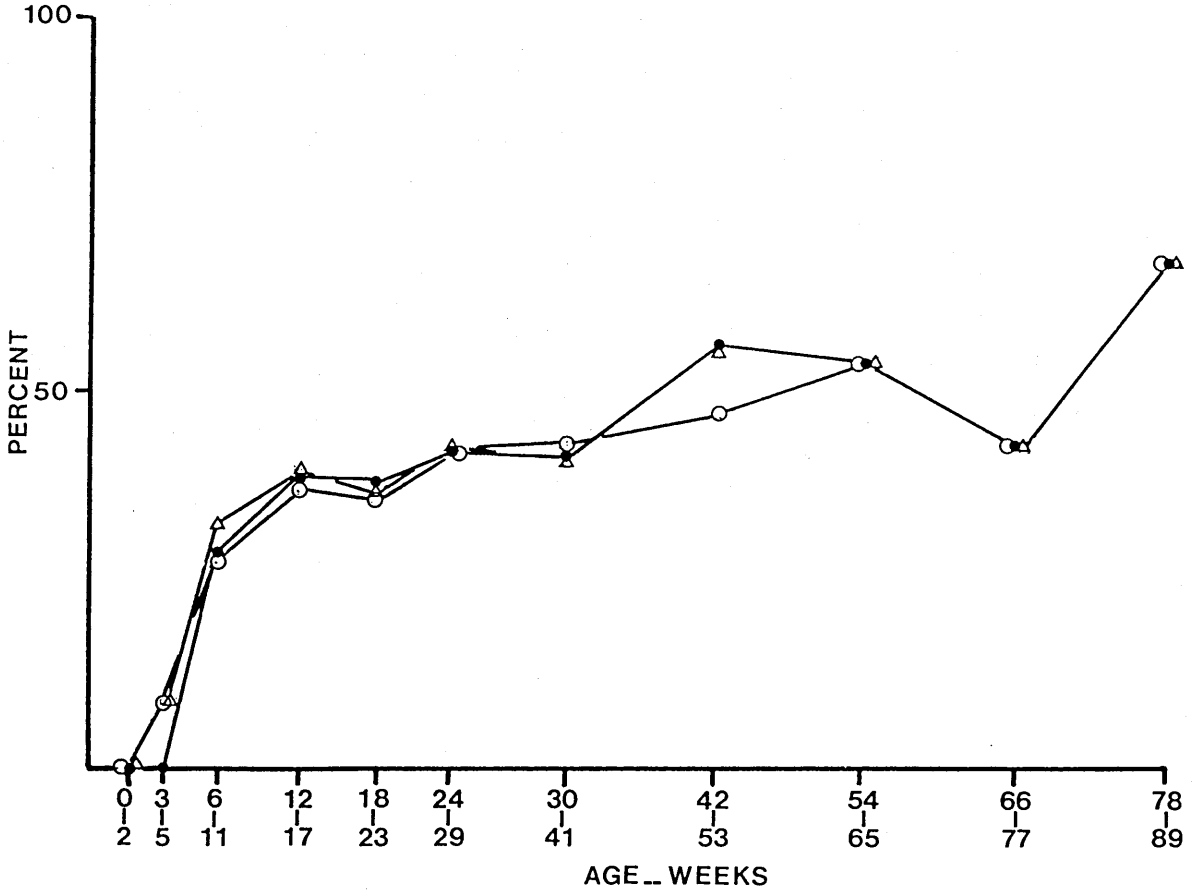


Figure 5. The percentage of off-nipple intervals with hold and mouth. Comparison between measures of central tendency. Key as in Figure 1.

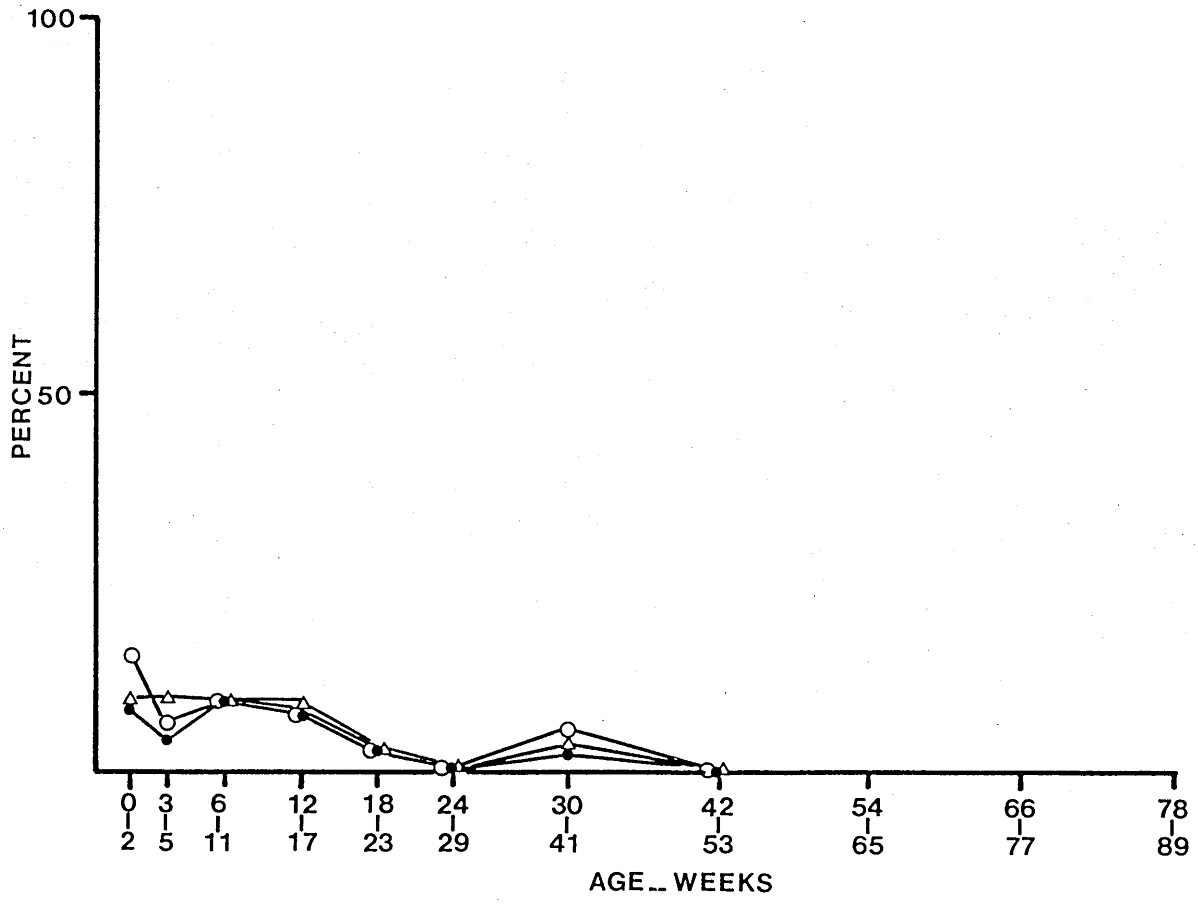


Figure 6. The percentage of intervals on mother with lean out. Comparison between measures of central tendency. Key as in Figure 1.

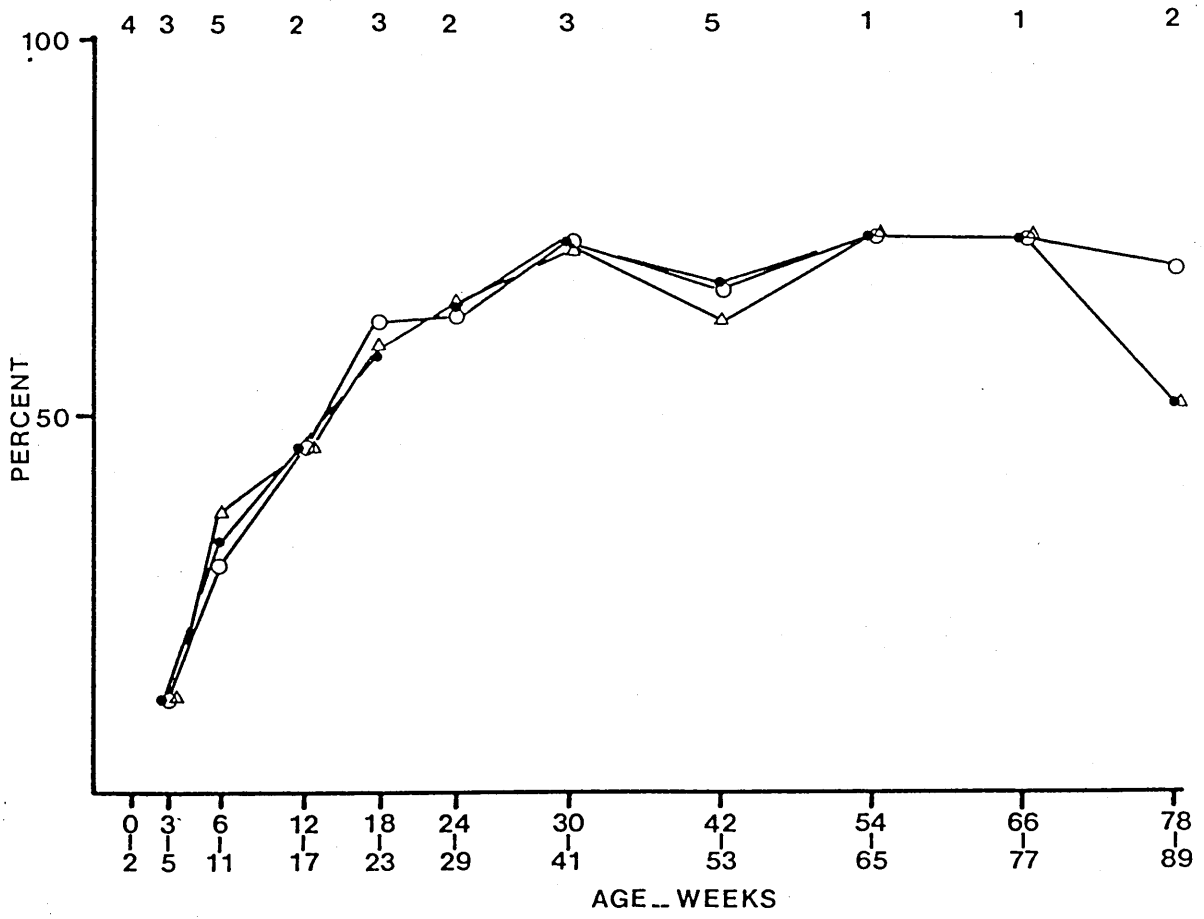


Figure 7. The percentage of intervals with wrestling which contained little-contact wrestling. Comparison between measures of central tendency. Key as in Figure 1.

The number of subjects at each age is shown above the figure.

Of the six subjects, Gu and Da have the two lowest estimated off-nipple scores (59.5 and 16.2) and the mobile activity frequency of Da is also the lowest. Gu's frequency (52.1%) contributes to the median. The other median contributor is K (52.4%) with off-nipple score of 242.2. The median ignores the most reliable frequency, that of S based on 661 intervals off-nipple which also happens to be the highest percentage (87.4%). The arithmetic mean considers all the frequencies equally and so is pulled down in value by the low frequency of Da (18.5%) despite it being the least reliable datum, based on a very small sample of only approximately 16 intervals.

Only the weighted mean emphasizes the two most reliable frequencies, those of S and De. They are also the highest frequencies and so the weighted mean comes out higher than the median and the arithmetic mean.

These particular results are important because they provide a picture of how mobility developed and their interpretation clearly depends on which central measure is used.

ii. Medians, extremes and sample size

Tables 7-13 give the data for Figures 1-7. In each one data are ranked in order of the size of the denominator used to express frequency - the greatest denominator (biggest sample of observation intervals) ranking number one. In age blocks for which there are data from three or more subjects the highest and lowest in the range are marked H and L and the median (or values immediately adjacent to the median) marked M.

The purpose of this is to find whether there is a tendency for the small samples to yield extreme frequencies, H and L, and for larger samples to contribute to the medians, M.

Inspection shows that if there is such a tendency, it is not strong. To make the comparisons easier, Table 14 has been included. For each set of data the position of the average rank of the median or the extremes are displayed on a continuum from highest to lowest possible ranks. It can be seen that on average both the median and the extreme data come from medium-

Table 7. Comparison between three measures of central tendency

INTERVALS IN WHICH OUT OF CONTACT WITH MOTHER AS % OF TOTAL INTERVALS

AGE	RANK ORDER OF DENOMINATORS							Median %	Arith mean %	Weighted mean %	No. of subjects
	1	2	3	4	5	6	7				
0-2	3.8 1372	0 251	3.6 138	0 130	0 124	0 35	0 21	0	1.0	2.7	7
3-5	16.7 H 251	5.0 238	0 L 226	0 L 175	3.3 M 90	10.0 60	0 L 56	3.3	5.0	5.7	7
6-11	29.7 H 1403	24.0 1116	17.0 M 395	17.9 M 218	16.7 78	15.0 L 20		17.45	20.0	25.0	6
12-17	51.3 M 1349	56.0 H 1190	34.2 L 295					51.3	47.2	51.5	3
18-23	65.3 M 956	38.5 L 714	39.9 M 363	67.4 H 285				52.6	52.8	53.3	4
24-29	63.7 724	33.9 180						48.8	48.8	57.7	2
30-41	62.2 M 659	98.0 H 453	61.9 L 349	90.8 M 271				76.5	78.2	76.0	4
42-53	86.5 1594	95.9 321	92.1 M 267	67.4 L 178	96.1 H 51			92.1	87.6	87.2	5
54-65	100 822							100	100	100	1
66-77	100 387							100	100	100	1
78-89	100 195	100 153						100	100	100	2

Key for tables

FREQUENCY

DENOMINATOR

M median
H highest in range
L lowest in range

Table 8. Comparison between three measures of central tendency

INTERVALS WITH MOBILE ACTIVITY AS % INTERVALS IN WHICH OFF-NIPPLE

AGE	RANK ORDER OF DENOMINATORS							Median %	Arith mean %	Weighted mean %	No. of subjects
	1	2	3	4	5	6	7				
0-2	7.8 602	0 85.7	7.5 66.5	0 46.7	0 20.2	0 6.2	0 4.2	0	2.2	6.25	7
3-5	45.3 139.1	0.9 87.3	0 57.5	14.6 48.0	0 38.9	0 24.8		0.45	10.1	19.7	6
6-11	87.4 H 661.0	74.3 601.6	52.4 M 242.2	30.5 114.7	52.1 M 59.5	18.5 L 16.2		52.25	52.5	72.0	6
12-17	93.5 H 946.7	86.1 M 839.8	4.3 L 167.1					86.1	61.3	86.0	3
18-23	83.2 M 851.0	80.8 L 433.9	91.4 M 263.6	95.7 H 155.7				87.3	87.6	84.8	4
24-29	83.4 510.6	79.1 70.8						81.25	81.25	82.9	2
30-41	81.7 H 461.4	72.0 L 453.0	79.4 M 261.8	73.1 M 251.6				76.25	76.5	76.7	4
42-53	79.3 H 1564.3	67.5 M 317.2	68.8 247.0	63.5 149.5	56.6 L 53.0			67.5	67.1	75.0	5
54-65	63.3 822.0							63.6	63.6	63.6	1
66-77	67.4 378.0							67.4	67.4	67.4	1
78-89	35.9 195.0	64.7 153.0						50.3	50.3	48.6	2

Table 9. Comparison between three measures of central tendency

INTERVALS WITH RUNNING AS % INTERVALS OFF–NIPPLE

AGE	RANK ORDER OF DENOMINATORS							Median %	Arith mean %	Weighted mean %	No. of subjects
	1	2	3	4	5	6	7				
0-2	7.0 602	0 85.7	0 66.5	0 46.7	0 20.2	0 6.2	0 4.2	0	1.0	0.7	7
3-5	4.3 139.1	0 87.3	0 57.5	0 48.0	0 38.9	0 24.8	0	0	0.7	1.5	6
6-11	29.2 H 661	21.1 601.6	3.3 L 242.2	9.6 114.7	11.8 M 59.5	18.5 M 16.2		15.1	15.6	20.6	6
12-17	37.1 H 946.7	33.7 M 839.8	22.1 L 167.1					33.7	31.0	34.3	3
18-23	25.4 M 851.0	23.7 L 433.9	41.0 M 263.6	52.0 H 155.7				33.2	35.5	29.8	4
24-29	42.5 510.6	36.7 70.8						39.6	39.6	41.8	2
30-41	37.9 M 461.4	50.5 H 453.0	34.4 M 261.8	19.5 L 251.6				36.1	35.6	38.0	4
42-53	34.3 H 15643	23.6 L 317.2	34.0 247.0	33.4 M 149.5	28.3 53.0			33.4	30.7	32.6	5
54-65	26.3 822							26.3	26.3	26.3	1
66-77	24.0 387							24.0	24.0	24.0	1
78-89	13.3 195.0	248 153.0						19.0	19.0	18.4	2

Table 10. Comparison between three measures of central tendency

PLAY RUNNING AS % ALL RUNNING

AGE	RANK ORDER OF DENOMINATORS							Median %	Arith mean %	Weighted mean %	No. of subjects
	1	2	3	4	5	6	7				
0-2	0	0	0	0	0	0		0	0	0	6
3-5	0	0	0	0	0	0		0	0	0	6
6-11	20.7 193	17.3 127	0 11	0 8	0 7	0 3		0	6.3	17.8	6
12-17	31.9 H 351	27.2 M 283	10.8 L 37					27.2	23.3	28.8	3
18-23	32.4 H 216	14.8 L 108	27.2 M 103	25.9 M 81				26.5	25.1	26.6	4
24-29	42.8 217	53.8 26						48.3	48.3	44.0	2
30-41	64.6 H 229	37.1 M 175	43.3 M 90	32.6 L 49				40.2	44.4	49.3	4
42-53	52.8 536	39.3 84	54.7 H 75	40.0 M 50	13.3 L 15			40.0	40.0	49.9	5
54-65	65.7 216							65.7	65.7	66.7	1
66-77	49.5 93							49.5	49.5	49.5	1
78-89	2.6 38	46.1 26						24.3	24.3	20.3	2

Table 11. Comparison between three measures of central tendency

PERIODS WITH 'HOLD AND MOUTH OBJECT' AS % PERIODS OFF-NIPPLE

AGE	RANK ORDER OF DENOMINATORS							Median %	Arith mean %	Weighted mean %	No. of subjects
	1	2	3	4	5	6	7				
0-2	0.3 602	0 85.7	0 66.5	0 46.7	0 20.2	0 6.2	0 4.2	0	0.05	0.2	7
3-5	18.7 139.1	0 87.3	0 57.5	0 48.0	0 38.9	32.3 H 24.8		0	8.5	8.6	6
6-11	28.4 M 661.0	29.3 M 601.6	12.4 L 242.2	41.0 114.7	26.9 59.5	55.7 H 16.2		28.8	32.3	27.5	6
12-17	38.4 M 946.7	33.1 L 839.8	46.7 H 167.1					38.4	39.4	36.8	3
18-23	39.5 M 851.0	25.1 L 433.9	36.8 M 263.6	45.6 H 155.7				38.1	36.7	36.0	4
24-29	42.1 510.6	42.4 70.8						42.2	42.2	42.1	2
30-41	52.0 H 461.4	46.1 M 453.0	28.6 L 261.8	36.2 M 251.6				41.1	40.7	43.1	4
42-53	41.9 L 1564.3	61.5 317.2	56.3 M 247.0	56.2 H 149.5	62.3 53.0			56.3	55.6	47.5	5
54-65	53.9 822.0							53.9	53.9	53.9	1
66-77	42.9 387.0							42.9	42.9	42.9	1
78-89	66.7 195.0	68.6 153.0						67.6	67.6	67.5	2

Table 12. Comparison between three measures of central tendency

LEAN OUT FROM MOTHER AS % INTERVALS IN WHICH ON MOTHER

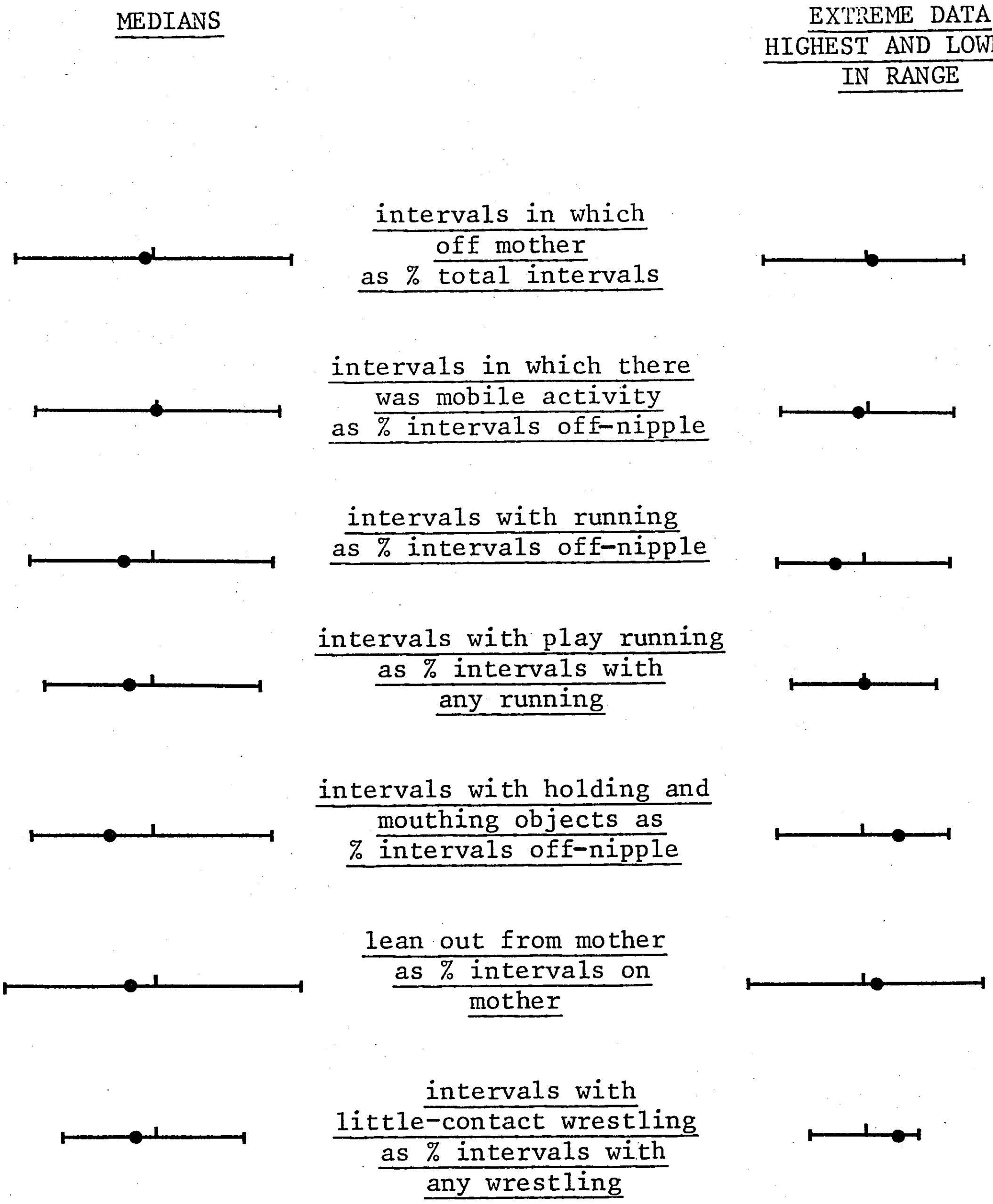
AGE	RANK ORDER OF DENOMINATORS							Median %	Arith mean %	Weigh-ted mean %	No. of sub-jects
	1	2	3	4	5	6	7				
0-2	17.7 1312	19.6 H 250	4.5 L 134	8.5 M 130	5.6 124	8.6 35	4.8 21	8.5	9.9	15.4	7
3-5	3.0 233	7.1 226	3.5 201	4.0 M 175	2.3 L 87	28.1 H 57	21.4 56	4.0	9.9	6.5	7
6-11	8.1 M 1098	11.1 M 901	11.3 354	6.4 188	17.6 H 74	0 L 19		9.6	9.1	9.6	6
12-17	5.2 L 824	7.7 M 611	14.1 H 205					7.7	9.0	7.2	3
18-23	1.8 L 496	2.5 M 405	2.1 M 232	4.0 M 75				2.3	2.6	2.2	4
24-29	0.7 264	0.8 126						0.75	0.75	0.8	2
30-41	8.0 H 261	1.4 M 71	0 L 68	2.9 M 29				2.15	3.1	5.6	4
42-53	0 214	0 54	0 26	0 4	0 4			0	0	0	5
54-65											
66-77											
78-89											

Table 13. Comparison between three measures of central tendency

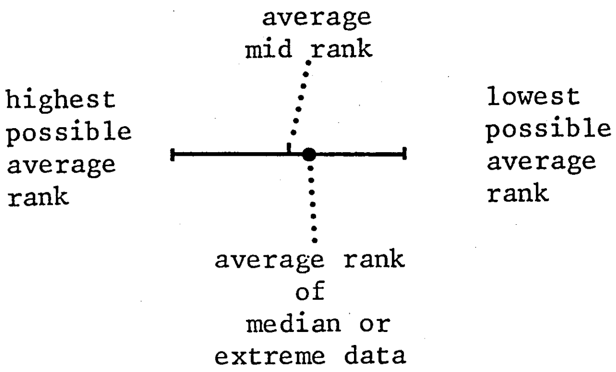
LITTLE-CONTACT WRESTLING AS % OF ALL WRESTLING

AGE	RANK ORDER OF DENOMINATORS							Median %	Arith mean %	Weigh-ted mean %	No. of sub-jects
	1	2	3	4	5	6	7				
0-2											0
3-5	12.5 16							12.5	12.5	12.5	1
6-11	28.6 L 63	33.3 M 6	50.0 H 4					33.3	37.3	30.1	3
12-17	46.6 204	44.7 152						45.6	45.6	45.8	2
18-23	68.5 H 130	58.1 M 74	52.2 L 46					58.1	59.6	62.4	3
24-29	63.1 152	66.7 12						64.9	64.9	63.4	2
30-41	73.2 M 86	73.4 H 79	70.0 L 40					73.2	72.2	72.7	3
42-53	58.8 136	79.4 68	67.8 M 28	90.5 H 21	16.7 L 6			67.8	62.6	66.8	5
54-65	74.4 176							74.4	74.4	74.4	1
66-77	73.6 53							73.6	73.6	73.6	1
78-89	78.9 19	25.0 4						51.9	51.9	69.6	2

Table 14. Is there a tendency for the extreme frequencies within an age block to come from subjects which were observed for a small number of 30-second intervals and for medians come from those observed for a large number of intervals?



KEY



sized samples (mid-ranking denominators) rather than from the largest or smallest samples. It would not be safe to assume that the highest and lowest frequencies were necessarily the results of small samples, and to be avoided. Neither is it safe to assume that the largest and most reliable sample will necessarily show up as the median. I submit that the weighted mean, which gives prominence to the larger samples, is the measure of central tendency most conducive to reliable interpretation of these data.

Symbols used in figures

A key to symbols which are used repeatedly in figures in the following results chapters is given in Appendix I. Other symbols are explained in the relevant figures.

Subject sample sizes and values of weighted mean frequency denominators

The number of subjects contributing to data points plotted in most of the figures is shown in Appendix II. Sample sizes different from these are shown in the relevant figures.

The denominators of weighted mean frequencies are shown in Tables A and B of Appendix III.

Rank correlation

The significance of changes in weighted mean frequency with age is tested using the Spearman method of rank correlation. The same test is used to measure the correlation between frequency changes in pairs of motor patterns. Eleven age blocks are shown in all relevant figures but the correlation coefficients are calculated using N = 10 (unless otherwise stated). That is because only one subject (Aubrey) contributed data to age blocks 54-65 weeks and 66-77 weeks; so to avoid having the coefficient influenced disproportionately by an individual the data in those blocks are combined for correlation tests.

Chapter 3. Results: the position of infants in relation to their mothers

This chapter deals with age changes in the proportion of time spent by young baboons in different positions relative to their mothers. This is an important dimension of behaviour development because it is a function of an infant's increasing independence from its mother and so forms a background against which to view other changes in behaviour. Furthermore it provides an opportunity to find out whether these safari park baboons were similar to baboons and other species in measures which can be compared with those reported in other studies. If they can be shown not to differ too greatly, then the descriptions of behaviour development in later sections might have some generality despite the particular living conditions of safari parks.

A number of authors have described the course of infant primates' increasing independence (e.g. Harlow and Harlow, 1965, 1969; Hinde, Rowell and Spencer-Booth, 1964; Hinde and Spencer-Booth, 1967; Hinde and White, 1974; Kaufman and Rosenblum, 1969 - captive macaques; Altmann, 1962; Berman, 1978, 1980; Kaufman, 1966 - wild rhesus; Rowell, Din and Omar, 1968 - captive baboons; Altmann, 1980; Bolwig, 1959; Chalmers, 1980a; De Vore, 1963; Hall, 1962; Rose, 1977 - wild baboons). Most studies of wild baboons have provided qualitative descriptions of this aspect of development but Altmann (1980), Chalmers (1980a) and Rose (1977) provided quantitative data as did Berman (1980) and Kaufman (1966) for wild rhesus.

Rowell, Din and Omar (1968), in their study of captive baboons, stressed the similarities in the development of mother-infant behaviour of caged baboons and caged rhesus, the latter having been described by Hinde, Rowell and Spencer-Booth (1964). This claim underlies my attempt to compare the safari park baboons with rhesus in the absence of other baboon data.

On mother and off mother

In the present study the earliest age at which an infant was first recorded out of contact with its mother was 4 days. Table 15 shows this,

Table 15. First records of infants out of contact with mother

	Sex	Species	Age (days)
Lilly	M	anubis	9
Davey	M	anubis	21
Safron	M	cynocephalus	23
Deag	F	anubis	47
Kenya	F	anubis	4

as well as the ages at which other infants were first seen away from their mothers. Only infants who were observed during their first week of life are included. Kaufman (1966) gave the earliest age at which wild rhesus were standing on the ground as 2 days, although another infant was not out of contact with its mother until 12 days. Chalmers (pers.comm.) saw all of his wild baboons off their mothers when they were 7 days old. The result of Kenya in the present study is therefore within the range observed elsewhere, but Safron, Davey and Deag were very much older when first seen out of contact. There is no implication here that these were the ages at which they first left their mothers. Kenya was observed much more than the others during the first few days and so was more likely to have been seen on the day of her first excursion from mother.

Comparisons with data from captive macaques

Figure 8 shows changes in the percentage of observation intervals in which infants were off mother. The weighted mean percentage in the first 3 weeks was 7.7% and this rose until they were recorded off mother in every interval at 54-65 weeks. It should be noted that after that age the young baboons may still have been associating with their mothers in ways other than being supported by them, and that they may indeed have returned to them at night. Up until 24-29 weeks these results are very similar to those obtained for captive rhesus by Hinde and Spencer-Booth (1967). Figure 8 also shows their results, estimated from the 1967 paper. After 24-29 weeks the baboons spent a greater proportion of observation intervals off mother.

Figure 9 shows the percentage of intervals in which infants were on mother. It falls from approximately 97% to 0% by 24-29 weeks. In the same Figure are results for captive rhesus. estimated from Hinde and White (1974), and for pigtail and bonnet macaques, from Kaufman and Rosenblum (1969). The safari park baboons, between 6-11 and 18-23 weeks, were on mother in a greater proportion of intervals than were captive macaques. From 24-29 weeks pigtail and bonnet macaques came within the ranges of

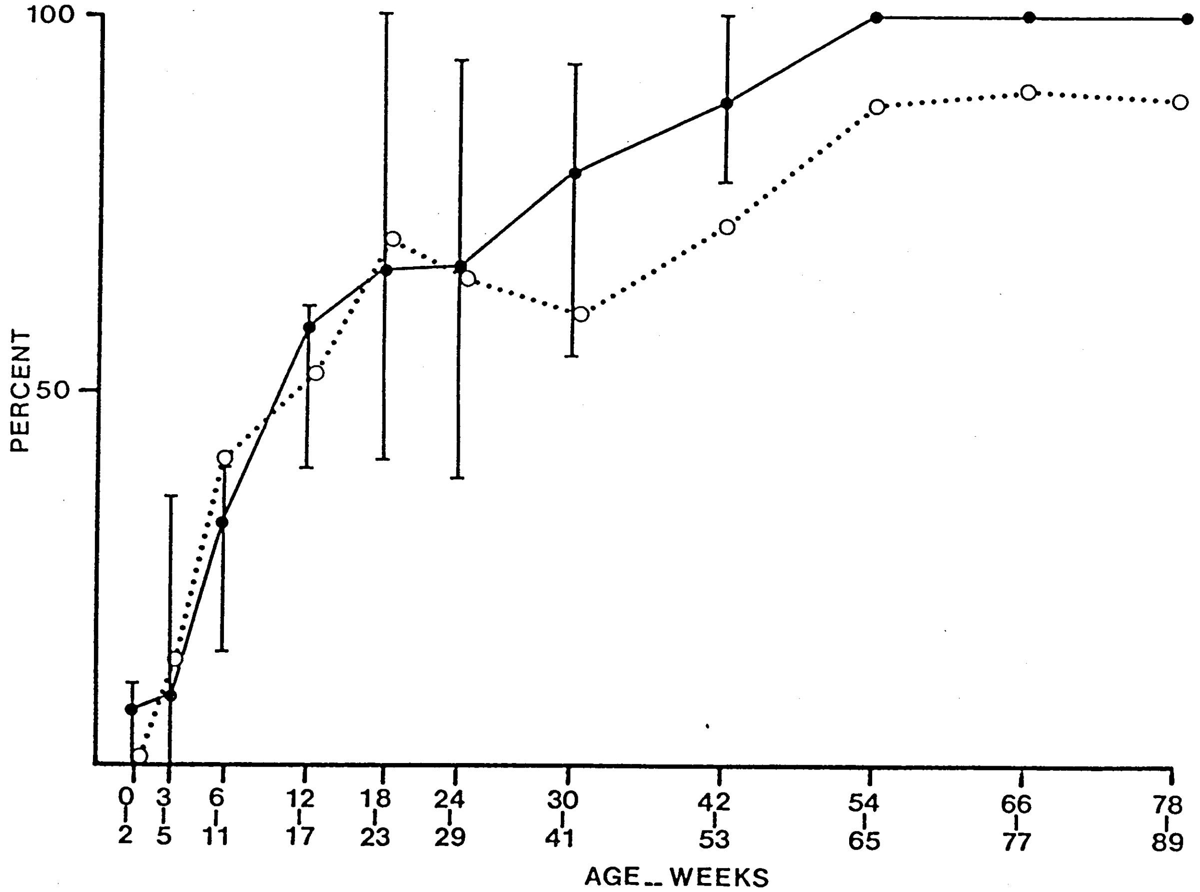


Figure 8. The percentage of 30-second intervals in which infants were off mother. Results are from safari park baboons in the present study and captive rhesus macaques (Hinde and Spencer-Booth 1967).

●——● safari park baboons
○·····○ captive rhesus

Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

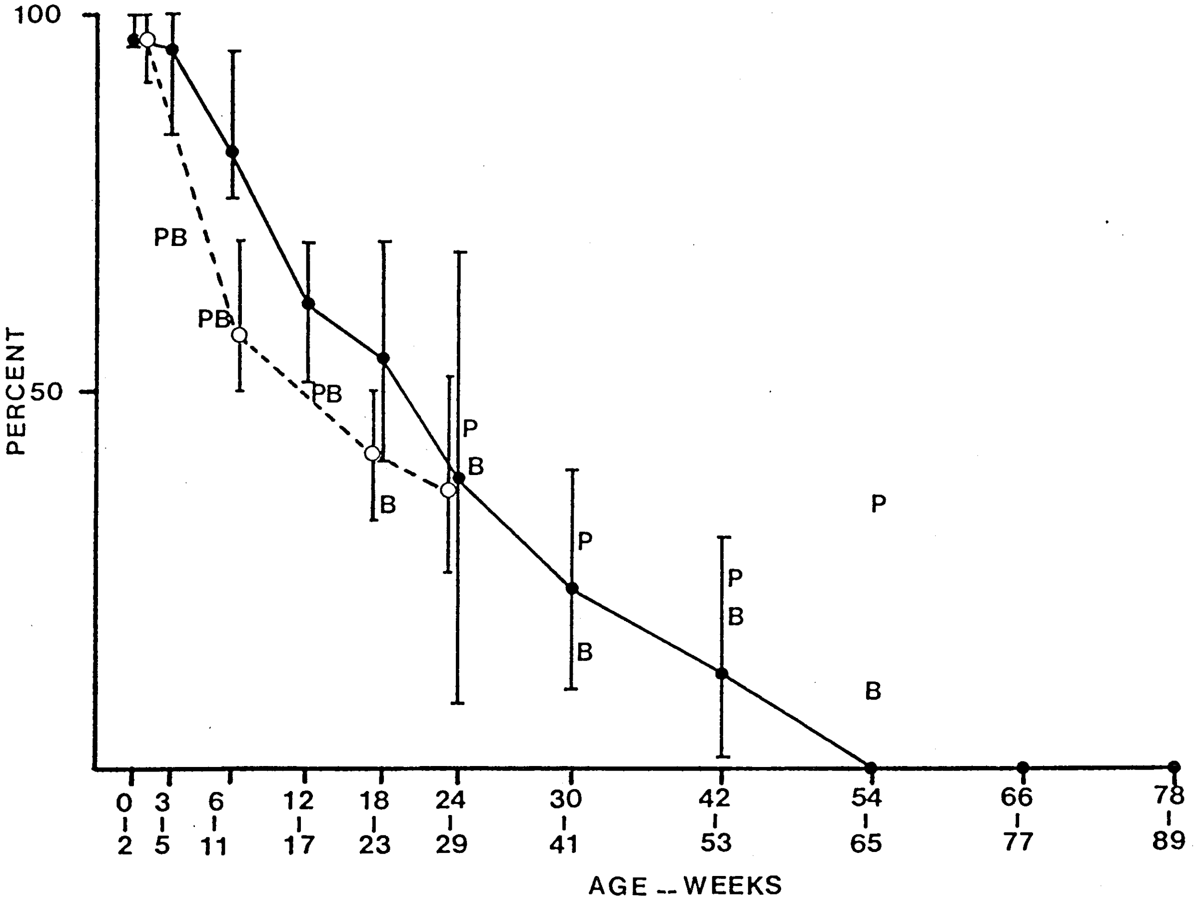


Figure 9. Time spent by infants on mother. Results are from safari park baboon in the present study, captive rhesus macaques (Hinde and White 1974) and captive pigtail and bonnet macaques (Kaufman and Rosenblum 1969). The measures are: Safari park baboons, percentage of 30-second intervals in which infants were on mother; captive rhesus macaques, percentage of 30-second intervals in which infants were in ventro-ventral contact with mother; captive pigtail and bonnet macaques, mean duration of ventro-ventral contact.

●——● safari park baboons
○----○ captive rhesus
P captive pigtail macaques
B captive bonnet macaques

Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

safari park baboons.

Altmann (1980) also compared mother contact times of wild baboon infants with those of feral rhesus infants (data from Berman, 1978). The baboons spent more time in contact. In this respect the safari park infants behaved similarly to wild infants.

Two more subtle measures of the infant-mother relationship are the length of bouts on or off mother and the rate of making and breaking contact. Hinde and Spencer-Booth (1967) gave an index of off mother bout length which was the number of intervals in which an infant was both on and off its mother as a proportion of intervals in which it was off. The data from the present study have yielded the same index. Hinde and White (1974) calculated an "activity score" which was the sum of contact makes and contact breaks in a standard observation time. A measure of the rate of contact makes and breaks has been calculated from the present data but it is less precise and in different units from the Hinde and White measure. It is the number of intervals in which contact was made or broken expressed as a proportion of the total observation intervals.

The bout length index is inversely proportional to the length of off mother bouts. Age changes in this index are shown in Figure 10. It can be seen that bout length increased with age, but up to and including 18-23 weeks the off mother bouts of safari park baboons were of shorter duration than those of captive rhesus. After that age the baboon mean bout lengths were the greater.

The absolute values of the present index of contact makes and breaks are not comparable with the Hinde and White activity score, but trends are; particularly the ages at which peaks occur. These measures are shown in Figure 11. The peak rate of contact makes and breaks for captive rhesus was around 6-11 weeks (Hinde and White gave 9-12 weeks) whereas the peak for safari park baboons was later, at 18-23 weeks.

To summarize: prior to 18-23 weeks the baboons spent more of their time on mother and had shorter bouts off mother than did rhesus, and from 30-41 weeks the baboons spent more time off mother, and in longer

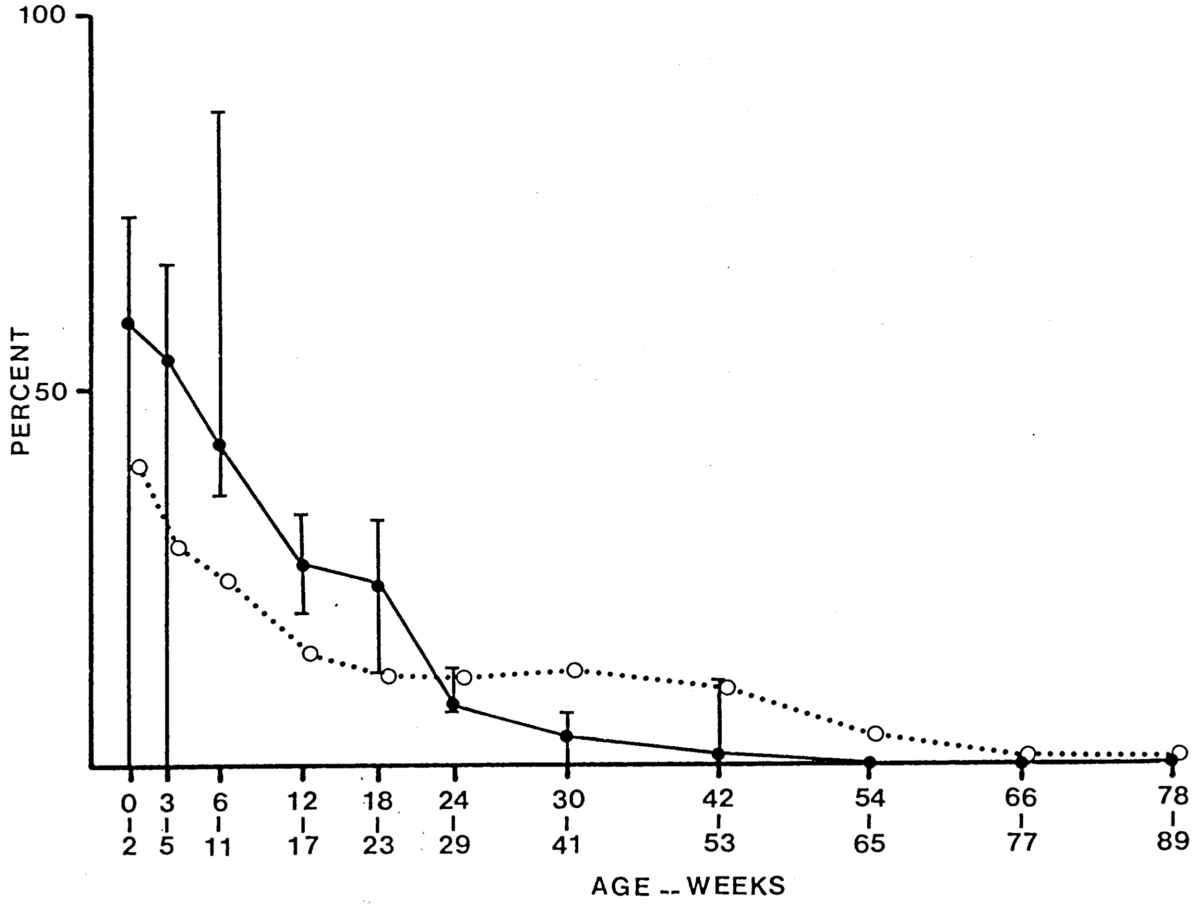


Figure 10. Changes in an index of the length of bouts off mother. Results are from safari park baboons in the present study and captive rhesus macaques (Hinde and Spencer-Booth 1967). The index is the percentage of intervals that infants were off mother in which they were also recorded on mother.

●——● safari park baboon
○·····○ captive rhesus
Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

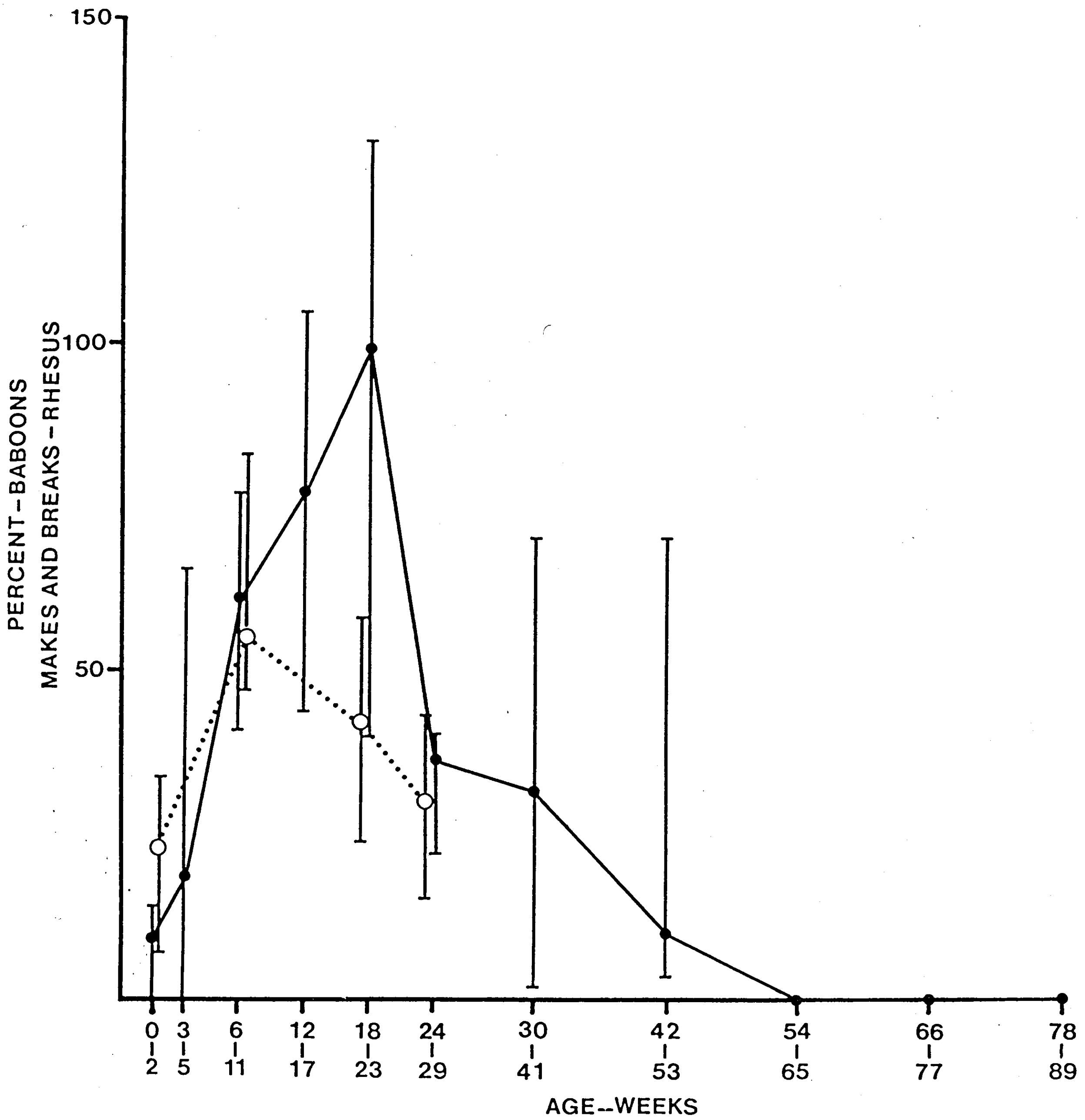


Figure 11. Changes in measures of the amount of making and breaking contact between infant and mother. Results are from safari park infants in the present study and captive rhesus macaques (Hinde and White 1974). The measure for baboons is the number of intervals in which contact was broken plus the number in which contact was made expressed as a percentage of total intervals. The measure for rhesus is the number of contact makes plus the number of contact breaks per standard 6 hour observation sessions (medians and interquartile ranges are plotted).

●——● safari park baboons
○·····○ captive rhesus
Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age:
see Appendix III, Table A, for the denominators of weighted means.

bouts, than rhesus. Whereas rhesus displayed their peak frequency of contact makes and breaks around 6-11 weeks, the baboon peak frequency occurred later at 18-23 weeks.

Comparison of positional and postural data with that from wild baboons in Kenya

The wild baboon data are taken from Rose's (1977) study of olive baboons of the "Pumphouse" troop at Gilgil, and Altmann's (1980) account of yellow baboons at Amboseli.

Safari park infants spent considerably more time on mother than did wild infants (Figure 12). It is not clear, however, whether Rose included in his "riding" category instances when infants were holding their mothers ventrally while the mothers were stationary and sitting. My "on mother" category did include this.

Figure 13compares changes in mother-infant contact time (from instantaneous samples) between safari park infants and Altmann's wild infants. The wild infant data are separated into "restrictive" and "laissez-faire" maternal styles. Safari park infant data are more similar to those from maternally restricted wild infants. This could mean that safari park mothers tended to be restrictive rather than laissez-faire in relationships with their offspring, but equally the effect might have been due more to the actions of the infants. I did not record who was responsible for makes and breaks of contact and so this question remains unresolved.

Altmann found that peak transition rate (rate of making and breaking contact) occurred during months 4 to 6. The peak for safari park infants comes within that range (Fig.11, peak = 18-23 weeks).

At those ages when mother-infant associations were recorded (0-53 weeks) safari park infants spent less time sitting (Figure 14) and standing (Figure 15) unsupported by their mothers than did Rose's wild infants. Presumably, this was because they were on mother more. Lying was rare in both groups (Figure 16).

From 65 weeks when they were no longer carried by their mothers the safari park infants, juveniles and adults spent more time sitting than

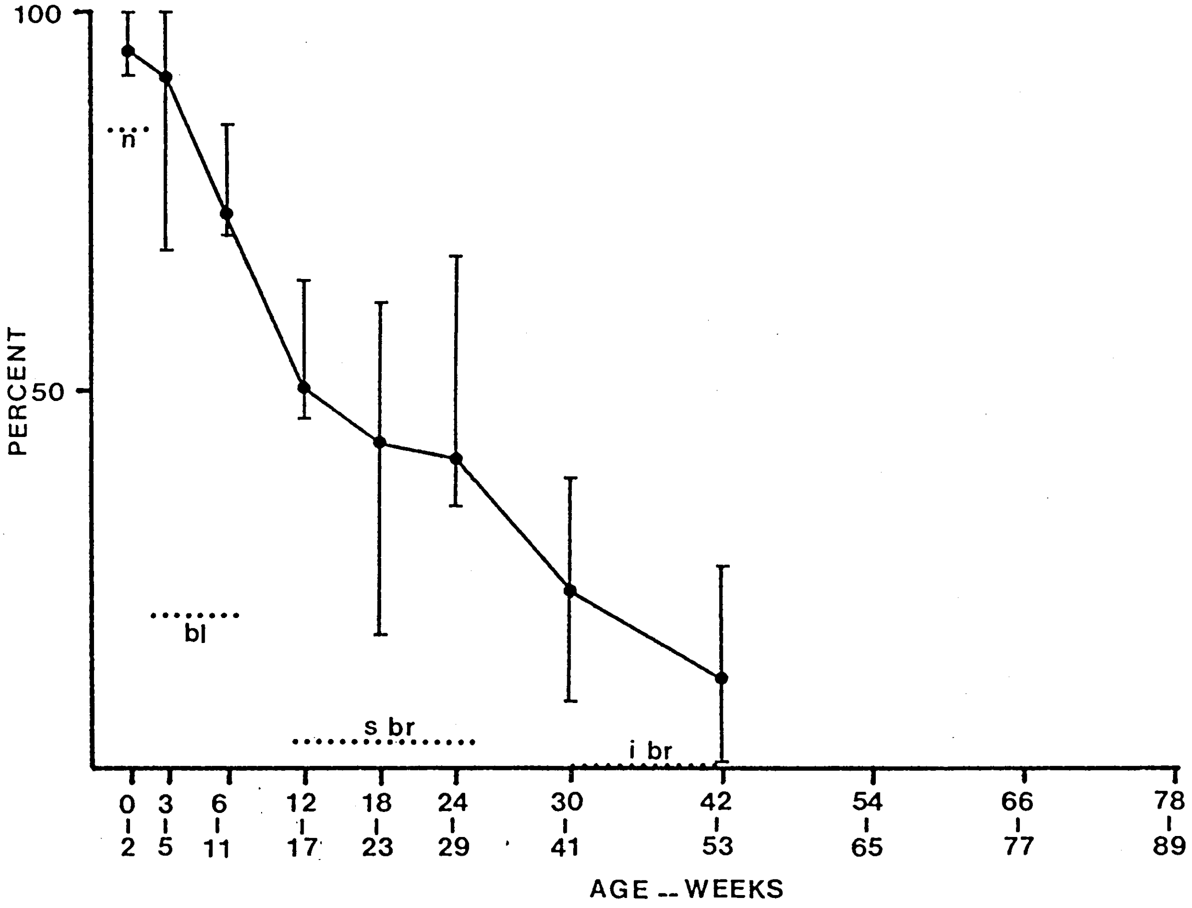


Figure 12. The proportion of time spent on mother. Results are for safari park baboons from the present study and for wild baboons from Rose (1977). The measure for safari park baboons is the percentage of total 30-second instantaneous samples which scored on mother. The measure for wild baboons is the percentage of total observation time spent riding on mother.

●——●	weighted means for safari park baboons
·······	results for wild baboons
n	neonate
bl	black infant
s br	small brown infant
i br	intermediate brown infant

Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

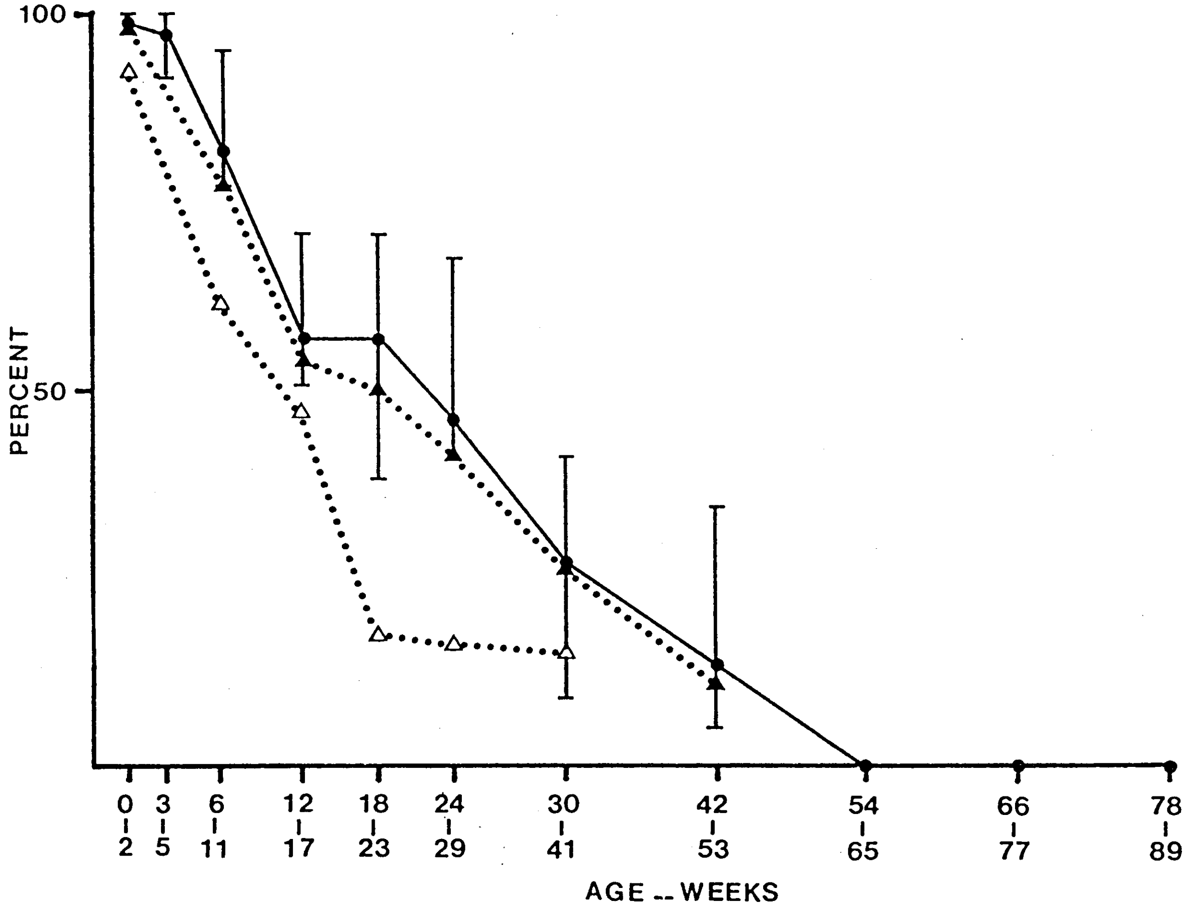


Figure 13. The proportion of time spent on or in contact with mother. Results are for safari park baboons from the present study and for wild baboons from Altmann (1980). The measures from both studies are based on instantaneous samples. The wild baboon results are from infants of restrictive and laissez-faire mothers.

●——● weighted means for safari park baboons

▲·····▲ means for wild baboons; infants of restrictive mothers

△·····△ means for wild baboons; infants of laissez-faire mothers

Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

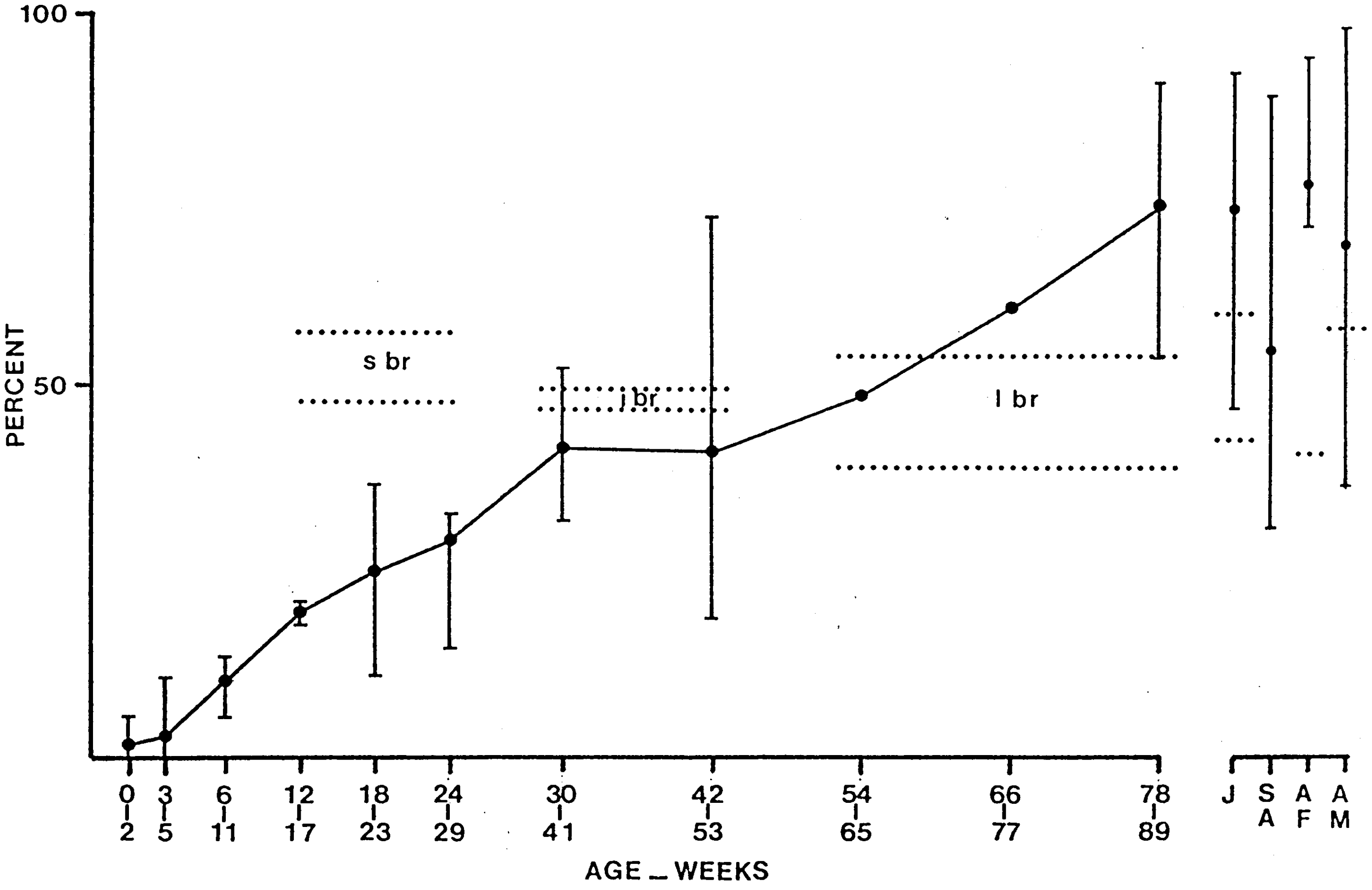


Figure 14. The proposition of time spent sitting. Results are for safari park baboons from the present study and for wild baboons from Rose (1977). The measure from safari park baboons is the percentage of total 30-second instantaneous samples which scored sitting. The measure for wild baboons is the percentage of total observation time spent sitting.

●——●	weighted means for safari park baboons
·······	results for wild baboons
s br	small brown infant
i br	intermediate brown infant
l br	large brown infant

Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

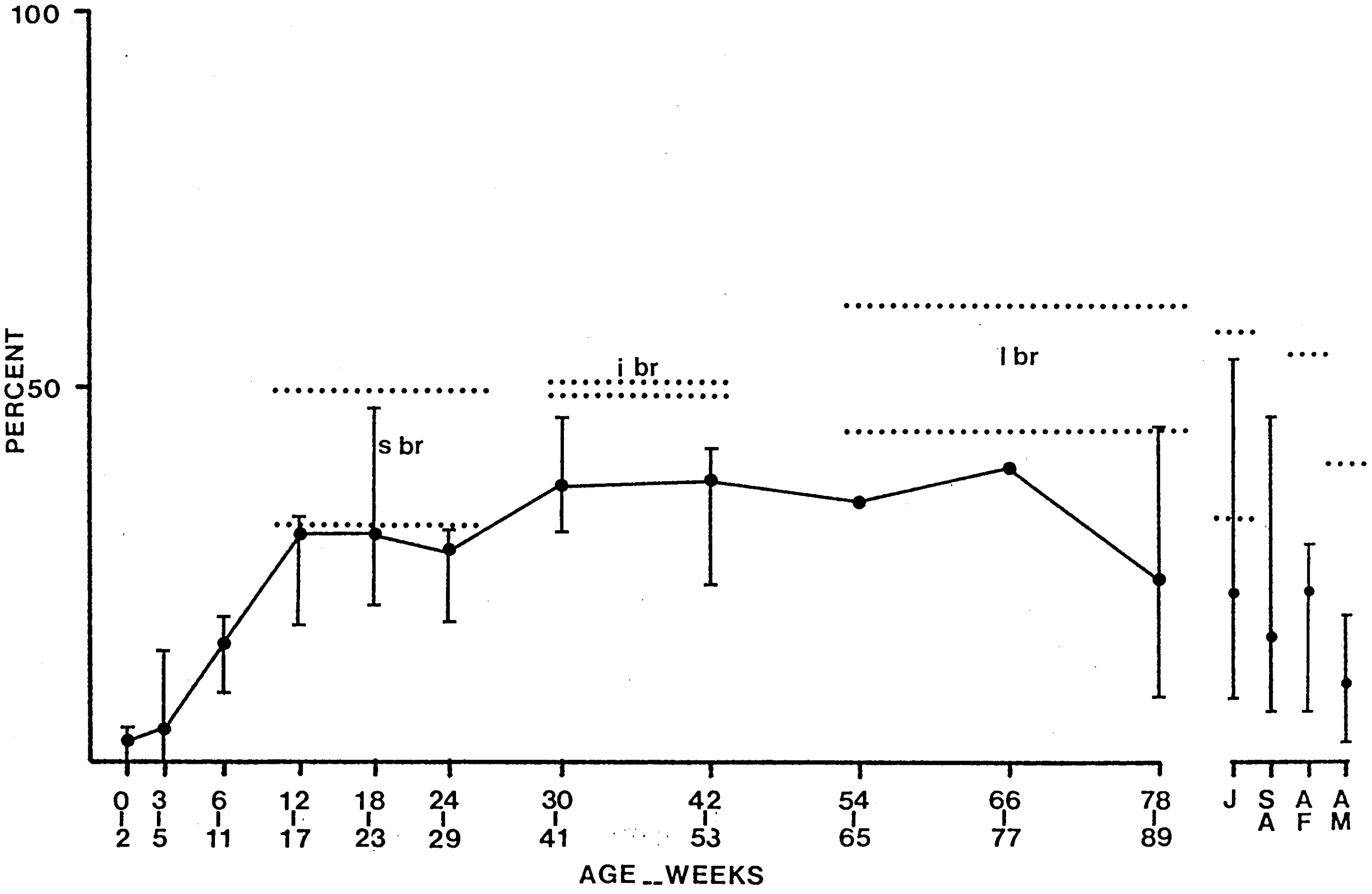


Figure 15. The proportion of time spent standing. Results are for safari park baboons from the present study and for wild baboons are from Rose (1977). The measure from safari park baboons is the percentage of total 30-second instantaneous samples which scored standing. The measure for wild baboons is the percentage of total observation time spent standing.

Key as for Figure 14.

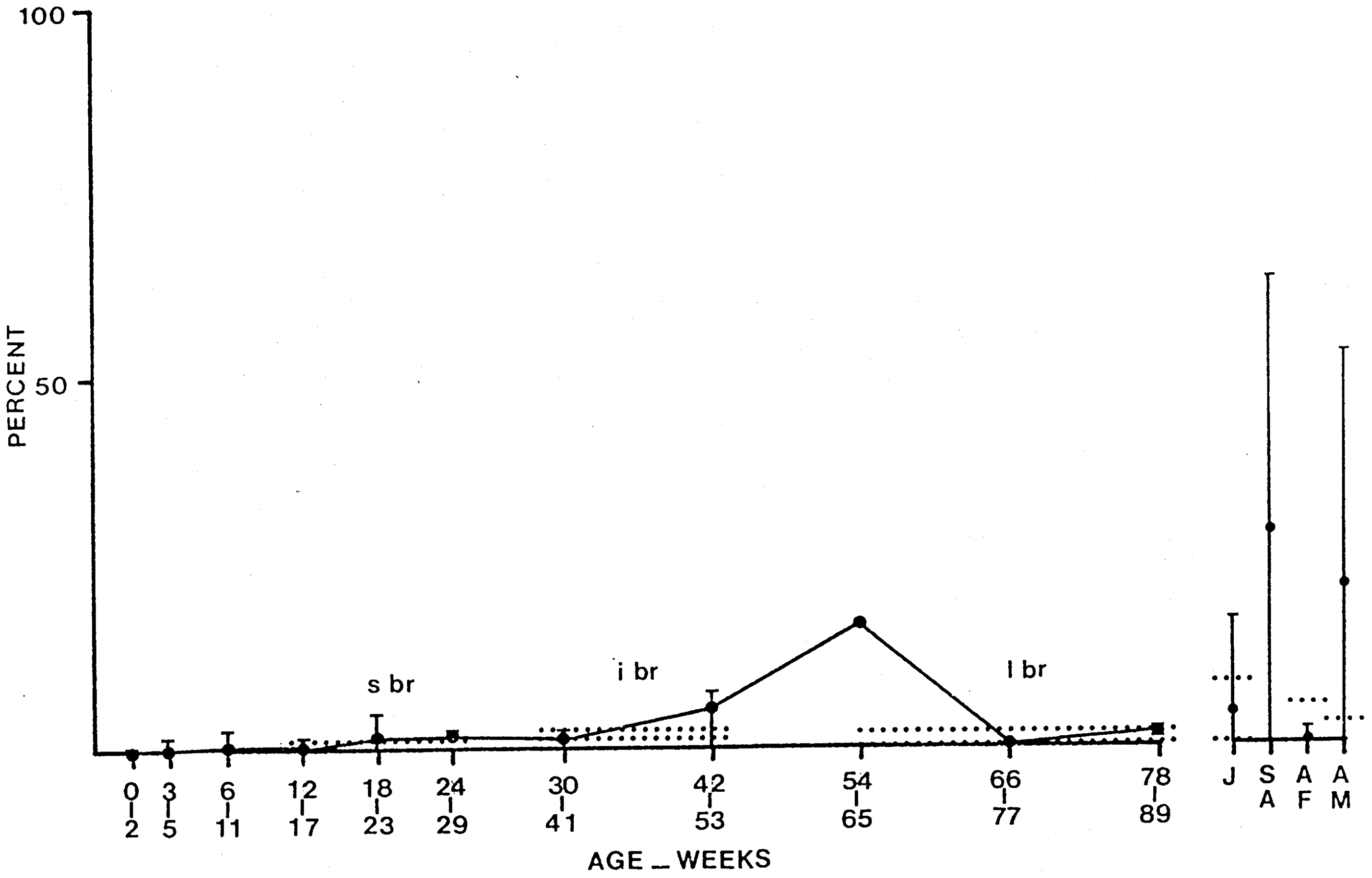


Figure 16. The proportion of time spent lying. Results are for safari park baboons from the present study and for wild baboons are from Rose (1977). The measure from safari park baboons is the percentage of total 30-second instantaneous samples which scored lying. The measure for wild baboons is the percentage of total observation time spent lying.

Key as for Figure 14.

did Rose's wild baboons but less time standing. Adult males in the safari parks spent more time lying than did wild baboons.

A major contrast between the safari park and wild condition is that wild groups are free to travel over a large home range whereas safari park animals are confined to a relatively small area. Rose estimated that the pumphouse troop travelled an average of 5.6 km. per day. In the safari parks such ranging was impossible or unnecessary. This may have resulted in the older safari park baboons standing less and sitting and lying more than their wild counterparts.

Coat colour

Infant baboons are born with black hair and a light coloured face. This neonatal coloration is gradually replaced by brown hair and black face. The safari park infants passed through a transition period of about 4 months in which first the face and then the hair around it changed colour, followed by shoulders and chest, then the legs, flanks and back and finally the top of the head. The ages at which major changes were noted for individuals are shown in Table 16.

Although not all infants began to change colour during the same age block, half started to show signs of yellow or brown at 6-11 weeks. The transition period can be considered to have been 6-11 weeks until 18-23 weeks.

Altmann gave the colour transition period to be from the third to the sixth month. Chalmers (pers.comm.) has described infants as having completely lost their black coats by 28 weeks. The ages of colour transition in safari park infants therefore corresponded with those reported for wild baboons.

Measures of time on-nipple in captive and wild baboons

Age changes in the frequency of on-nipple scores for safari park baboons, caged baboons (Rowell, Din and Omar, 1968) and wild baboons (Chalmers, unpublished data) are shown in Figure 17. The measures for caged and wild baboons are based on one-zero scores but instantaneous sampling was used in the present study. The measure for safari park

Table 16. The ages at which major changes in coat colour were recorded

	Age blocks - weeks										
	0-2	3-5	6-11	12-17	18-23	24-29	30-41	42-53	54-65	66-77	78-89
Lilly	■	■									
Safron	■	■	▨	▨	▨	□	□	□			
Peg	■	■									
Aubrey							□	□	□	□	□
Gush		■	▨								
Davey	■	■	■								
Sigmund							□				
Capone								□			
Rover											□
Gilian		■	■	▨	▨						
Deag	■	■	▨	▨	▨	□	□	□			
Kenya	■		■		▨						
Booby	■										
Viola								□			

■ black

▨ black/brown

□ brown

Blank squares indicate age blocks for which there were no data.

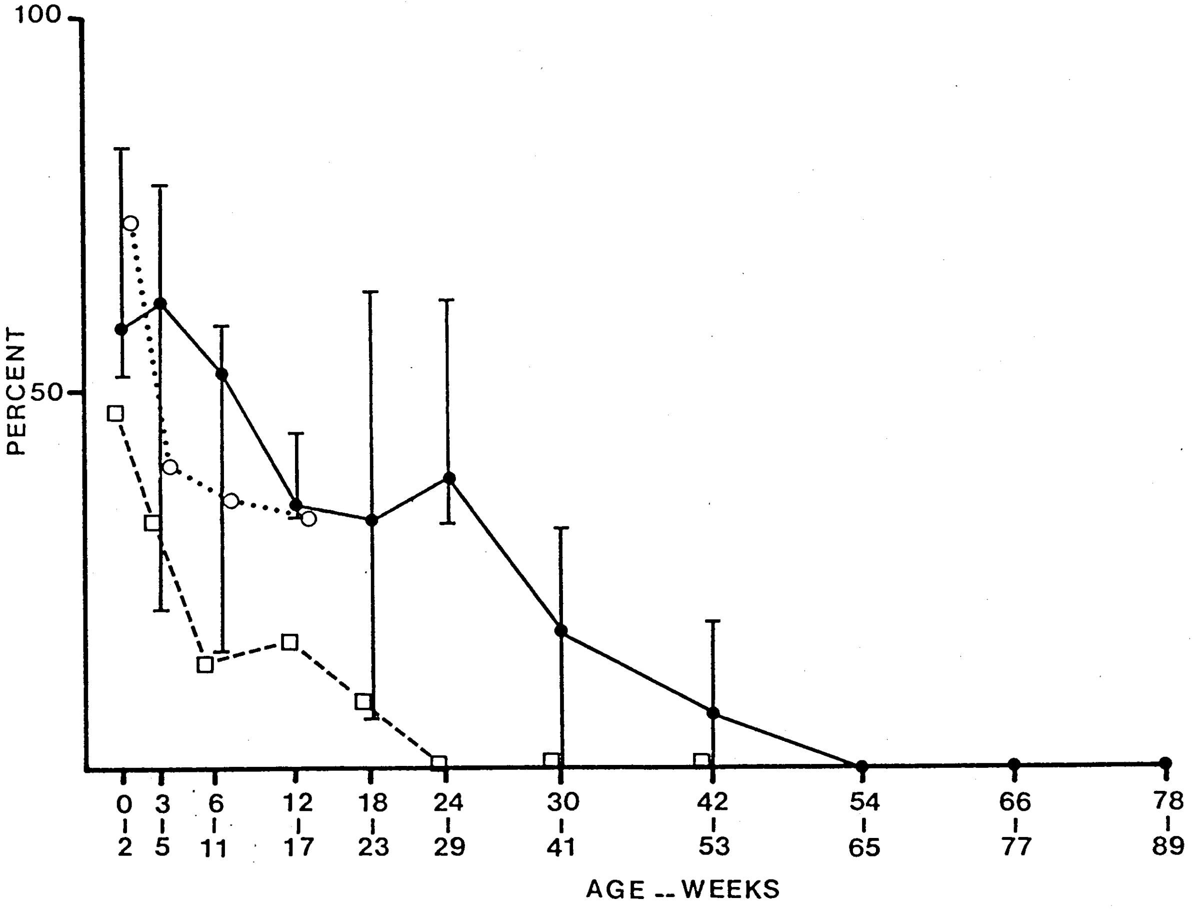


Figure 17. Time spent by infants on-nipple. Results are from safari baboons in the present study, wild baboons (Chalmers unpublished results) and captive baboons (Rowell, Din and Omar 1968). The measures are: safari park baboons, percentage of instantaneous samples which scored on-nipple; wild baboons, percentage of non-encounter 30-second intervals in which infants were on-nipple captive baboons, percentage of total 30-second intervals in which infants were on-nipple.

●——● safari park baboons
○·····○ captive baboons
□---□ wild baboons
Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

baboons is therefore an estimate of the proportion of time spent on-nipple. This means that it is possible to compare trends but not absolute values. It should also be noted that Chalmers' frequencies are not proportions of total sample intervals but of "non-encounter intervals", that is, of intervals sampled between social encounters with group members other than the mother. If they had been expressed as proportions of total intervals they would have been lower by virtue of larger denominators.

All three studies show that the on-nipple measures decreased over the age range covered (although the Figure shows the weighted mean frequency for safari park baboons increasing between 0-2 weeks and 3-5 weeks, there is a downward shift in the ranges). It is of interest here that safari park baboons were more similar in this measure to caged than to wild baboons who at every age were on-nipple in a smaller proportion of intervals.

One-zero scores tend to be higher than instantaneously sampled scores of the same events (Rhine and Linville, 1980; Simpson and Simpson, 1977). It could be significant that the wild baboon frequencies, which were from one-zero scores, were lower than those for safari park baboons, which were instantaneously sampled. It might indicate a real difference in either time on-nipple or frequency on-nipple such that safari park baboons were on-nipple more than wild baboons.[1]

The most marked decrease with safari park baboons happened at 30-41 weeks. Nash (1978) also reported a sharp decrease in the time spent by wild infant olive baboons on the nipple, but at the slightly later age of

---

[1] This argument has been used by Berman (1980) to compare different measures of off mother frequencies in wild and captive rhesus macaques.

10 to 12 months. She considered that this marked a decrease in infants' dependence on their mothers for food and security.

Differences between safari park infants and wild infant baboons

To summarize, safari park infants tended to be off mother less and on-nipple more than wild infants, except for those wild infants which were more restricted by their mothers, but safari park infants might have started weaning earlier than at least one group of wild infants.

I suggest there were five factors contributing to the apparently closer association between safari park infants and mothers:

1) adult sex ratios;
2) the absence of mothers' kin;
3) climate;
4) the presence of humans;
5) feeding in trees.

1. Adult sex ratios:

There may have been more stress within the safari park groups because of higher male:female ratios than in the wild. Fights between males were common in the safari parks. I saw them on most days, involving sparring, biting and extended chases with loud vocalization. Injuries were common. Such fights were rare in the wild (Altmann, 1980; Chalmers, pers.comm.). Safari park mothers may have been more restrictive as a result of stress.[2]

2. Absence of kin:

Berman (1980) has suggested that a factor affecting the degree of maternal restrictiveness in rhesus might be the availability of kin with which a mother can associate. She considered that a kin-organized group might be less stressful than one with few kin-relationships and mothers

---

[2] See comment on p.48 regarding restrictiveness at feeding times.

might be less restrictive.

At both Woburn and Blair Drummond the adults, sub-adults and juveniles had been brought together from several sources. The infants described in this study were the first generation to be born in captivity. While one cannot rule out the possibility that some of the older baboons might have been related, it is certainly reasonable to assume that there were fewer kin-relationships than at Gilgil or Amboseli.

3. Climate:

The temperature at Gilgil was higher than British summer temperature. It is possible that the closer association of safari park infants with their mothers was a temperature regulatory response. Furthermore, it is reasonable to suppose that the safari park baboons experienced more rainy days than those in Kenya. Rowell, Din and Omar (1968) showed that rain increased the time spent on-nipple by captive infant baboons.

4. The presence of humans:

An obvious difference between safari park and wild conditions was the continual presence in the safari parks of large numbers of visitors in cars, and keepers who were usually in vehicles but sometimes on foot.

Altmann (1980) has said that mothers with newly born infants are the class most sensitive to being observed. She (along with other field primatologists) has stressed the need for a period prior to data collection in which the animals can habituate to the presence of observers in or out of vehicles. The safari parks had existed for over one year before the present study began and the baboons had become tolerant of humans but in a different way from those studied by Altmann, Chalmers and Rose. Those researchers became neutral entities; neither dangerous nor benevolent. To safari park baboons the visitors were always potential sources of food, as were the keepers at feeding time. On the other hand, keepers were a potential threat when they carried rifles (loaded with blanks or syringes charged with medicine).

Thus, it is reasonable to suggest that the presence of humans in the safari parks might have contributed more to maternal stress than the presence of researchers in field studies.

5. Feeding in trees:

It was mentioned in the previous chapter that the safari park baboons spent much of their time in trees feeding on leaves, fruit, bark, etc. This might have caused mothers to restrict the mobility of their infants. However, Chalmers (pers.comm.) has pointed out that at Gilgil there were plenty of shrubs and bushes from which mothers fed while holding their infants. Also they frequently restricted their infants while climbing on cliffs.

Conclusion

On the basis of the measures of mother-infant behaviour and infant colour transition that this study has in common with others, the following general statements can be made. Safari park baboons resembled both caged and wild macaques and baboons enough to suggest that findings in this study may have some general application and may be comparable with those in the published literature. In measures of mother-infant association and time spent on-nipple, safari park baboons resembled caged rather than wild baboons and mothers showed restrictive rather than laissez-faire maternal styles. This may have been a result of climate or stressful conditions in safari parks.

Chapter 4. Results: behaviour associated with mother

One of the aims stated in Chapter 1 was to describe motor pattern development in the context of other changes in infant life such as relationship with the mother and coat colour change. The results presented in this chapter, as well as some from the previous chapter, will provide part of the necessary contextual background.

1. Closer consideration of positions relative to mother

The off mother position was sub-divided into "in contact with mother" and "out of contact with mother". Changes in their one-zero frequencies are shown in Figures 18 and 19.

All three mother-related positions (on , in contact and out of contact) are shown in Figure 20. At ages 0-2 and 3-5 weeks the proportion of intervals on mother was high compared with in contact and out of contact, which had approximately equal frequency. The proportion with out of contact increased at ages 6-11 weeks and 12-17 weeks so that infants were out of contact more than in contact, yet still on mother in most intervals. From 24-29 weeks the intervals with out of contact continued to increase, with an accompanying decrease in intervals on and in contact. Infants were now out of contact with their mothers in most intervals.

At 18-23 weeks there were equal proportions of intervals with on and out of contact, while in contact reached a peak. By comparison with Figure 11 it can be seen that this was the age with the maximum rate of contact makes and breaks. The question arises whether the peak frequency of intervals with in contact is an artifact of transitions between on mother and out of contact, in which case it may not have been an important state for the infants, or whether in contact with mother was an extended state which may have been important in infants' lives.

Instantaneous sampling has a low probability of scoring events of short duration, such as contact with mother which is simply a transition, whereas it is likely to score extended states with a frequency proportional

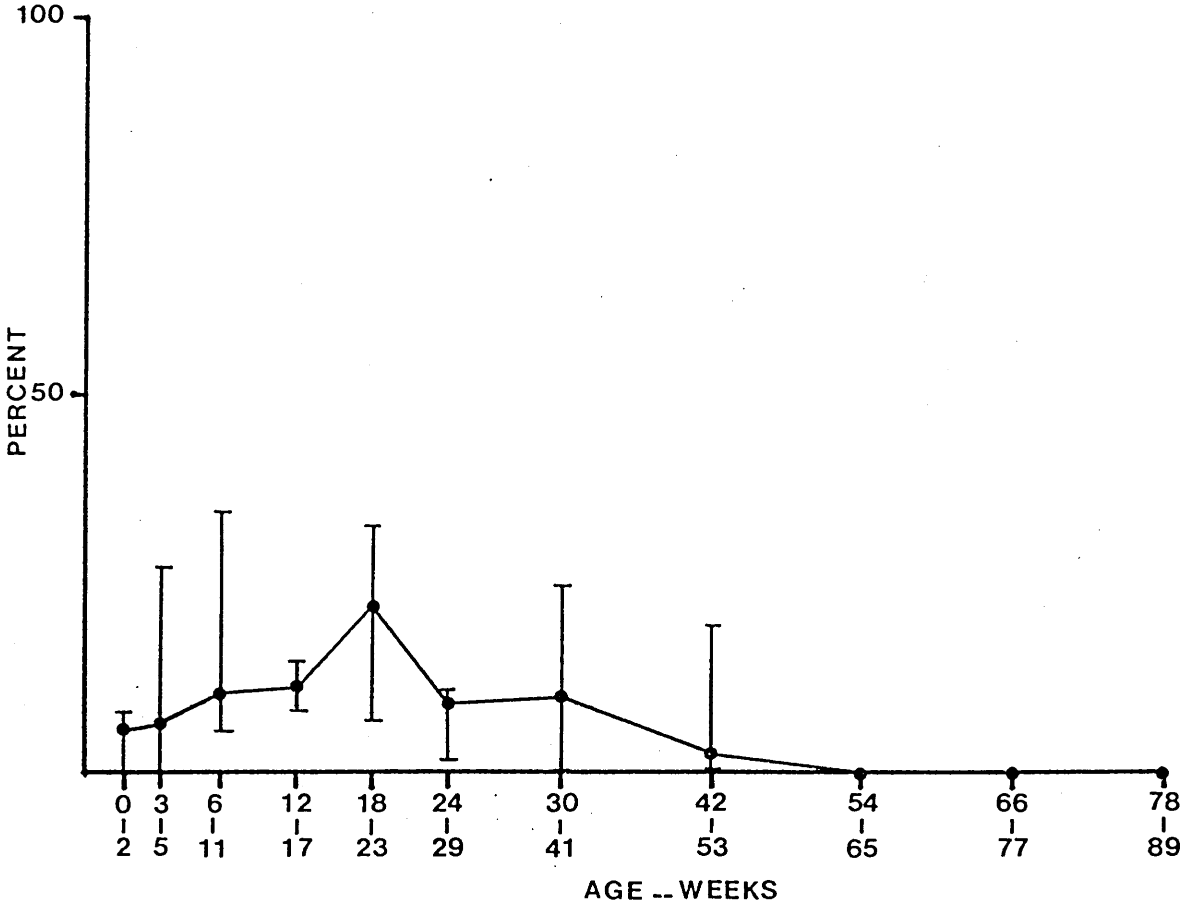


Figure 18. The percentage of 30-second intervals in which infants were in contact with mother.

For key to symbols see Appendix I.

Sample Sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

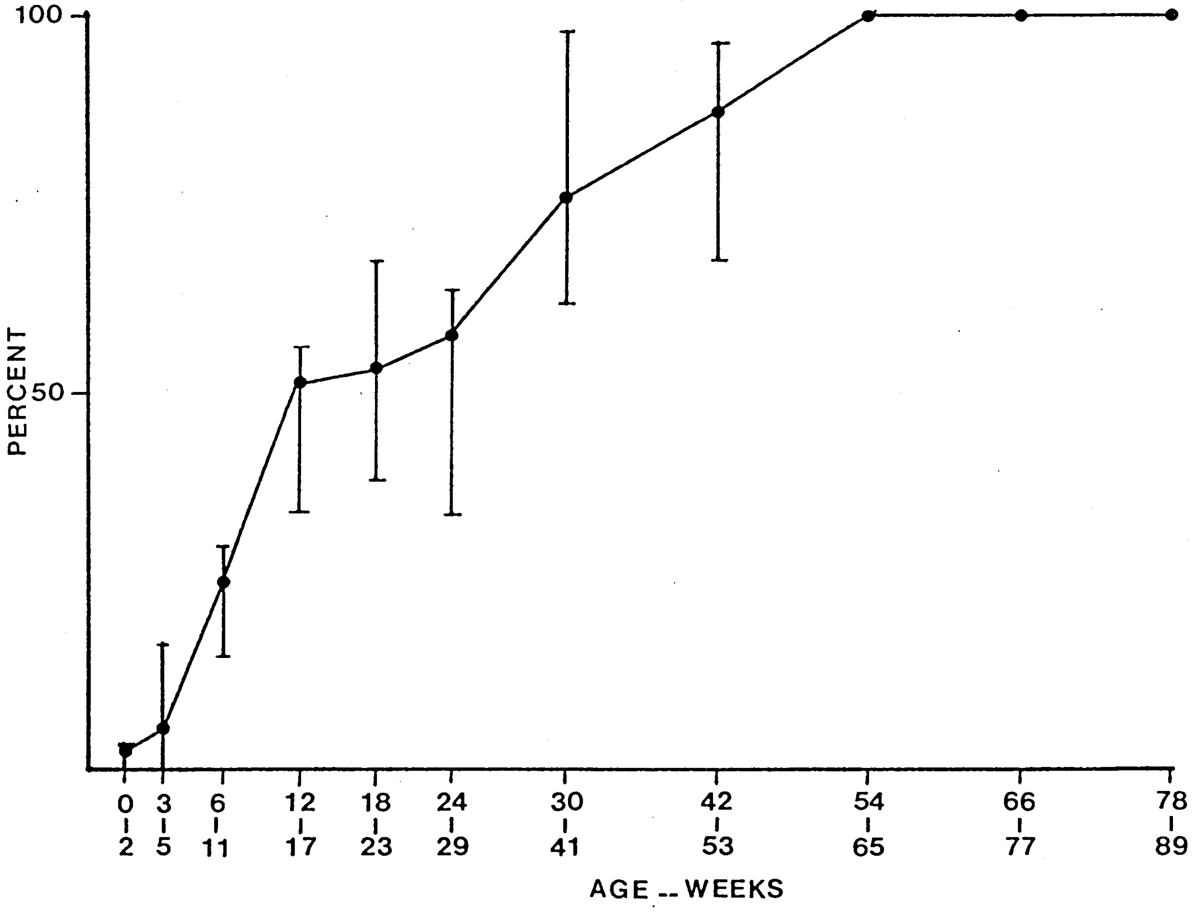


Figure 19. The percentage of 30-second intervals in which infants were out of contact with mother.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

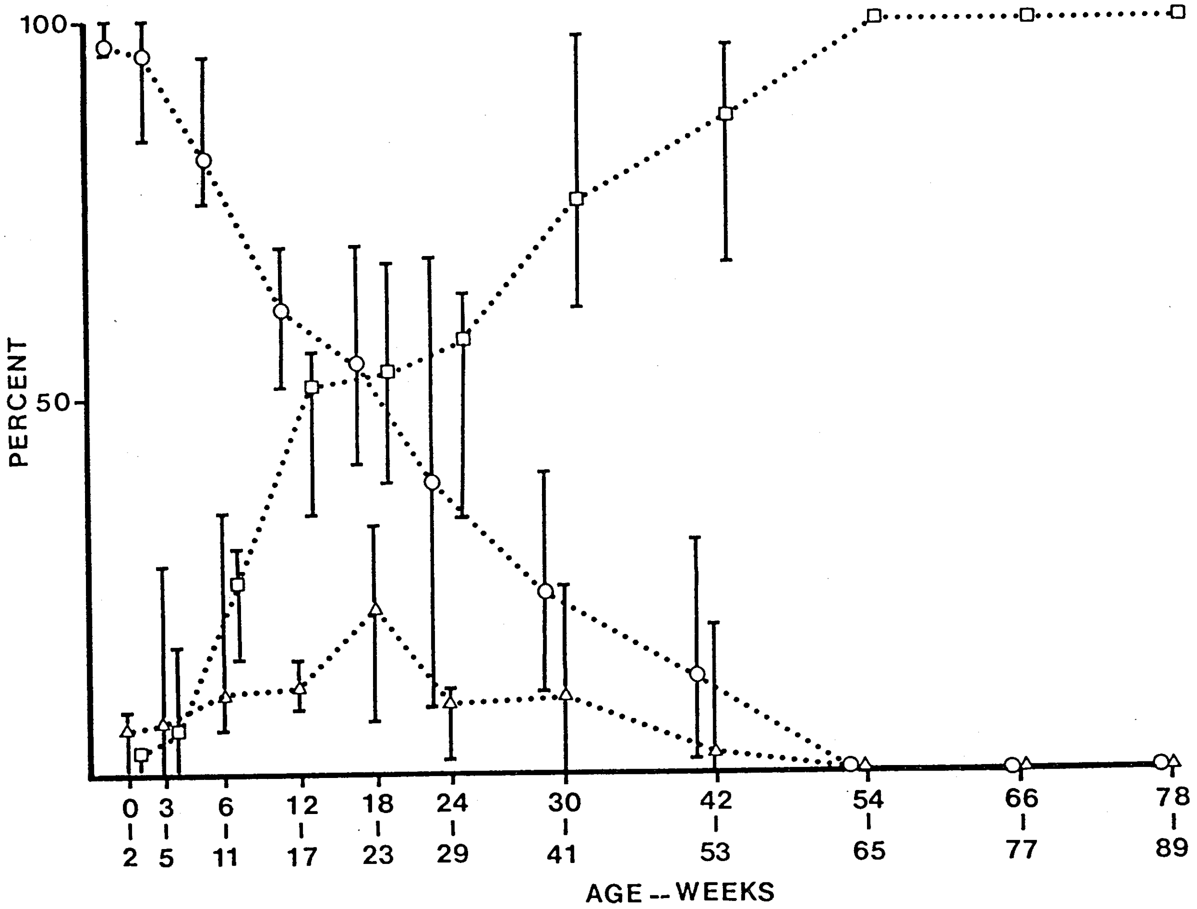


Figure 20. The percentage of 30-second intervals in which infants were on mother, out of contact with mother or in contact with mother. These data have already been given in Figures 9, 18 and 19.

O·····O	on mother
□·····□	out of contact with mother
△·····△	in contact with mother

Vertical lines show the ranges.

Sample sizes in the present study:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

to the total time involved. Changes in the percentage of instantaneous samples which scored in contact with mother are shown in Figure 21.

It is clear that in-contact was of sufficient duration to be picked up by instantaneous sampling. It was unlikely therefore to have been merely a position passed through when getting onto or leaving the mother. It was more likely to have been a positional state adopted by infants in the presence of their mothers. Eighteen to twentythree weeks was the age at which it was adopted most.

2. Behaviours performed on or in contact with mother

The behaviours dealt with here are:

on-nipple;
rooting;
shift position;
grip mother's fur;
lean out;
manipulation of mother's fur;
clamber on mother.

"Clamber on other" is also dealt with even though it was obviously not performed on-mother.

Object manipulation from on the mother is not included here but will be considered in the next chapter.

In order to determine how much of the infants' total time was taken up performing these behaviours, intervals in which each behaviour occurred are expressed as percentages of total intervals. The results are shown in Figures 22 to 27.

Most of the behaviours appeared during the earliest weeks with maximum or near maximum frequency and then decreased in frequency with age. Clamber on mother only became conspicuous between 6-11 weeks and 18-23 weeks during which time the one-zero frequency was fairly constant. Even so, its frequency did decrease with age. It has already been shown, in the previous section, that the proportion of time on-nipple decreased with age (Figure 17).

These results might be expected as a result of infants spending less

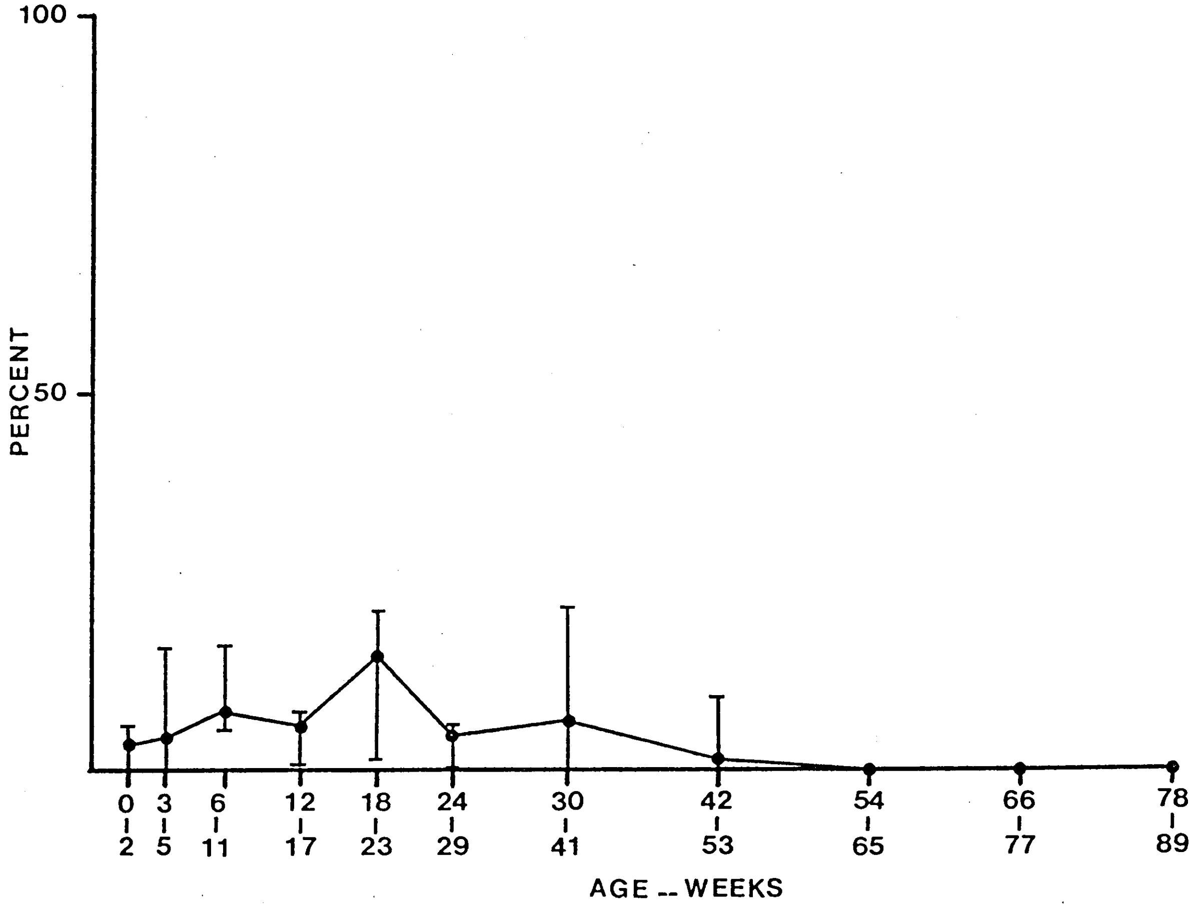


Figure 21. The percentage of 30-second instantaneous samples which scored in contact with mother.

For key to symbols see Appendix I.

Sample sizes:

See Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

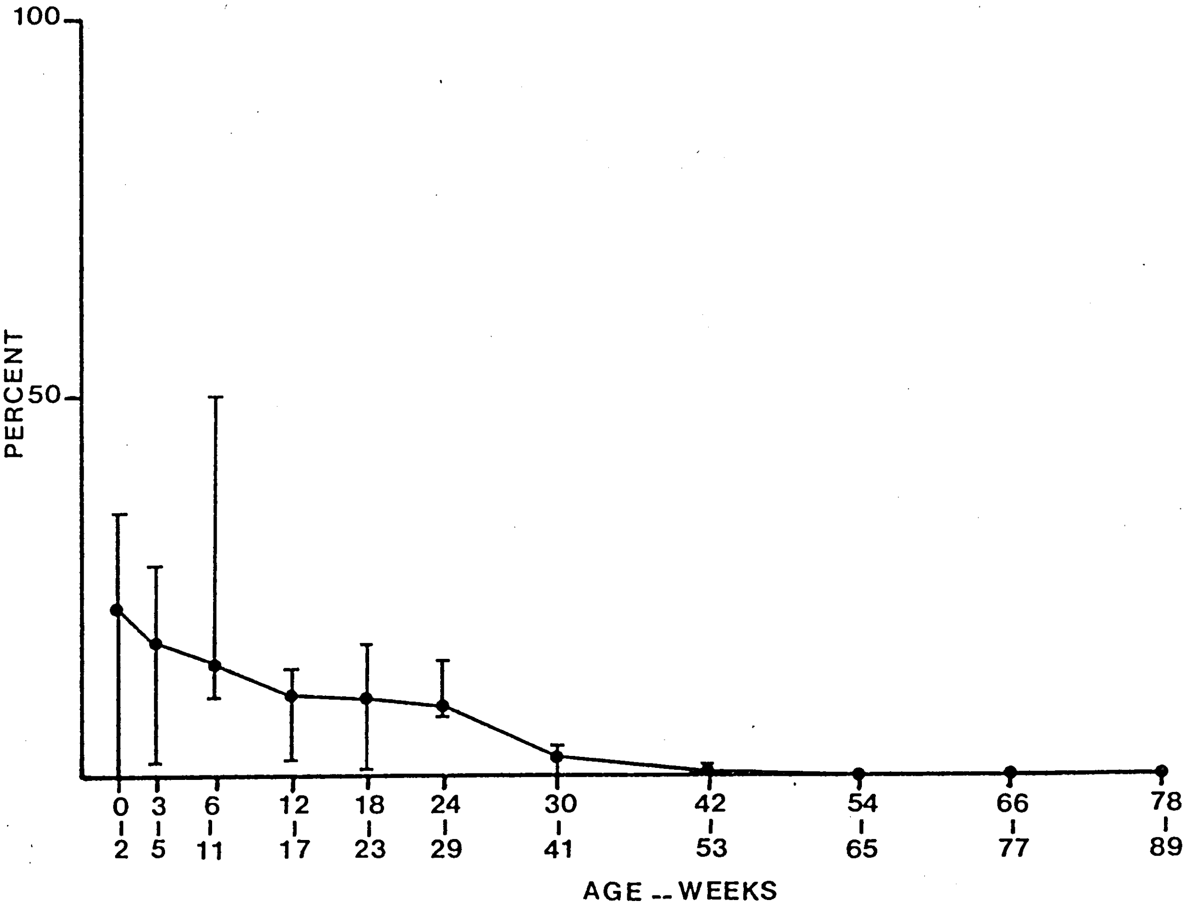


Figure 22. The percentage of 30-second intervals with shift position.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

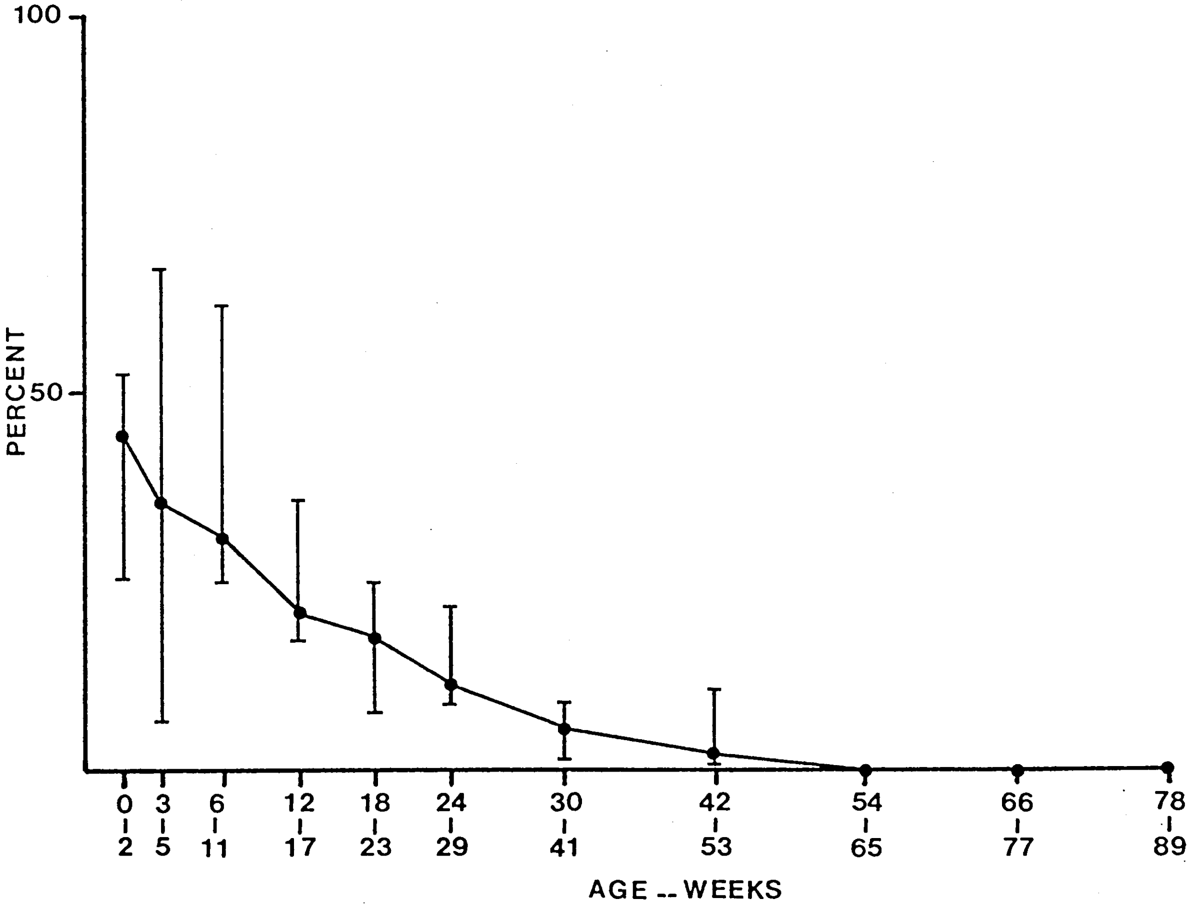


Figure 23. The percentage of 30-second intervals with rooting.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

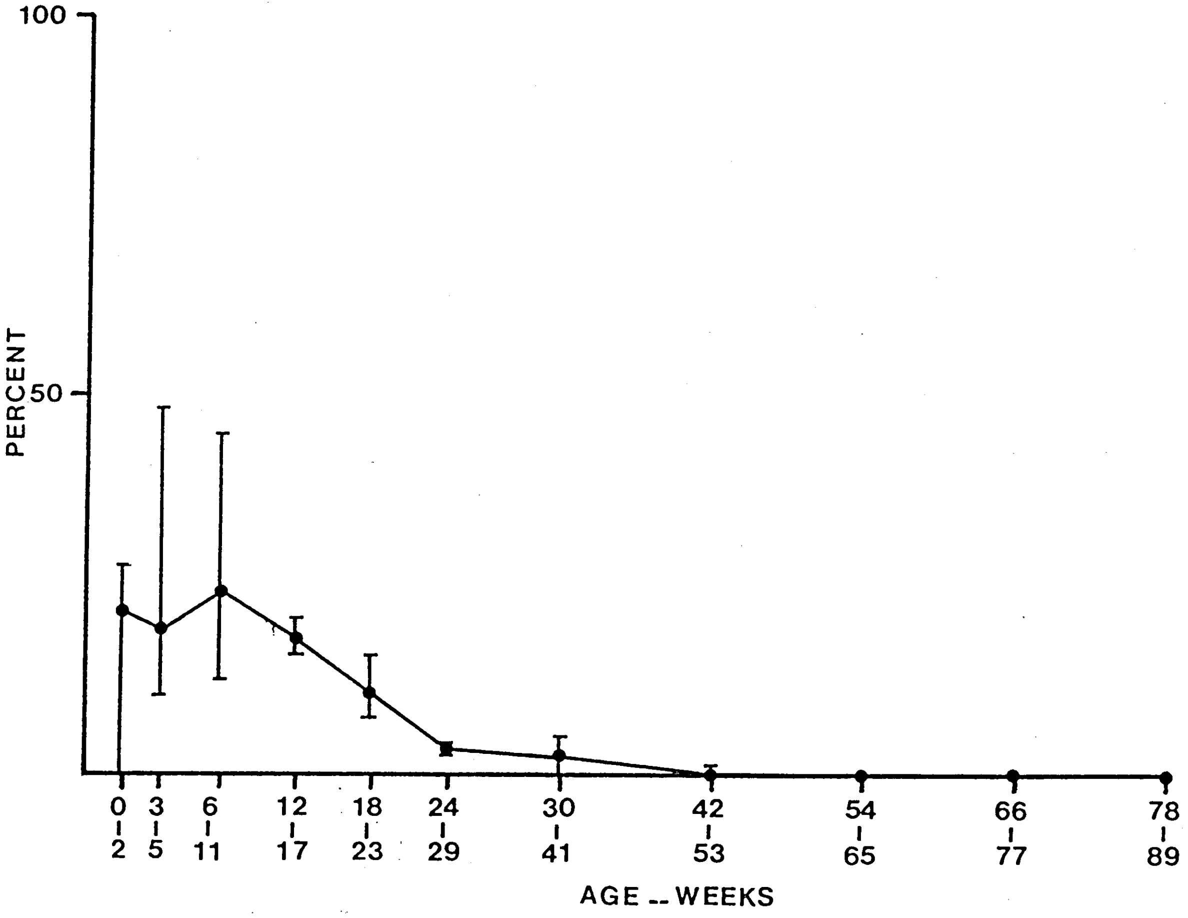


Figure 24. The percentage of 30-second intervals with grip fur.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

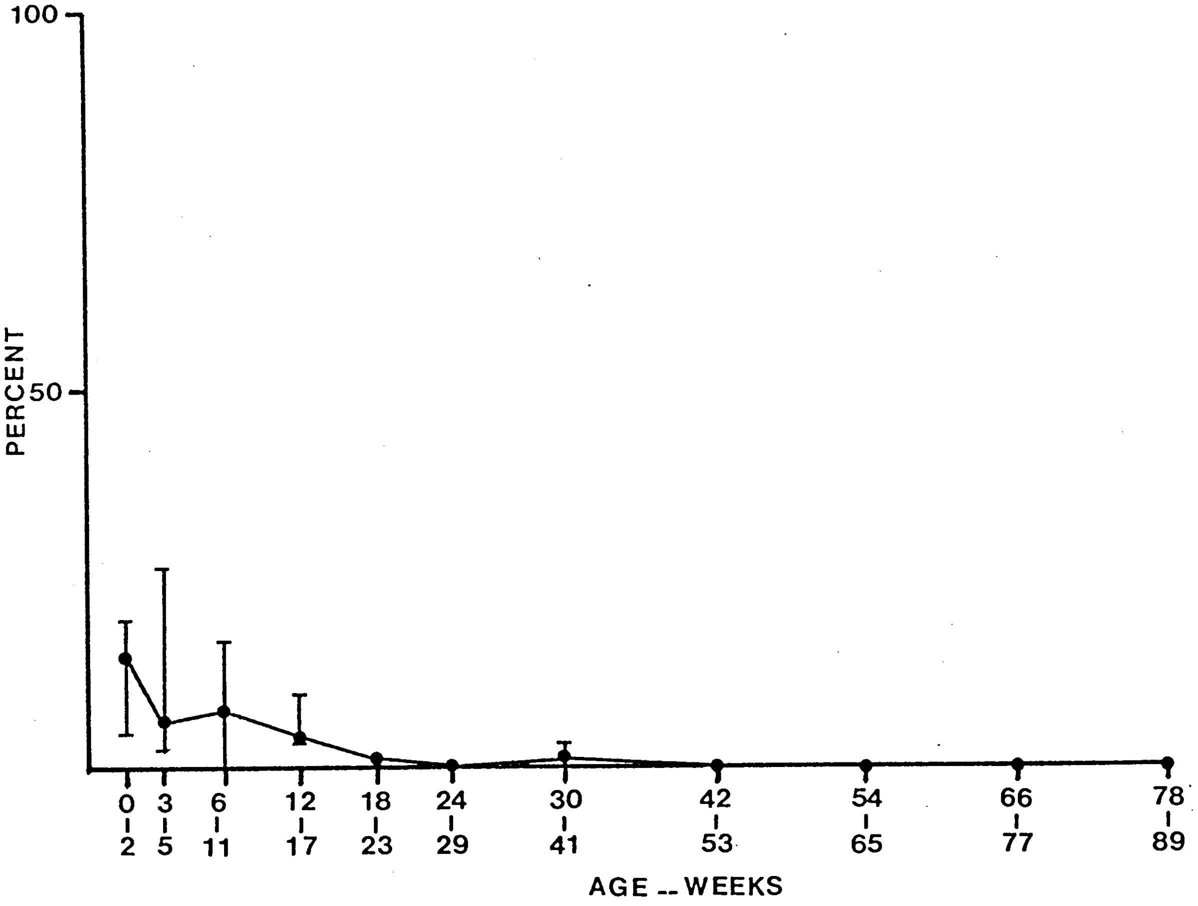


Figure 25. The percentage of 30-second intervals with lean out.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

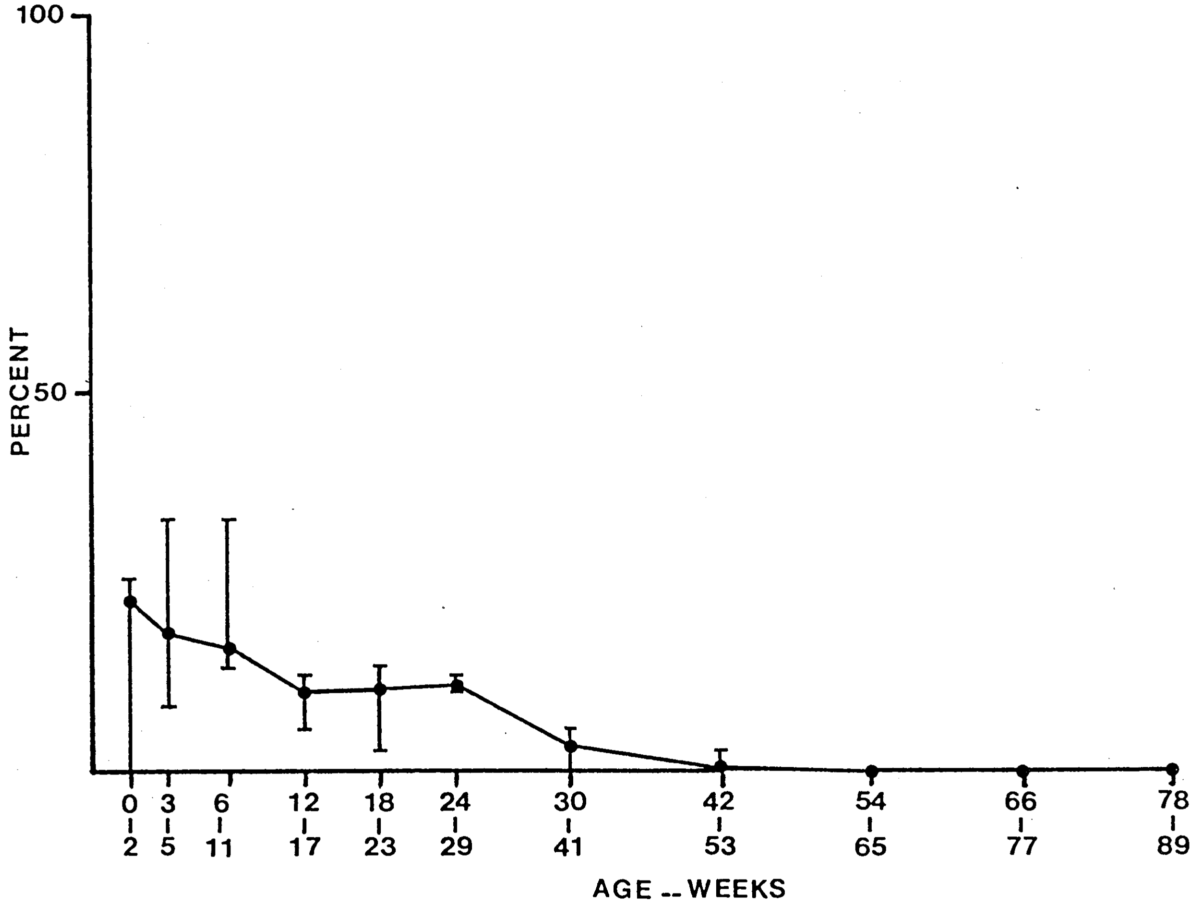


Figure 26. The percentage of 30-second intervals in which infants movec a hand or foot in the mother's fur.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

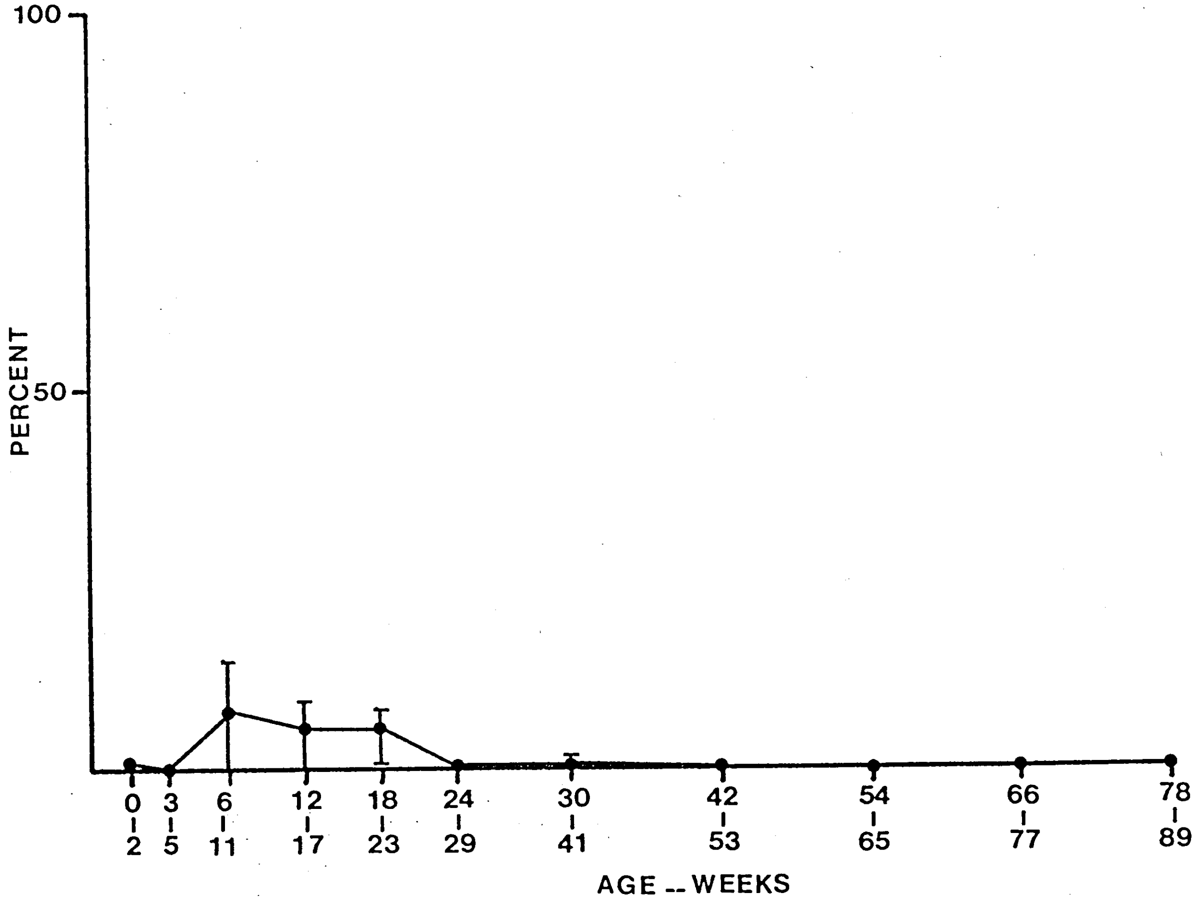


Figure 27. The percentage of 30-second intervals with clamber on mothe

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

time on mother with age.

More useful questions might be: what proportion of time spent on mother was occupied by a given behaviour and how did it change with age? These are addressed in Figures 28 to 36. They show age changes in the percentage of intervals in which infants were on or in contact with mother that a behaviour was scored.

On-nipple (Figure 28)

This shows the frequency of intervals beginning on-nipple as a percentage of intervals which began with the subject on or in contact with mother with its head visible. This is a measure of the proportion of time on or in contact with mother spent on-nipple. The results were very variable, shown by the wide ranges, but the weighted means show an increase with age (Spearman rs = +0.76, N = 8, $p < 0.05$). That is, with increasing age a greater proportion of time on or in contact with mother was spent on her nipple.

Rooting (Figure 29)

The proportion of time on mother spent rooting for the nipple decreased with age (Spearman rs = -0.98, N = 8, $p < 0.01$). The greatest rate of change was in the first few weeks.

The finding is remarkable in view of the increasing proportion of on mother time spent on-nipple. But it could mean that the amount of rooting in each session on-nipple decreased. Rooting was a motor pattern which brought the mouth to the nipple and marked the beginning of a bout on-nipple. It also occurred within such a bout, possibly when the infant was adjusting the nipple's position in its mouth. The decreasing frequency of rooting per unit time on-nipple could indicate a fall in the frequency with which bouts began, that is an increase in average bout length, or a decrease in the amount of rooting during bouts. Either case could be a sign of increasing skill at positioning and maintaining the nipple in the mouth.

This pattern is presented graphically in Figure 30. It shows an index of rooting per unit time on-nipple constructed by dividing the number

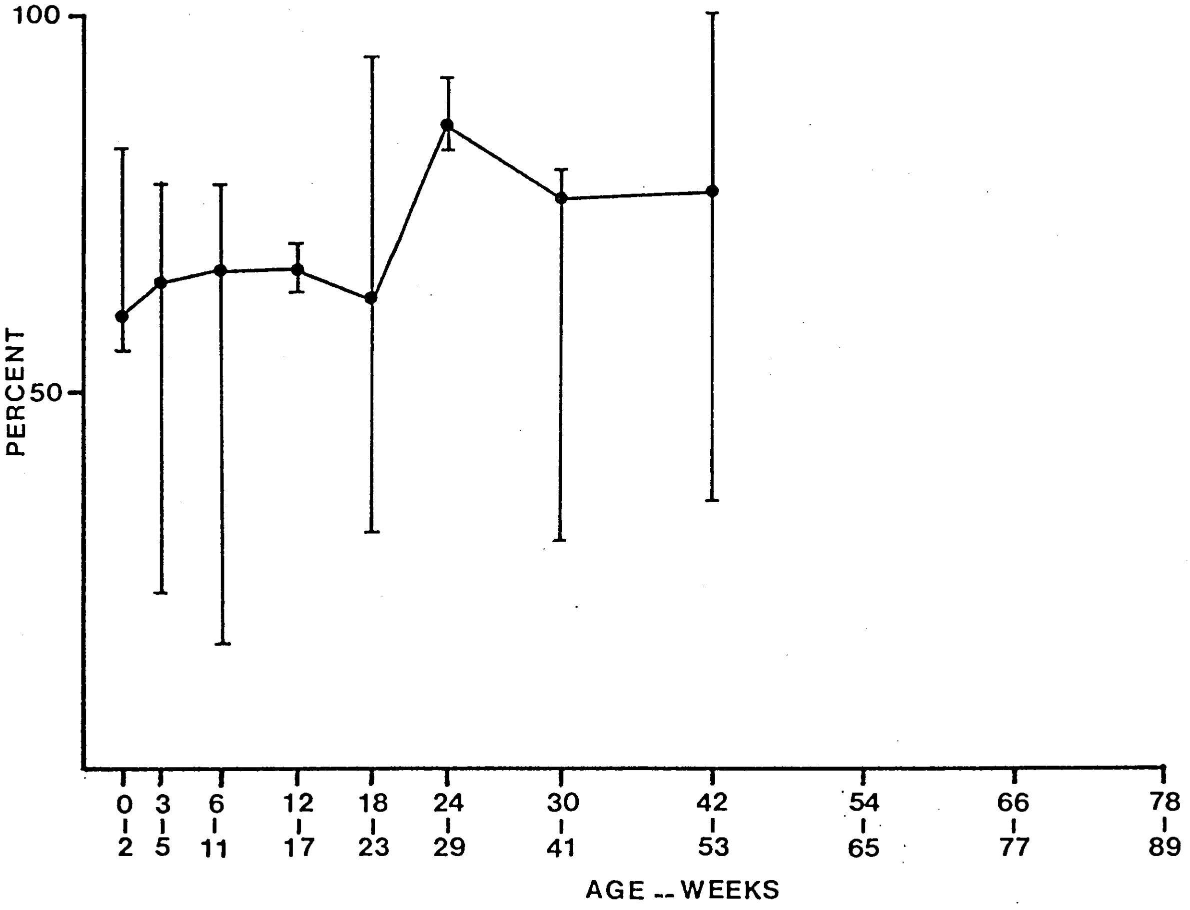


Figure 28. The proportion of time on or in contact with mother that infants spent on-nipple. Instantaneous samples scoring on-nipple are expressed as a percentage of those samples scoring on or in contact with mother in which the infant's head was visible.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

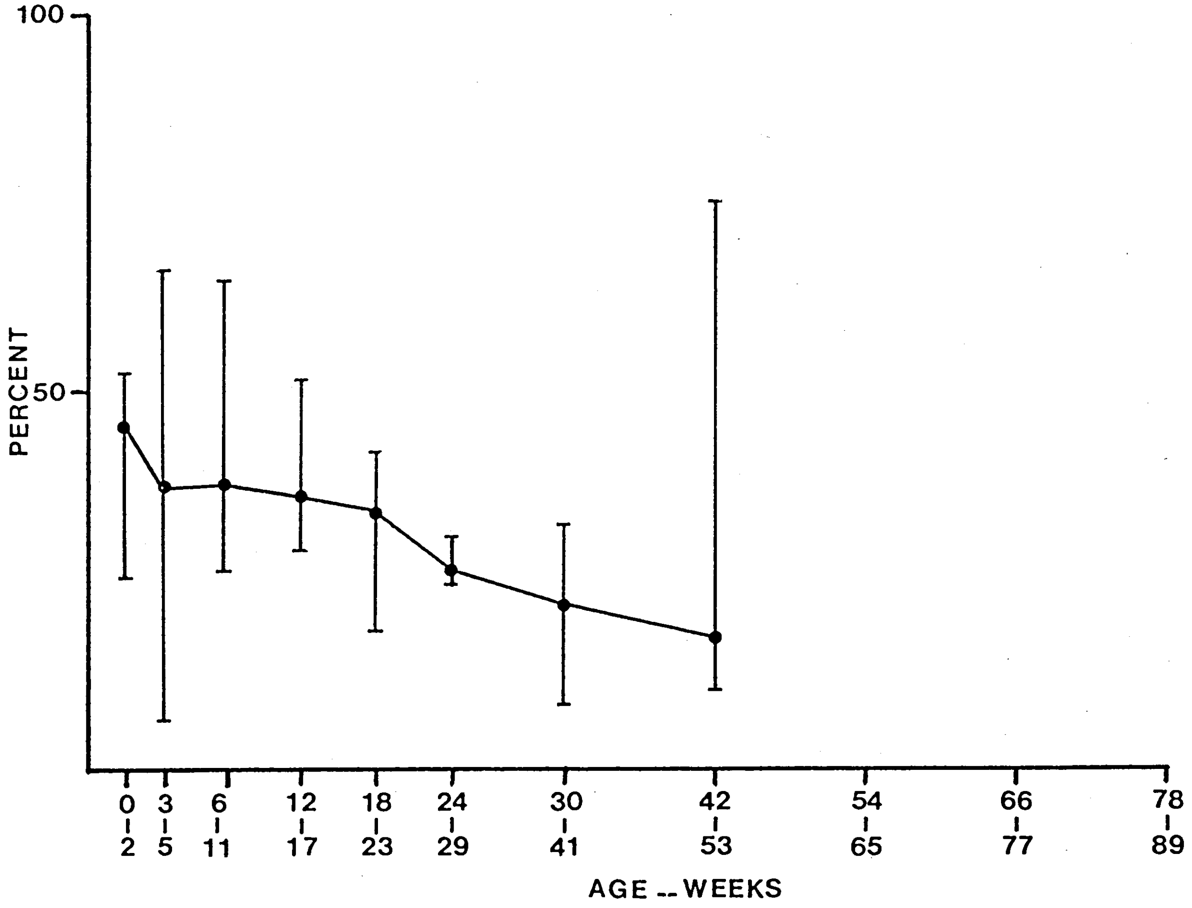


Figure 29. The percentage of on mother intervals with rooting for the nipple.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

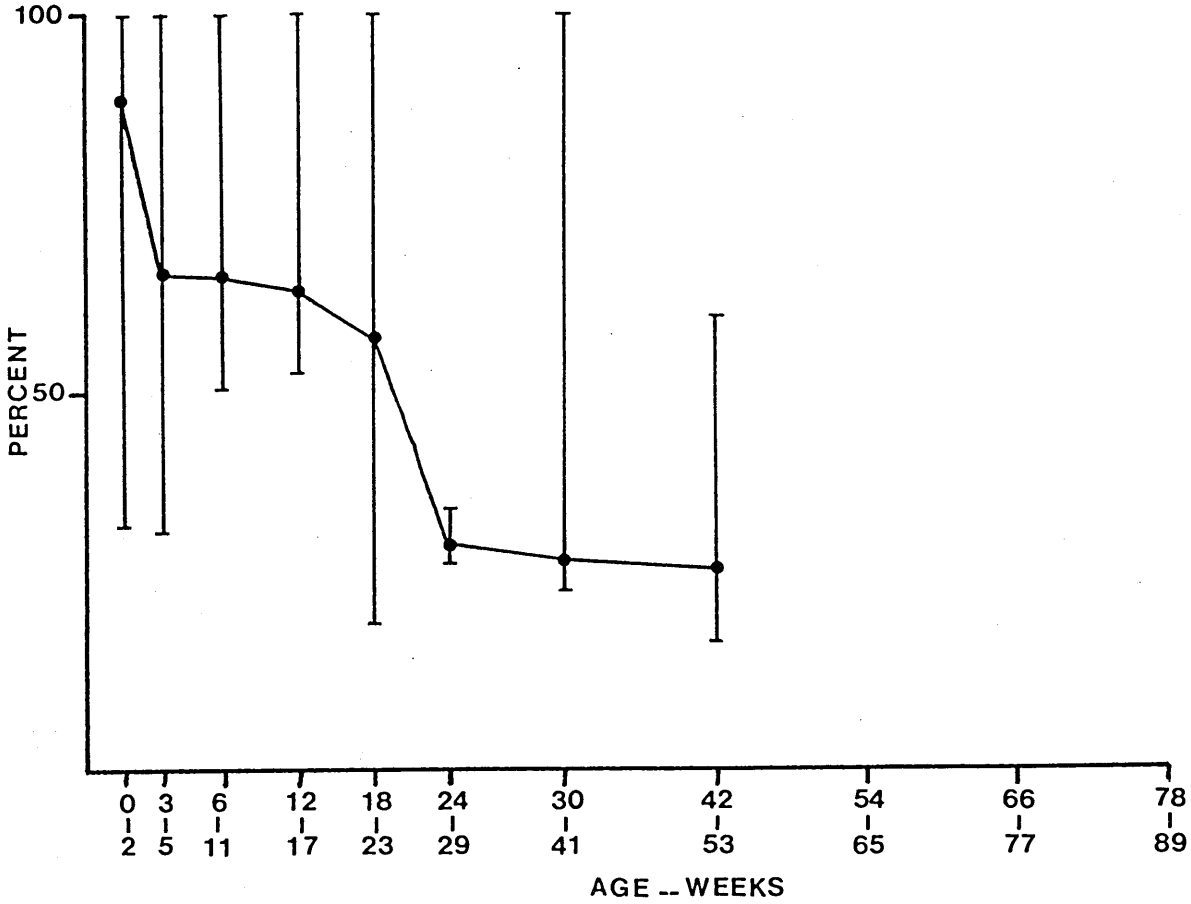


Figure 30. Age changes in an index of rooting bout length. The number of 30-second intervals with rooting are expressed as a percentage of 30-second instantaneous samples scoring on-nipple.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

of intervals with rooting by the number of intervals beginning on-nipple. The higher the index, the more rooting occurred per unit time on-nipple.

The index decreases with age as expected, but not with uniform rate. The decrease is rapid between 0-2 weeks and 3-5 weeks, perhaps because of rapidly increasing skill at rooting and holding the nipple. Between 3-5 weeks and 18-23 weeks the rate of decrease is much less. Perhaps there was little change in skill or bout length during this period. After 18-23 weeks the index falls to a lower level where it remains. This final stage is unlikely to represent the development of greater skill at rooting but might mean that bouts on-nipple were of longer duration; that is, less interrupted than before.

Shift position (Figure 31)

This was a "sink" category of small movements. The frequency remained at approximately 20% until 24-29 weeks, after which it fell to approximately 10%. There is a negative trend but it falls short of significance (Spearman rs = -0.55, N = 8, $p > 0.05$).

From 30-41 weeks infants were apparently more still, when on their mothers, than before.

Grip mother's fur (Figure 32)

This behaviour occurred consistently when an infant was holding the mother ventrally and she began to move after a period of sitting or standing still. It resulted, apparently, in a more secure grip on the mother. It was also scored if the infant was riding dorsally, but in this case it was not performed so consistently when the mother moved (casual observation).

Its frequency remained approximately the same in the early weeks but rose to a peak at 12-17 weeks. Between 24-29 weeks and 42-53 weeks it occurred with a fairly constant lower frequency. Overall there was a decrease with age (Spearman rs = -0.69, N = 8, $p < 0.05$).

Casual observation suggested that there was no obvious improvement in the effectiveness of gripping with age and any changes in frequency were unlikely to have been the result of maturational changes. I consider

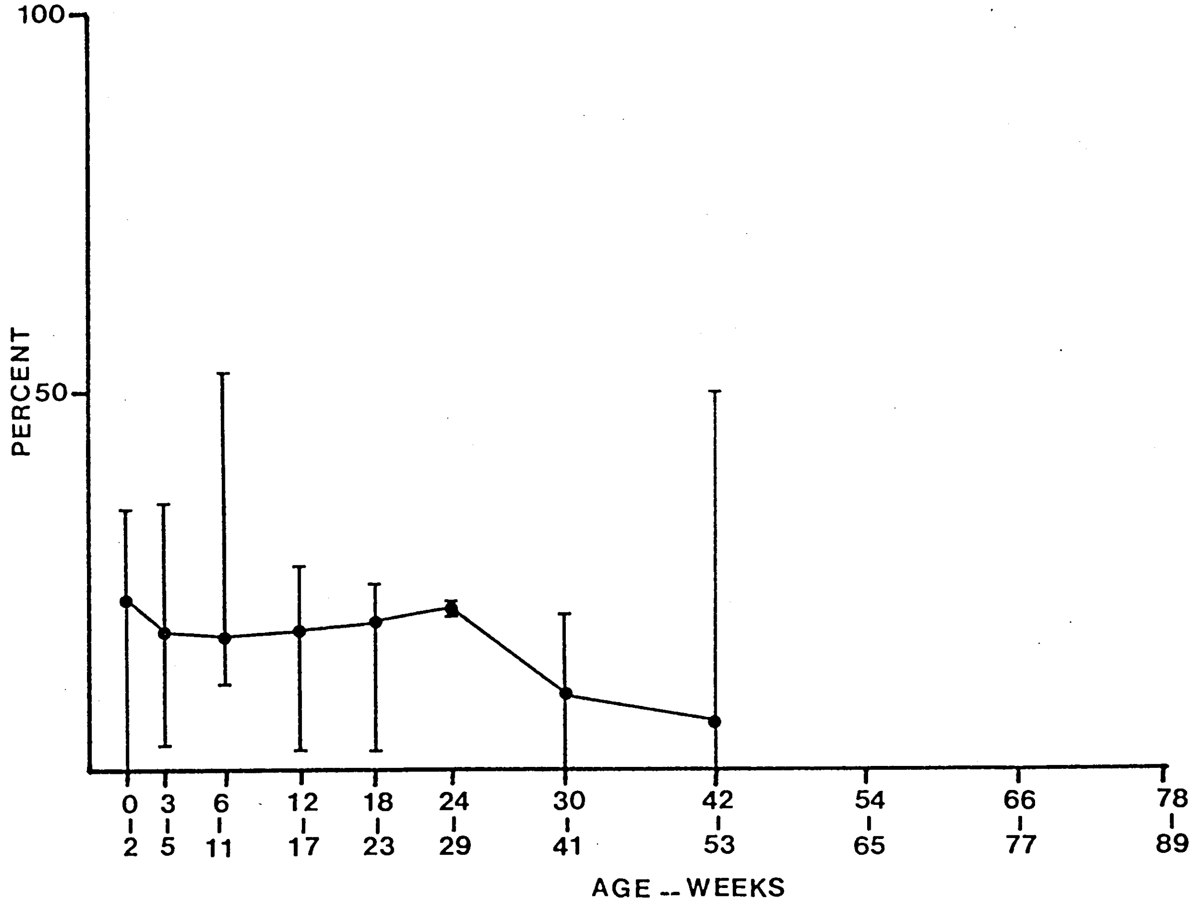


Figure 31. The percentage of on mother intervals with shift position.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

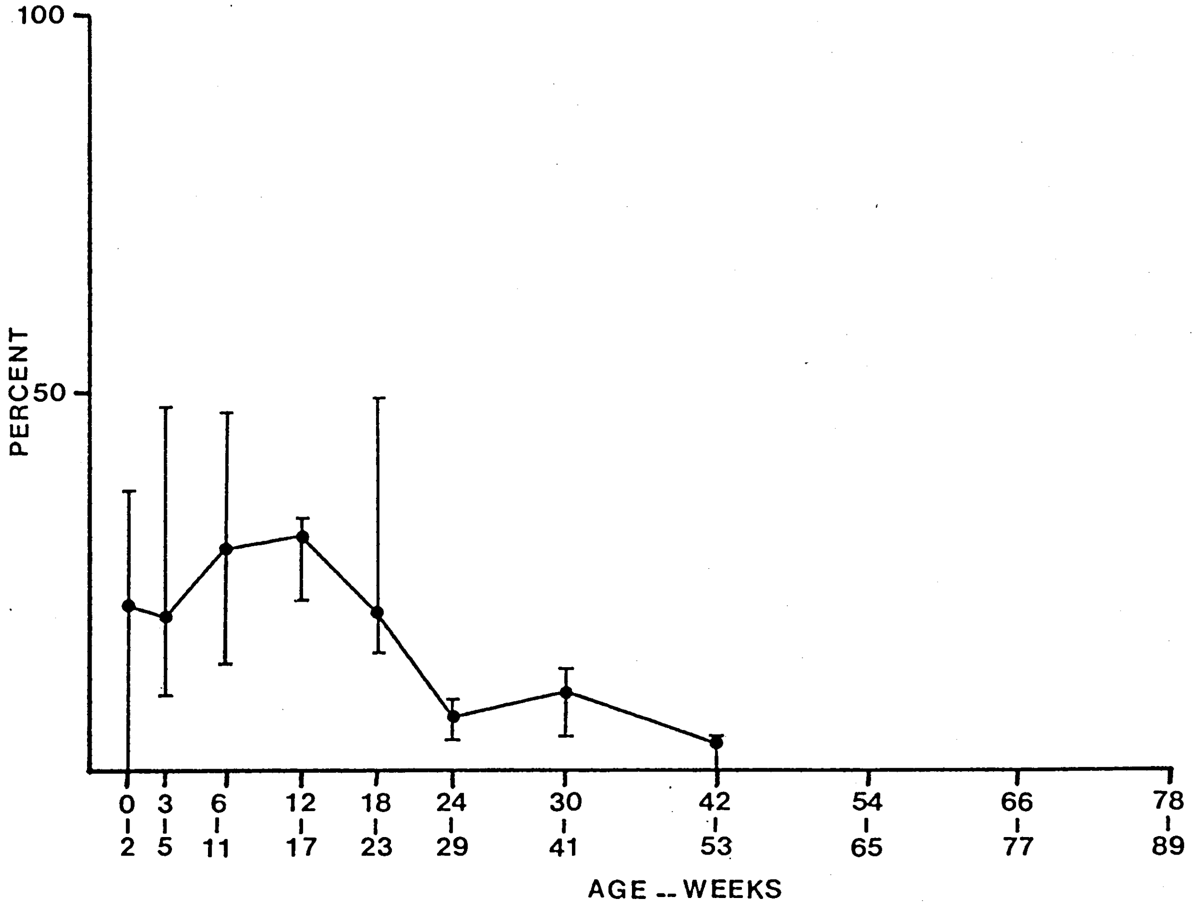


Figure 32. The percentage of on mother intervals with grip fur.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

it more likely that they reflect changes in the mothers' behaviour. The lower frequency in the earlier weeks compared with the later peak may have been the result of mothers giving their very young infants more support with their arms when they walked. This is in accord with casual observation. Alternatively, the higher frequency at 6-11 weeks and 12-17 weeks may mean that mothers moved more frequently with infants of this age. It was when infants were leaving and returning to their mothers with the highest frequency (see Figure 11), perhaps as a result of the infants' own actions or because the mothers were retrieving them more frequently. The low frequencies from 24-29 weeks may have been the result of an increased incidence of dorsal riding (casual observation) and also an increased tendency to leave the mother and move independently in those circumstances when a mother might change her position.

Lean out (Figure 33)

No attempt was made to determine the reasons why infants leant out from their mothers, although one could imagine it being a response to an object or another baboon at a distance.

Frequency decreased with age (Spearman rs = -0.79, N = 8, $p<0.05$); most steeply between 0-2 weeks and 3-5 weeks. This first decrease might reflect the cephalocaudal maturation of voluntary control over the clasping reflex described by Mowbray and Cadell (1962). They found that rhesus infants, up to 24 days, frequently developed the ability to voluntarily release their arms from clasping a surface before they could do the same with their legs. They would hang away from the surface still holding on with their legs. The lower frequency at 3-5 weeks in the present study could have resulted from infants releasing themselves more easily from their mothers. If it is assumed that leaning out facilitated interacting with the world away from the mother, then its occurrence might indicate some degree of ambivalence - attempting to maintain contact with mother while also attempting to approach something away from her. Alternatively, it might reflect a mother's restrictiveness - attempts to leave being thwarted by the mother holding the infant to her. Primate mothers have been shown

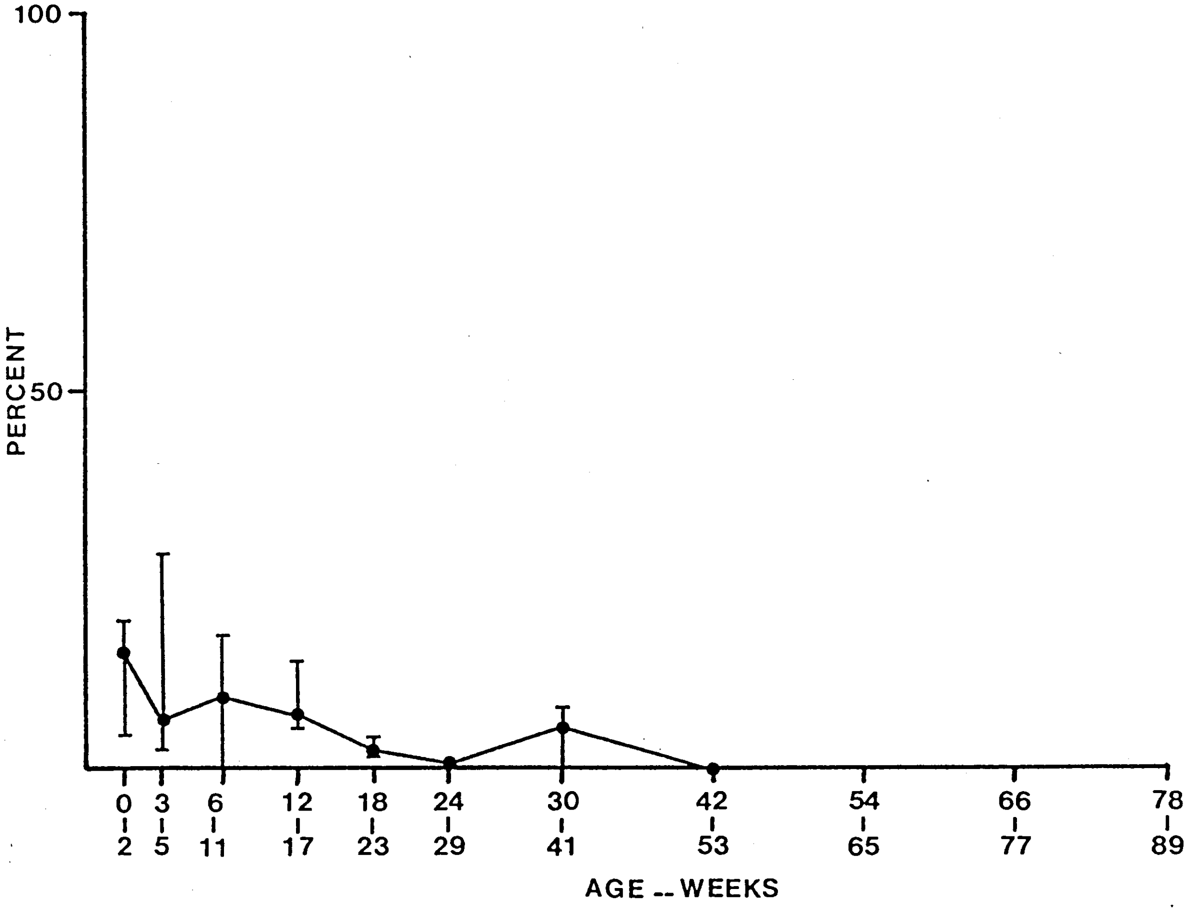


Figure 33. The percentage of on mother intervals with lean out.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

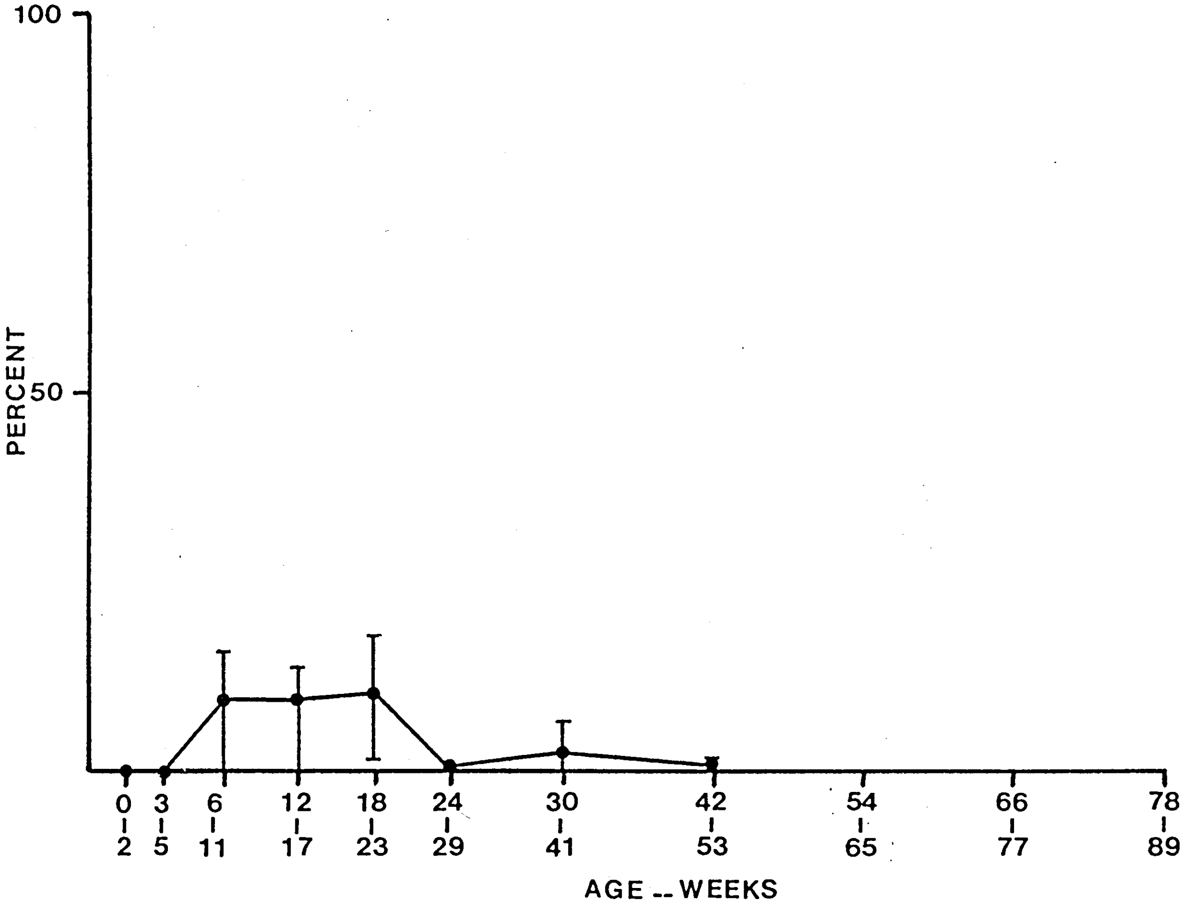


Figure 34. The percentage of on mother intervals with clamber on mother.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

to become less restrictive as their infants become older (Hinde and White, 1974; Hinde and Spencer-Booth, 1967) which might explain the decreasing frequency of lean out.

Clamber on mother (Figure 34) or other (Figure 35)

Infants did not clamber on their mothers until 6-11 weeks. Prior to that they might have lacked the necessary strength and coordination. Between 6-11 weeks and 18-23 weeks it occurred in approximately 10% of intervals on mother and after that in less than 2.5%. The same pattern of development is seen in clambering on baboons other than the mother (Figure 35, frequencies expressed as percentage of total intervals). The rank correlation between the weighted means of these two measures is positive and significant (Spearman rs = +0.95, N = 8, $p<0.01$).

Clambering was most common during the period of coat colour transition. A contributory factor might have been adult tolerance of infants still with some black neonatal fur but intolerance of close attention from brown infants. The infants' changing colour and increasing size and weight might have stimulated rejection from adults. I did not score any measures of rejection and so cannot test the hypothesis that the decline after 18-23 weeks was in any way determined by the adults.

Moving hand or foot in mother's fur (Figure 36)

This was scored whenever the infant made what seemed to be an intentional movement of the hand or foot over or through the fur. In Figure 36 frequencies are expressed as percentages of intervals in which the subject was on or in contact with its mother. There was a decrease in frequency over the whole period of close association with mother, despite a minor peak at 24-29 weeks, although rank correlation with age is not significant (Spearman rs = -0.59, N = 8, $p>0.05$). As they became older infants spent less of the time in which they were in the company of their mothers manipulating her fur.

Summary

As infants spent less time on or in contact with their mothers they spent a greater proportion of that time on her nipple, possibly in increas-

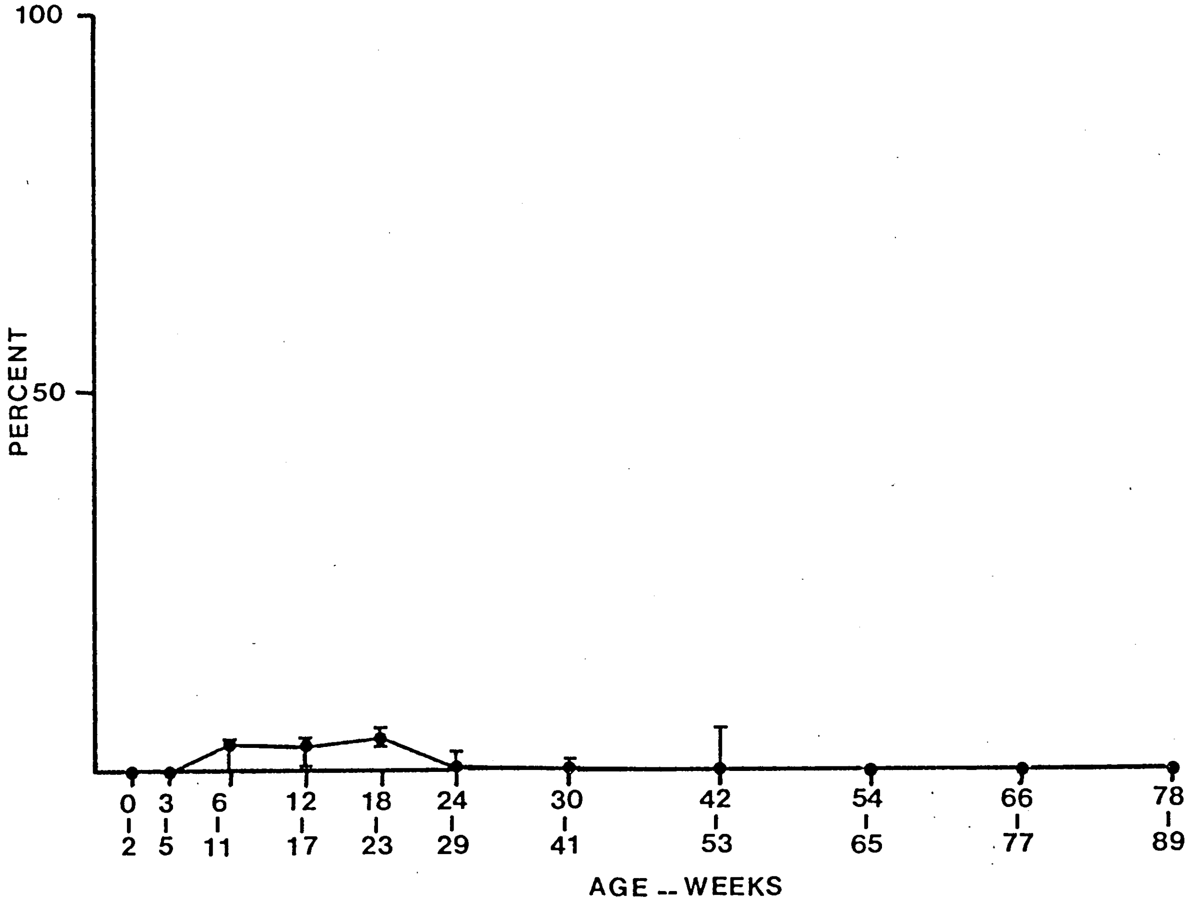


Figure 35. The percentage of total intervals with clamber on other.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

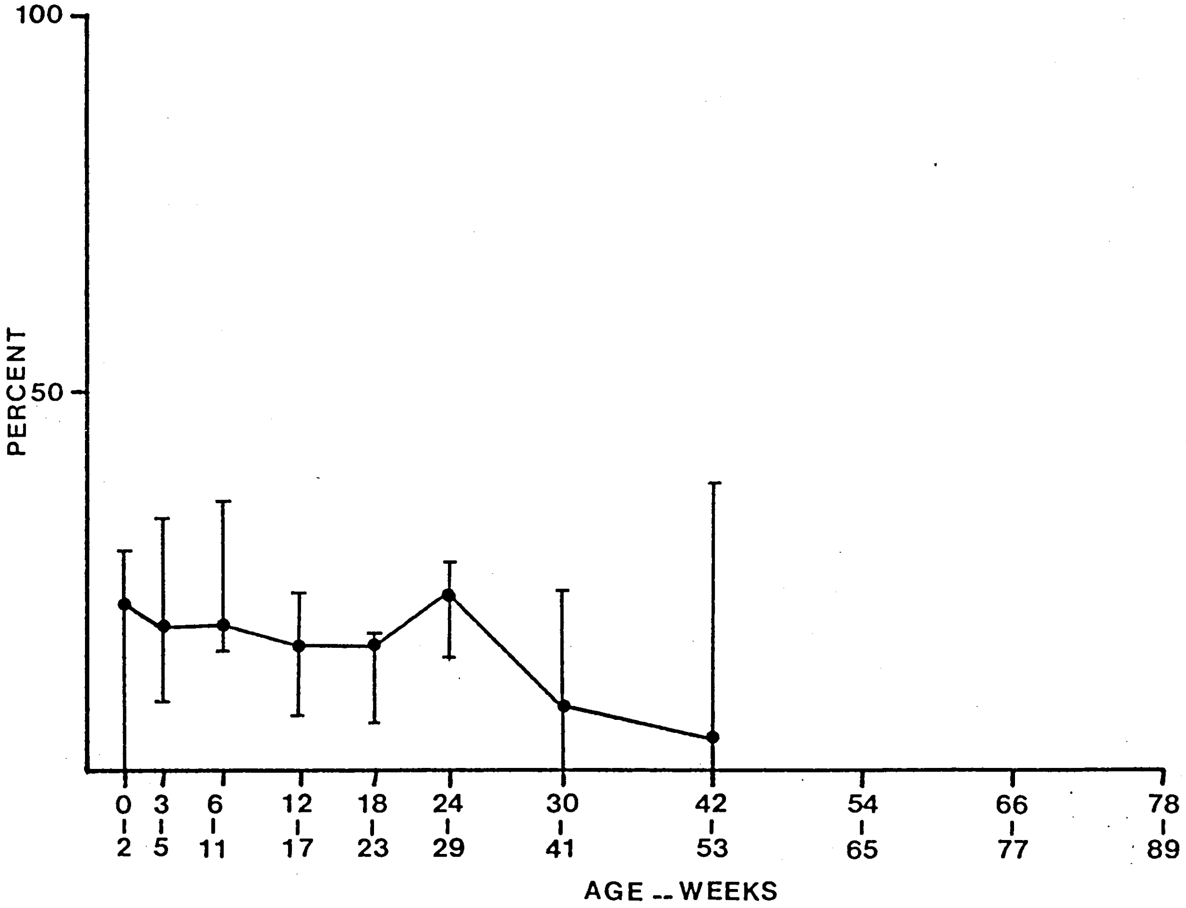


Figure 36. The percentage of on mother intervals in which infants moved a hand or foot in the mother's fur.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

ingly uninterrupted bouts, and a lesser proportion of that time performing other behaviours.

Table 17 summarizes the trends analysed in this chapter, and some of their interpretations.

The most noticeable feature is the coincidence of several changes between age blocks 18-23 and 24-29 weeks. Neonatal black coloration was finally lost. Time spent in contact with mother decreased along with the rate of contact makes and breaks. There is indirect evidence that infants moved more independently. Clambering on adult baboons became infrequent. It will be shown in later chapters that this was also a period of significant change in other behaviours.

Table 17. Major age changes in colour and behaviour associated with the mother

age blocks	0-2	3-5	6-11	12-17	18-23	24-29	30-41	42-53	54-65	66-77	78-89
colour	black		transition			brown					
on mother	decreasing					less than half time spend on mother			never recorded on mother		
out of contact with mother	increasing					more than half time spent out of contact			always recorded out of contact		
in contact with mother	increasing				max. time	decreasing					
making and breaking contact	increasing				max. rate	decreasing					
on-nipple	decreasing absolute time constant proportion of time with mother				sharp increase		constant proportion of time with mother				
rooting	bouts on-nipple becoming less interrupted										
grip fur	mother moving more frequently with infant					more dorsal riding or infant moving independently					
lean out	decreasing - possibly infant becoming less restricted										
clamber on mother or other				maximum frequency		very low frequency					
manipulate mother's fur	decreasing										

Chapter 5. Results: the development of object manipulation

The manipulation of objects is a conspicuous feature of baboon behaviour. Its development is described here for the following reasons.

It gives an unsophisticated index of changes in sensori-motor coordination.

It provides a measure of an infant's developing involvement in the world away from the mother, particularly its increasing self-reliance for gathering food.

Objects may sometimes have been manipulated in an apparently non-functional or "playful" way[1]. This proposition is analysed in Chapter 10 but the present chapter provides a background for that analysis.

It provides another point of comparison between development in safari park baboons and in wild baboons as reported by Chalmers (1980b).

1. Age changes in the frequency of various motor patterns

The motor patterns dealt with are:

reach
touch
pick-up
hold and mouth
scratch ground

Reach was scored only when a subject was on its mother. The other motor patterns were scored in any position. Figures 37 and 38 show the development of reaching and touching by infants when on-mother. One-zero frequencies are expressed as percentages of intervals in which subjects were on-mother. In weeks 0-2 and 3-5 there was slightly more reaching than touching but from 6-11 weeks touching was the greater. This would indicate that with improving hand/eye coordination, after 6-11 weeks infants were able to touch most of the objects they reached for.

---

[1] Note that the operational definition of play did not include any form of object manipulation.

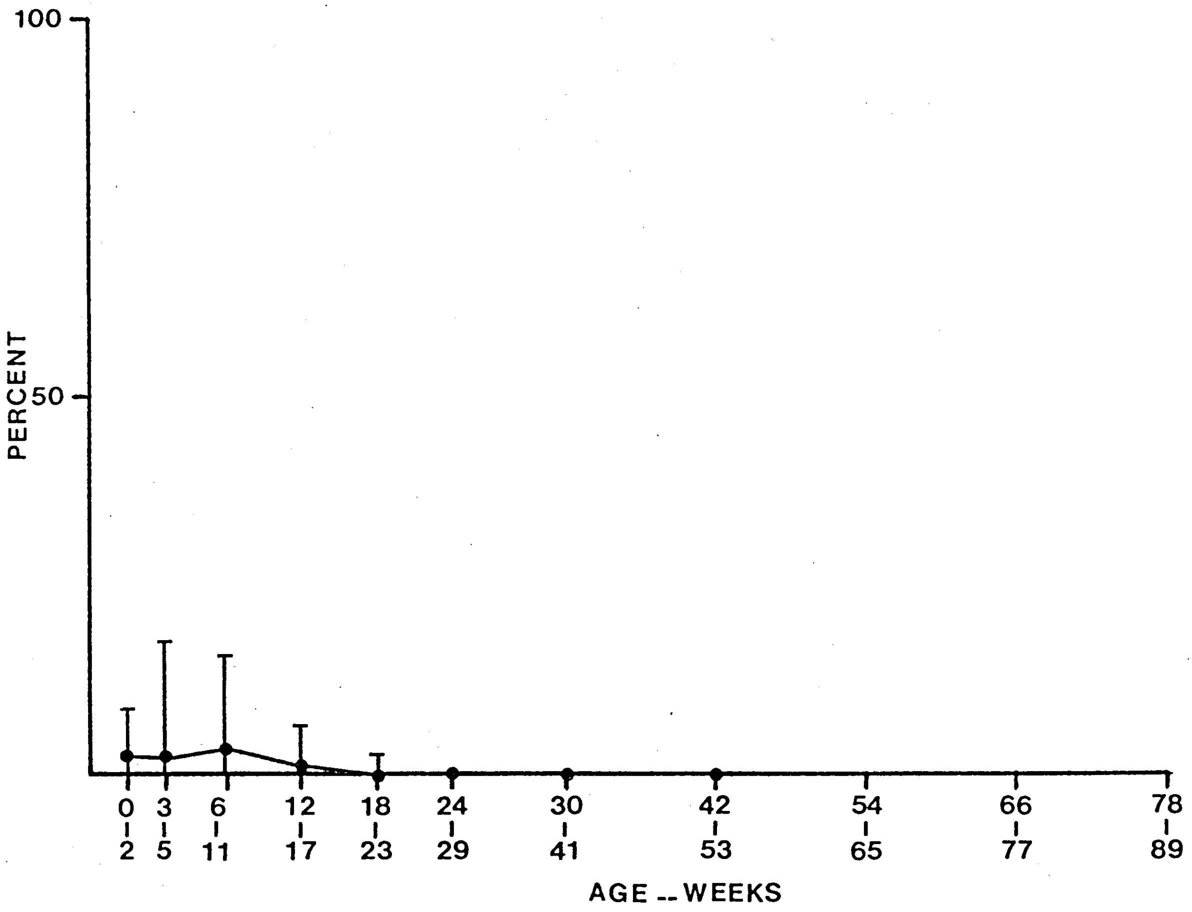


Figure 37. The percentage of on mother intervals with reach.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects of each age;
see Appendix III, Table A, for the denominators of weighted means.

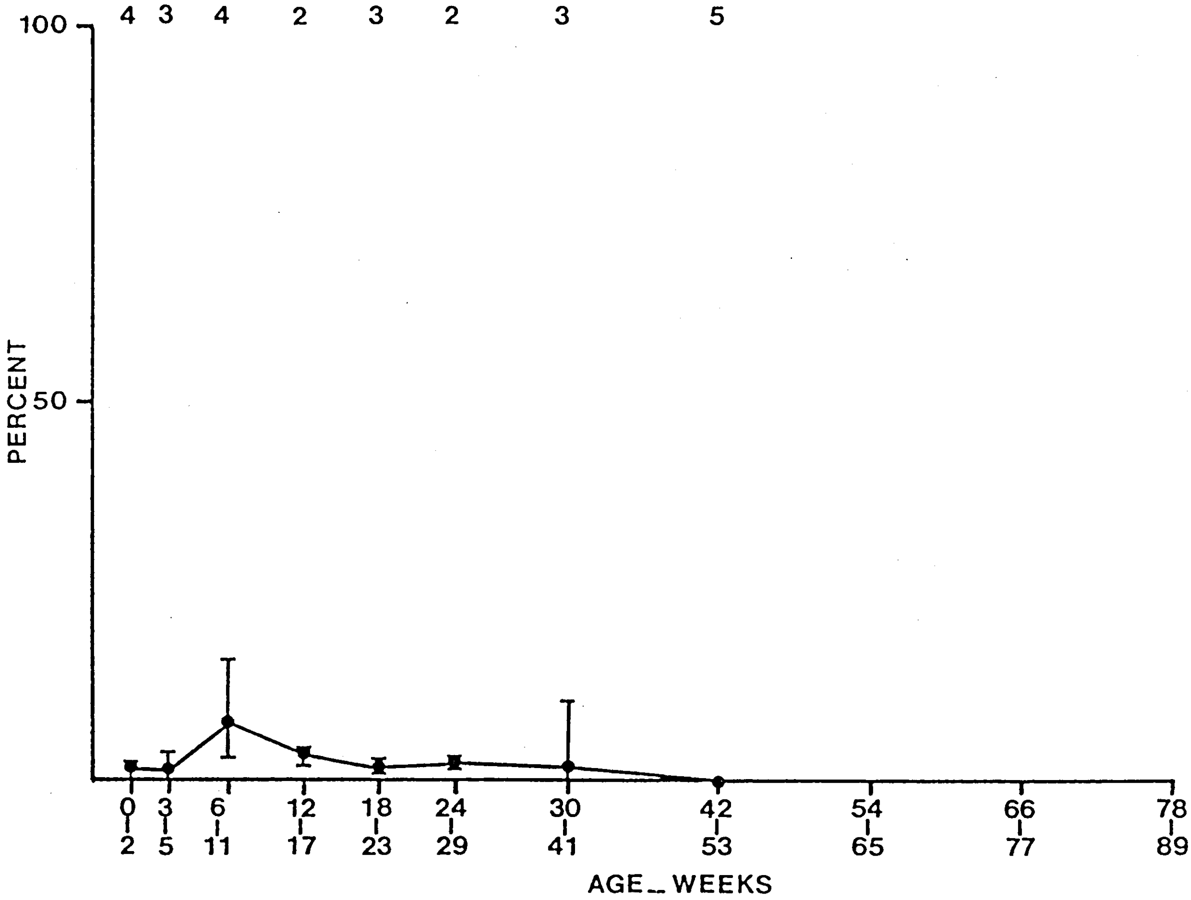


Figure 38. The percentage of on mother intervals with touch.

For key to symbols see Appendix I.

Sample sizes:

the number of subjects at each age is shown above the figure; see Appendix III, Table A, for the denominators of weighted means.

Figures 39 to 41 show changes in touch, pick-up and hold and mouth (scored in any position relative to the mother) expressed as percentages of intervals off-nipple. Pick-up and hold and mouth both increased with age (Spearman rs = +0.99, N = 10, $p < 0.01$) but touch showed no consistent change (Spearman rs = -0.22, N = 10 $p > 0.05$).

At ages 0-2 and 3-5 weeks, touch was scored more than pick-up or hold and mouth. It reached a peak at 6-11 weeks and then continued at a lower but fairly constant level until 78-89 weeks. Touching was still shown by older baboons (juvenile to adult) but at a lower level still. This development is similar in shape and one-zero frequency values to that described for wild olive baboons by Chalmers (1980b), except that in that study touching peaked earlier at 2 weeks.

Pick-up and hold and mouth increased most rapidly between 0-2 weeks and 6-11 weeks, when they became more frequent than touch. They continued to increase but less rapidly, after 6-11 weeks. The results from 54-65 weeks to adulthood probably represent a plateau at approximately 50%.

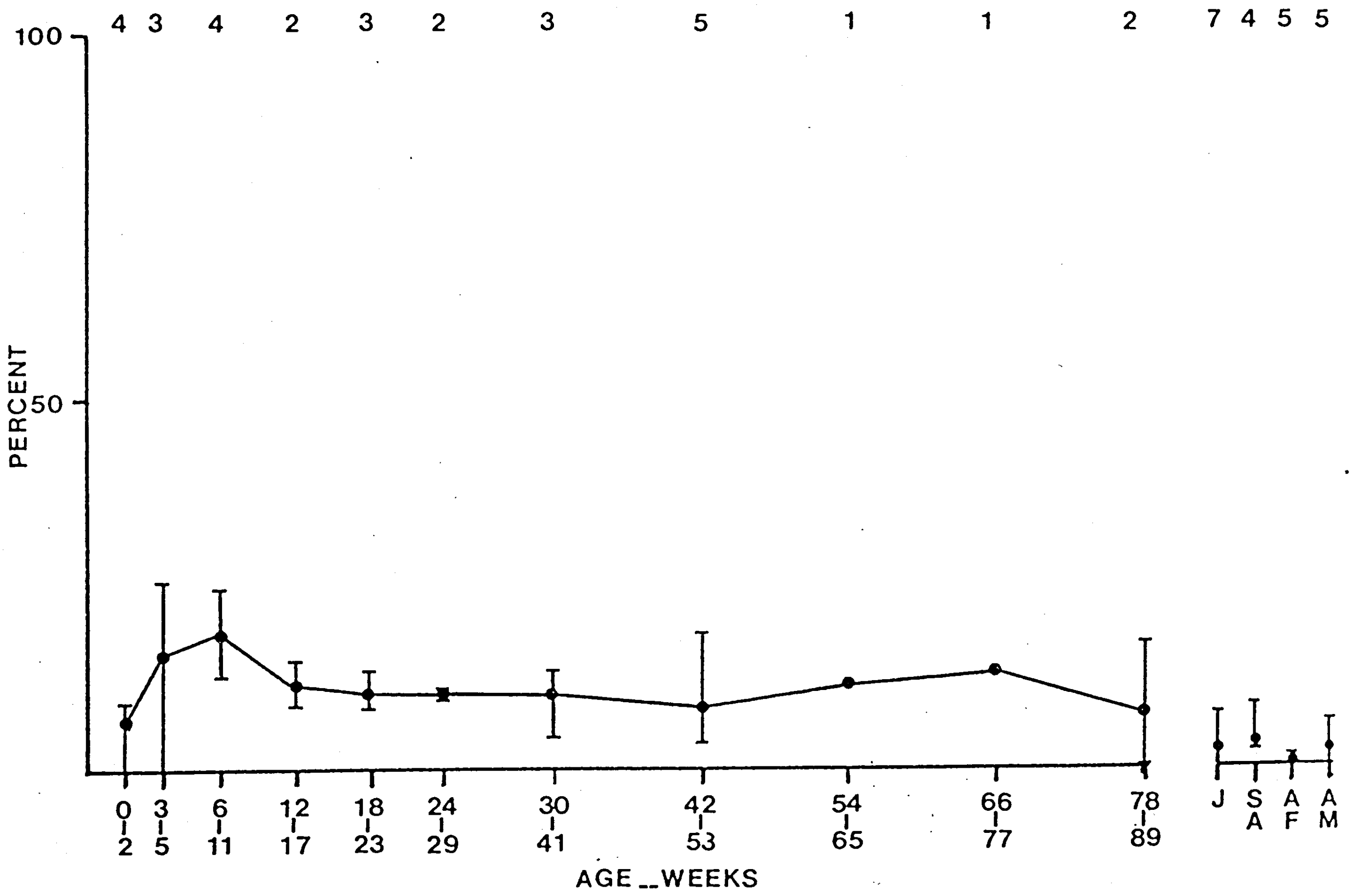


Figure 39. The percentage of off-nipple intervals with touch.

For key to symbols see Appendix I.

Sample sizes:

the number of subjects at each age is shown above the figure;
see Appendix III, Table A, for the denominators of weighted means.

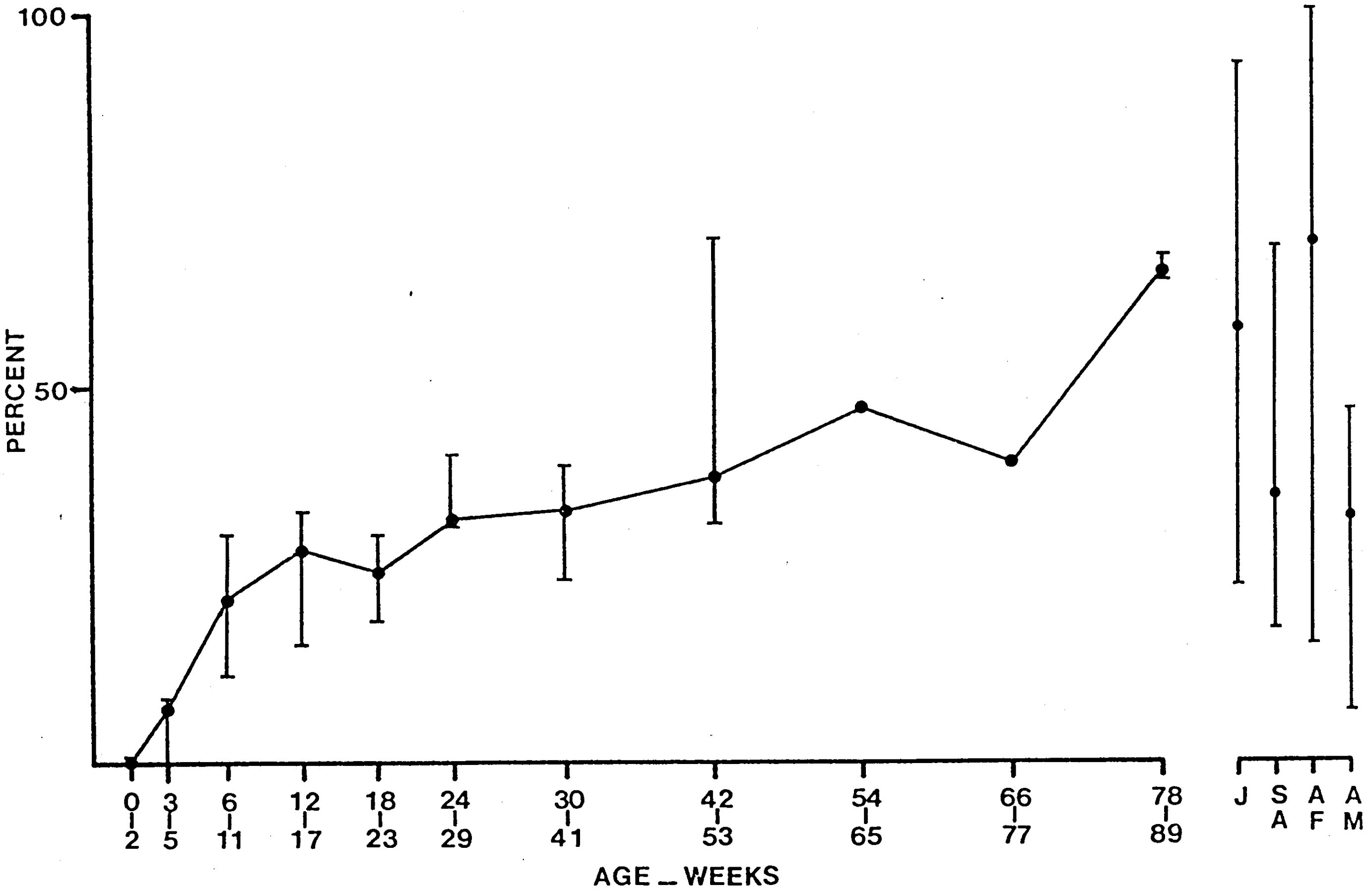


Figure 40. The percentage of off-nipple intervals with pick-up.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

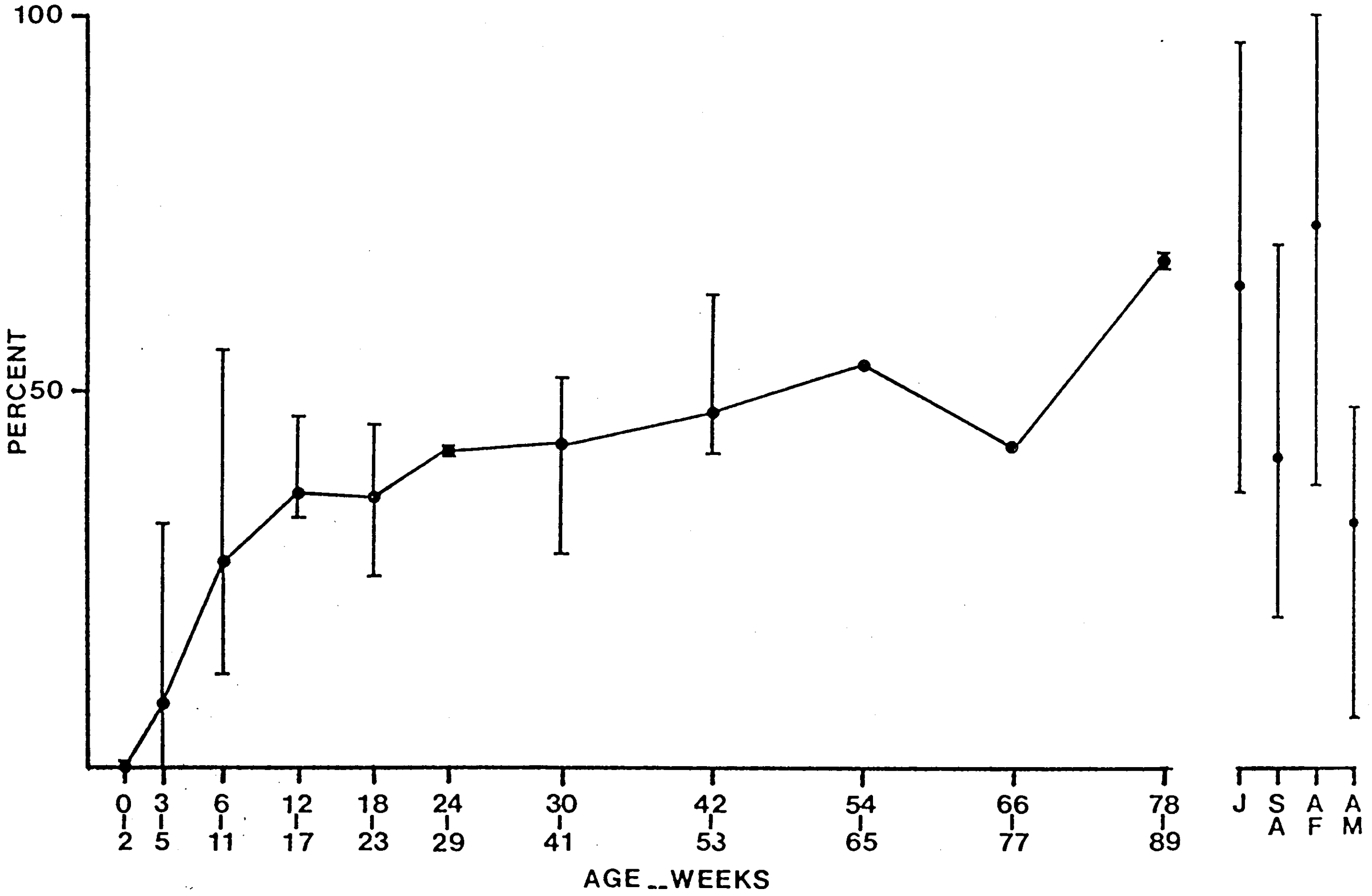


Figure 41. The percentage of off-nipple intervals with hold and mouth.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

Mason, Harlow and Rueping (1959) demonstrated that infant rhesus increasingly manipulated objects from the first to the eleventh or twelfth week, after which the level decreased slightly. They concluded that increasing responsiveness was due to maturation. A phase of steeply increasing frequency of mouthing edible objects was shown in wild baboons by Chalmers (1980b) between the first and eighth weeks. The same period of increasing object manipulation in safari park baboons might have resulted from a growing interest in solid food combined with improving sensori-motor coordination.

Pick-up and hold and mouth were more similar to each other in development than to touch (see Table 18 for Spearman rank correlation coefficients). This was to be expected since casual observation had suggested that pick-up was very often followed by hold and mouth, whereas touching an object may not have preceded its being picked up and held and mouthed. But the results suggest that touch might have been an ontogenetic precursor of pick-up. Until 6-11 weeks coordination might have been only sufficiently developed to allow objects to be located (touched) more frequently than picked up. Touch was in the repertoire even after 6-11 weeks and so it is unlikely to have always represented unsuccessful attempted to pick objects up. It probably remained as an adaptive part of object manipulation.

Hold and mouth was scored consistently more frequently than pick-up despite the fact that most instances of holding and mouthing an object had to be preceded by picking the object up. Pick-up was an instantaneous event whereas hold and mouth could have been a continuing state recorded in two or more consecutive intervals without interruption by pick-up. This fact is used later in this analysis to generate a measure of mouthing bout length (long bout mouthing).

Scratch ground (Figure 42)

This appeared at 0-2 weeks and gradually increased through the infant age range (Spearman rs = +0.89, N = 10, $p < 0.01$). Although its rate of increase was less than those of pick-up and hold and mouth, its development correlates highly with theirs but not significantly with that of touch (see Table 18 for Spearman rank correlation coefficients).

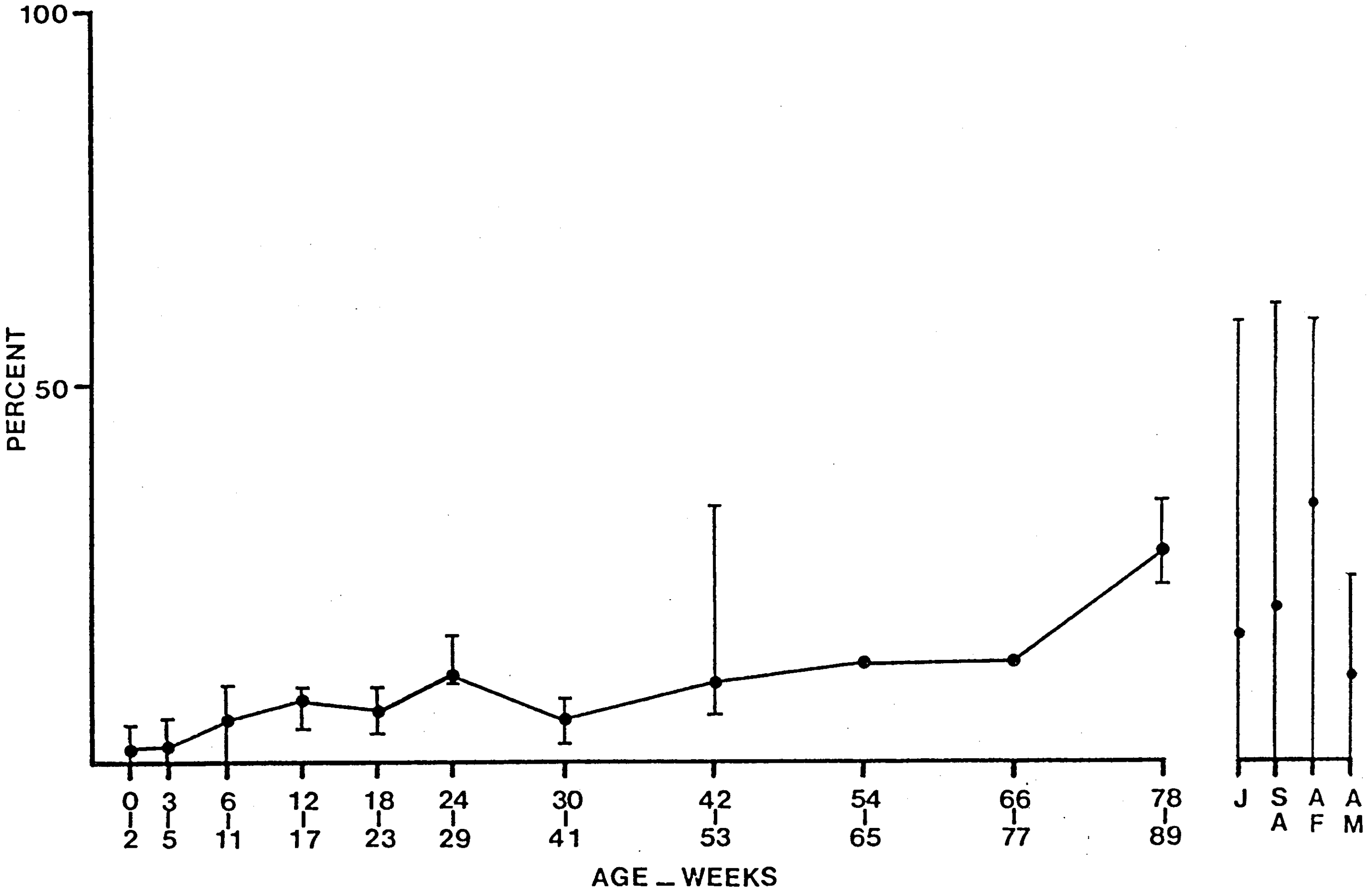


Figure 42. The percentage of off-nipple intervals with scratch ground.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

Table 18. Spearman rank correlation between age changes in the weighted mean one-zero frequencies of object manipulation patterns. N = 10 unless stated otherwise.

	pick-up	hold and mouth	scratch ground	short bout mouthing	long bout mouthing	on-nipple N = 9
Touch	-0.19	-0.19	-0.13	-0.28	-0.03	+0.22
pick-up		+1.00 ***	+0.90 ***	0.99 ***	+0.34	-0.92 ***
hold and mouth			+0.90 ***	+0.99 ***	+0.34	-0.92 ***
scratch ground				+0.99 ***	+0.36	-0.75 *
short bout mouthing					+0.31	-0.87 **
long bout mouthing						-0.62

* two tailed $p < 0.05$

** two tailed $p < 0.01$

*** two tailed $p < 0.001$

From casual observation scratch ground was a commonly used motor pattern when baboons were feeding on small articles in or on the ground, for instance on roots, shoots or "animal feed". Its increasing frequency might have been due to an increasing tendency to feed on solid food, which might also account for the positive correlations with pick-up and hold and mouth. If there was an increasing use of solid food there is likely to have been a corresponding decrease in the time spent feeding on mother's milk. The nearest available measure to "time feeding from mother" is "intervals beginning on-nipple", which, it should be noted, is not the same thing because an infant could have been on-nipple without sucking milk. The rank correlation coefficients between on-nipple and pick-up, hold and mouth and scratch ground are shown in Table 18 to be negative and significant. That with touch is not significant. These correlations support a fairly strong feeding association for scratch ground, pick-up and hold and mouth.

2. An analysis of preferred position relative to mother for object manipulation

Objects were manipulated in all positions relative to mother (on, in contact, out of contact). The questions arise whether infants were more likely to manipulate objects in one position as opposed to any other and whether such a likelihood changed with age.

During the following analysis the words "preferred" and "favoured" are used - for instance, "out of contact was a preferred position for picking up objects". Such an expression is only a short way of saying "pick-up appeared in a higher proportion of intervals in which infants were out of contact with mother than of intervals in which they were in contact with or on mother". Many factors could have contributed to a higher probability of manipulating objects in one position compared with another such as the restrictiveness of the mother, relative accessibility of objects or indeed the true preference of the infants. I recognize that no conclusion can be drawn from the present data about the relative contributions of these factors. I merely use "preferred" and "favoured" to simplify the structures of the sentences.

Figures 43 to 45 show how the proportion of intervals in each position occupied by touch, pick-up and hold and mouth changed with age. The proportion of on mother intervals with object manipulation was relatively small, but of the manipulation types touch was the most frequent.

0-2 to 3-5 weeks

In contact was the position in which the greatest proportion of intervals contained object manipulation and so might be considered the preferred position.

6-11 weeks onwards

A slightly higher proportion of intervals contained touching when out of contact with mother but this tendency was not strong. All that can safely be said is that between approximately 5% and 10% of intervals in each position contained touch.

Between 6-11 and 18-23 weeks

The probabilities of pick-up and hold and mouth were approximately the same when in contact as when out of contact. There may have been a preference for out of contact but it was not great.

During this period only hold and mouth increased (both in contact and out of contact). Pick-up remained at approximately the same frequency.

From 24-29 weeks onwards

A strong preference was shown for picking-up and holding and mouthing when out of contact compared with in contact with mother, and the proportion of intervals with these behaviours increased with age.

Summary of preference changes

On mother was never a favoured position from which to pick-up and hold and mouth objects although things were touched from this position more frequently.

During development there was a shift of preference away from the mother; from manipulating objects when in contact, through a period in which in contact and out of contact were similarly favoured to a time when

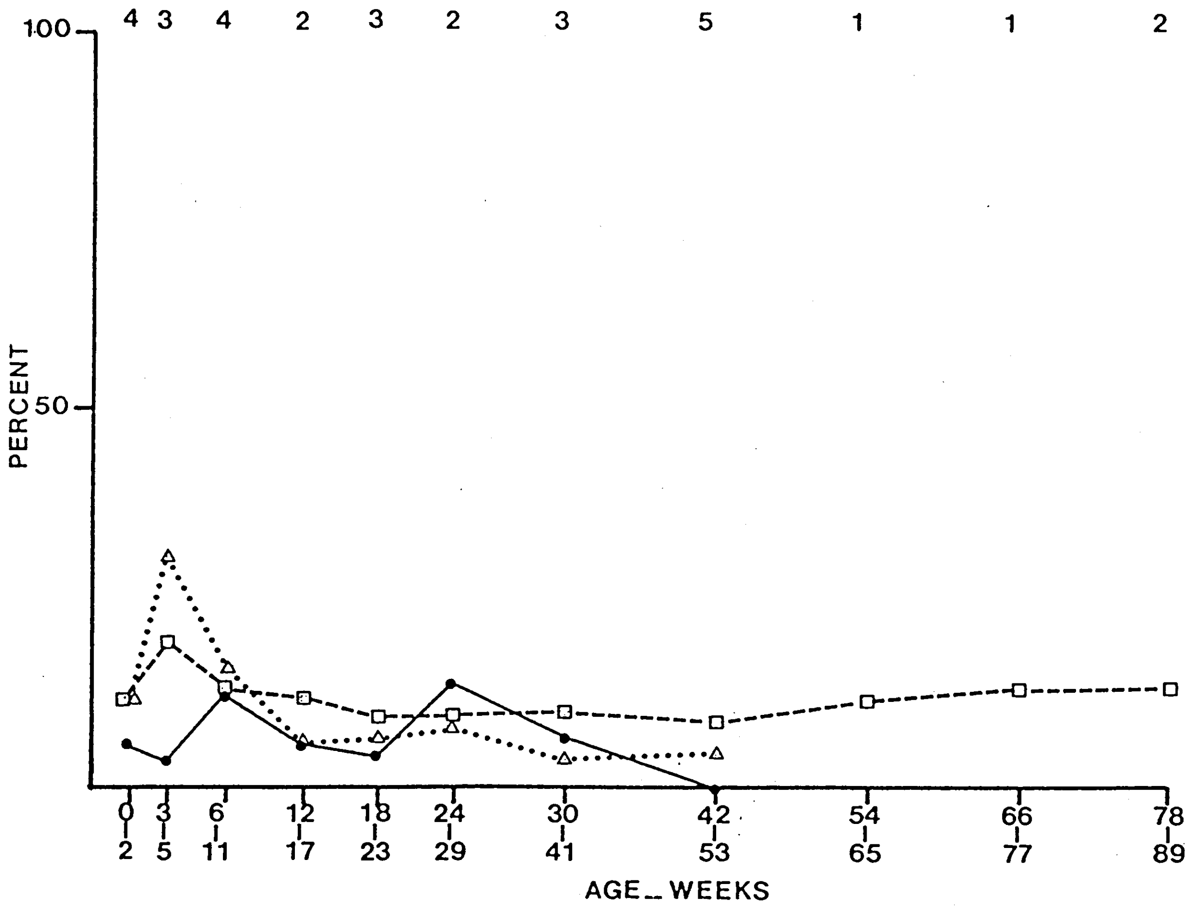


Figure 43. Age changes in preferred position for touching objects. Intervals with touch in each position relative to mother are expressed as percentage of intervals in which infants were in those positions.

●——● on
△·····△ contact
□----□ out of contact

Sample sizes:

the number of subjects at each age is shown above the figure; see Appendix III, Table A, for the denominators of weighted means.

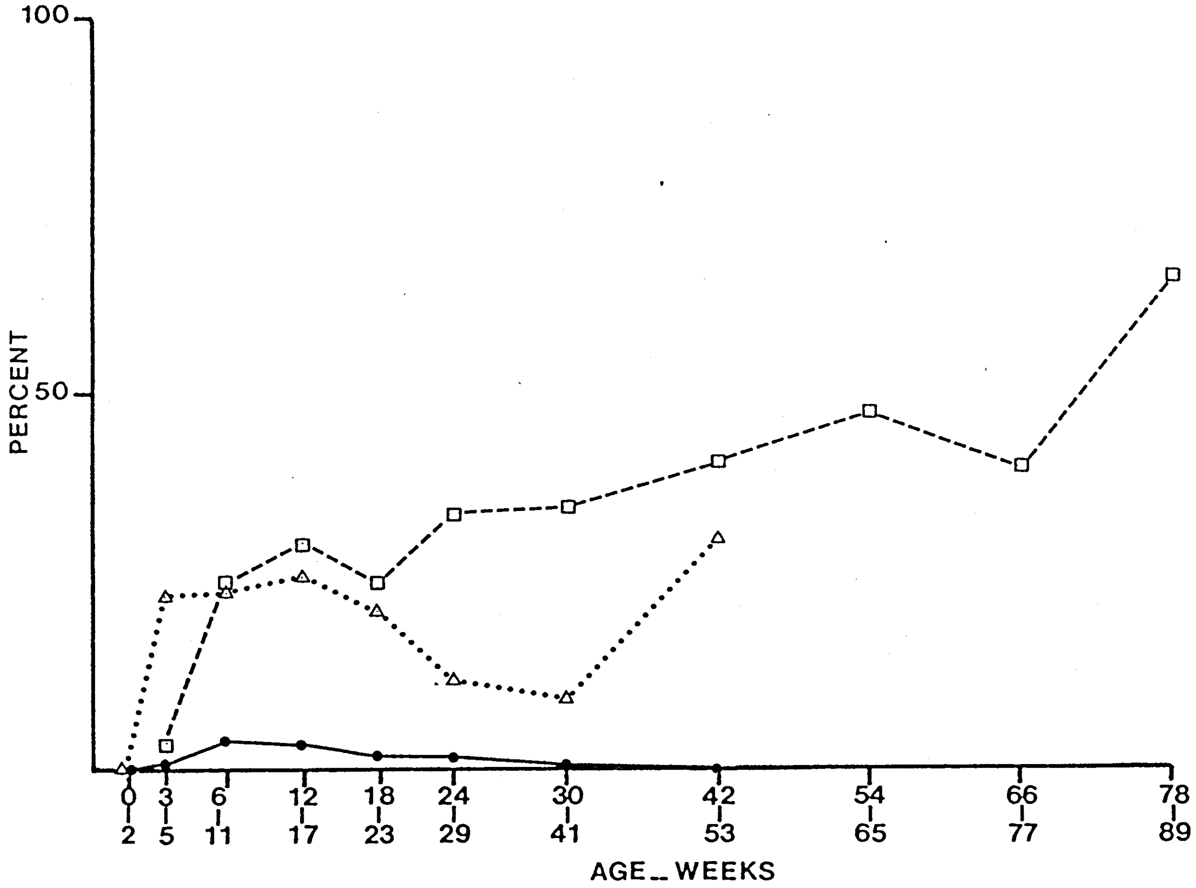


Figure 44. Age changes in preferred position for picking up objects. Intervals with pick-up in each position relative to mother are expressed as percentage of intervals in which infants were in those positions.

Symbols as for Figure 43.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

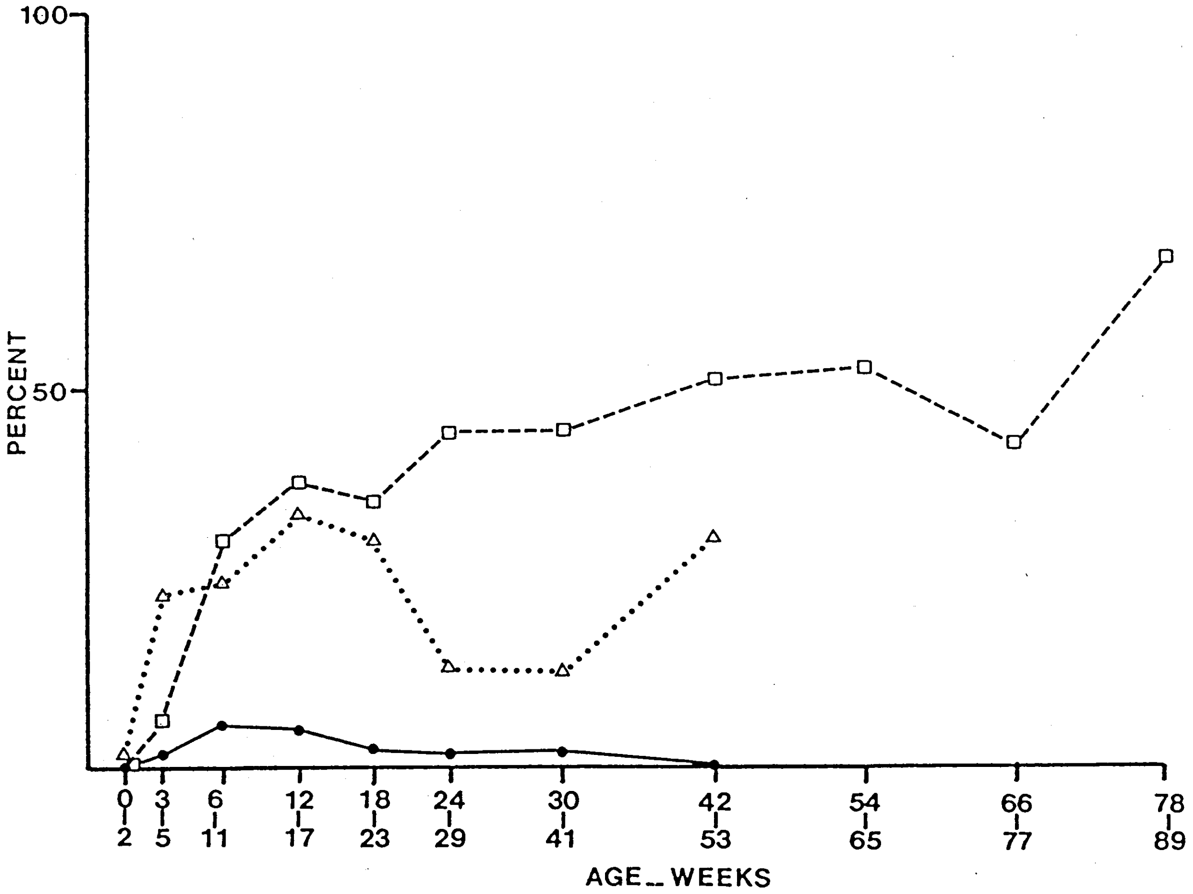


Figure 45. Age changes in preferred position for holding and mouthing objects. Intervals with hold and mouth in each position relative to mother are expressed as percentage of intervals in which infants were in those positions.

Symbols as for Figure 43.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

out of contact was clearly, and increasingly, preferred. In short, as infants became older they increasingly left their mothers to manipulate objects.

3. Functions of object manipulation

Object manipulation could have fulfilled a variety of functions depending on physical or social context, nature of the object and so on. There is little point listing all the possibilities but three obvious possible functions are:

i) feeding
ii) gaining information about the object
iii) improving manipulative ability through practice

The motor pattern data scored in this study made no distinction between food and non-food nor between instances which might or might not have provided the subject with information or served as practice. Such distinctions would necessarily have been subjective and, since they are not mutually exclusive, possibly quite artificial. How could one categorize the case of an obviously edible object being mouthed but not eaten, or of a number of small objects, some edible and some inedible, being picked up and put into the mouth? Despite this, it has been possible to make a distinction, during analysis rather than during data collection, between certain intervals with object manipulation on the grounds of the duration of mouthing. It will be shown that the two derived manipulation categories differ in their development.

Pick-up and hold and mouth together (short bout mouthing) and hold and mouth alone (long bout mouthing)

It was shown earlier that the frequency of hold and mouth was generally higher than that of pick-up, and the magnitude of this difference varied according to age. This was because holding and mouthing the same object may have been recorded in a number of consecutive intervals without pick-up also being recorded. On the other hand, if objects were picked up and mouthed in quick succession then successive intervals may have been scored with both pick-up and hold and mouth. Measures of bout length have been generated which are based on two rather simplistic assumptions:

1. the frequency of intervals containing both pick-up and hold and mouth is a measure of the amount of time spent holding and mouthing objects for durations of less than 30 seconds (short bout mouthing);

2. the frequency of intervals containing hold and mouth but not pick-up is a measure of the amount of time spent holding and mouthing for durations of more than 30 seconds (long bout mouthing).

There are several sources of error in these measures:

a. most sequences of intervals containing only hold and mouth had to be preceded by an interval with both pick-up and hold and mouth because objects were usually picked up before being held and mouthed. But such intervals were counted with, and so inflated, the short bout mouthing scores. But they did not prevent the identification of instances of long bout mouthing;

b. if an instance of short bout mouthing happened at the end of a 30 second interval pick-up might have been recorded in that interval and hold and mouth recorded on its own in the next. This would have been incorrectly identified as long bout mouthing, but such an eventuality would have had to occur almost simultaneously with the 30 second mark and therefore is likely to have been rare;

c. an interval at the end of a long bout of mouthing might have been scored with hold and mouth, for that bout, and then pick-up for the start of the next bout. This would have resulted in an interval with both pick-up and hold and mouth scored together, artificially inflating the short bout mouthing scores and reducing the score of long bout mouthing.

The intervals with both pick-up and hold and mouth are to some extent ambiguous. No firm conclusions can be drawn from the use of the measure, although it might serve to raise questions.

On the other hand, intervals with only hold and mouth are less easy to dismiss as being ambiguous. It is difficult to account for most of them as anything other than mouthing which had been extended into the next 30 second interval.

Figures 46 and 47 show the development of short bout and long bout mouthing (frequencies expressed as percentages of intervals off-nipple).

Short bout mouthing was identified first at 3-5 weeks and increased to a minor peak at 12-17 weeks. After a trough at 18-23 weeks the frequency increased at a lower rate than before until the end of the infant age range. The results for older baboons suggest no further increase. The increase with age between 0-2 and 78-89 weeks is significant (Spearman rs = +0.96, N = 10, $p<0.01$).

The proportion of intervals with long bout mouthing increased between 0-3 weeks and 18-23 weeks after which a plateau was maintained until 42-53 weeks. Gradually the proportion then decreased, and this downward trend continued into adulthood.

By inspection it is clear that the development trend of short bout mouthing was similar to that of pick-up (Figure 40), hold and mouth (Figure 41) and scratch ground (Figure 42) and opposite the trend of time on-nipple (Figure 17). The development of long bout mouthing was different from all of them. These conclusions are supported by the Spearman rank correlation coefficients shown in Table 18. The high correlations between short bout mouthing and both pick-up and hold and mouth is because most of the pick-up and hold and mouth scores were combined as short bout mouthing. That is, on most occasions when an object was picked up it was immediately mouthed. This is a casual observation supported by the closeness of the one-zero frequency values for pick-up and short bout mouthing. The one-zero frequency of short bout mouthing was always greater than long bout mouthing, which means that most intervals with hold and mouth were included as short bout mouthing.

The correlations of interest here are between:

1. short bout mouthing and scratch ground - positive and significant;
2. short bout mouthing and on-nipple - negative and significant;
3. long bout mouthing and scratch ground - not significant;
4. long bout mouthing and on-nipple - negative and significant.

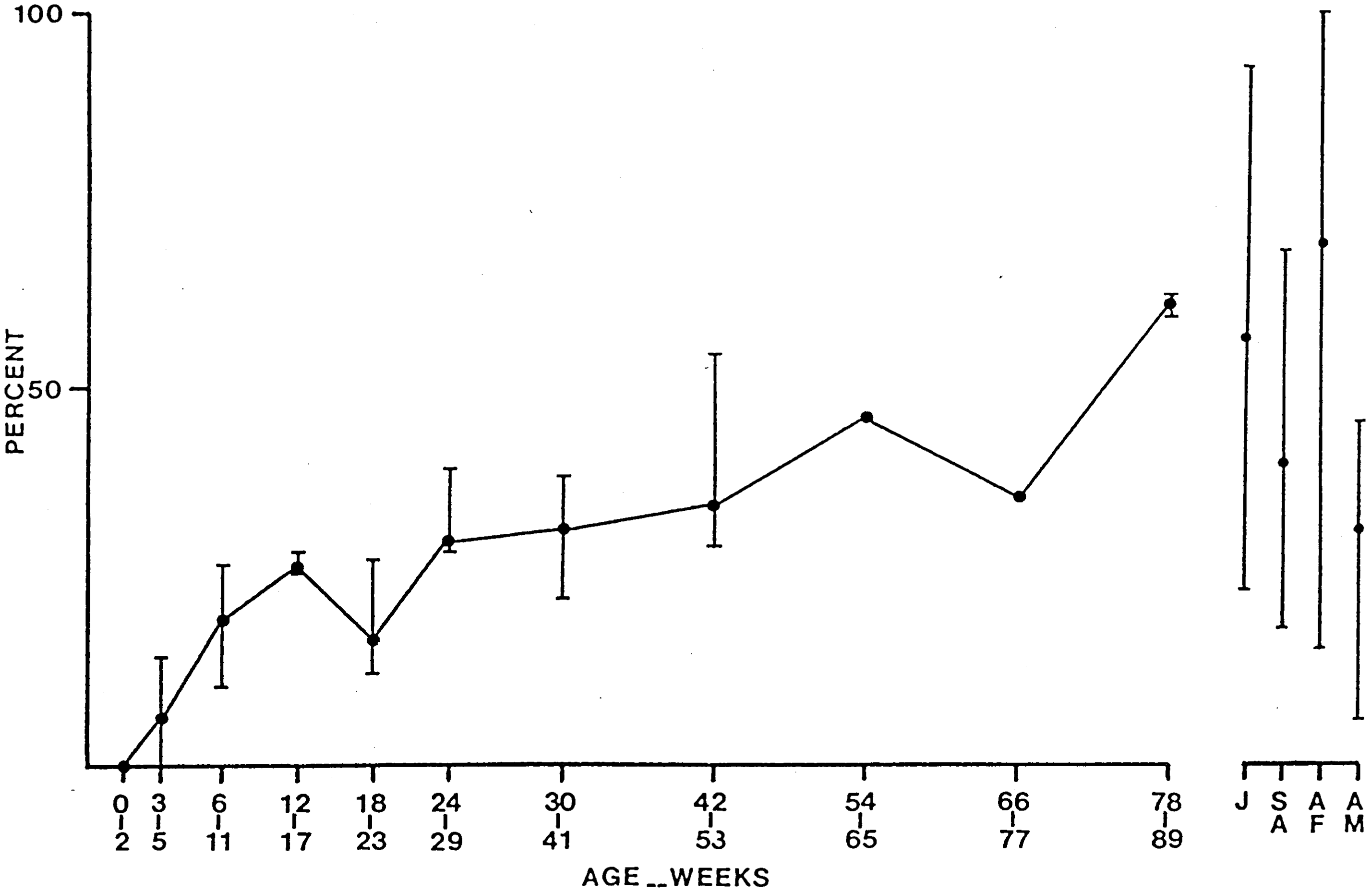


Figure 46. The percentage of off-nipple intervals with short bout mouthing.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

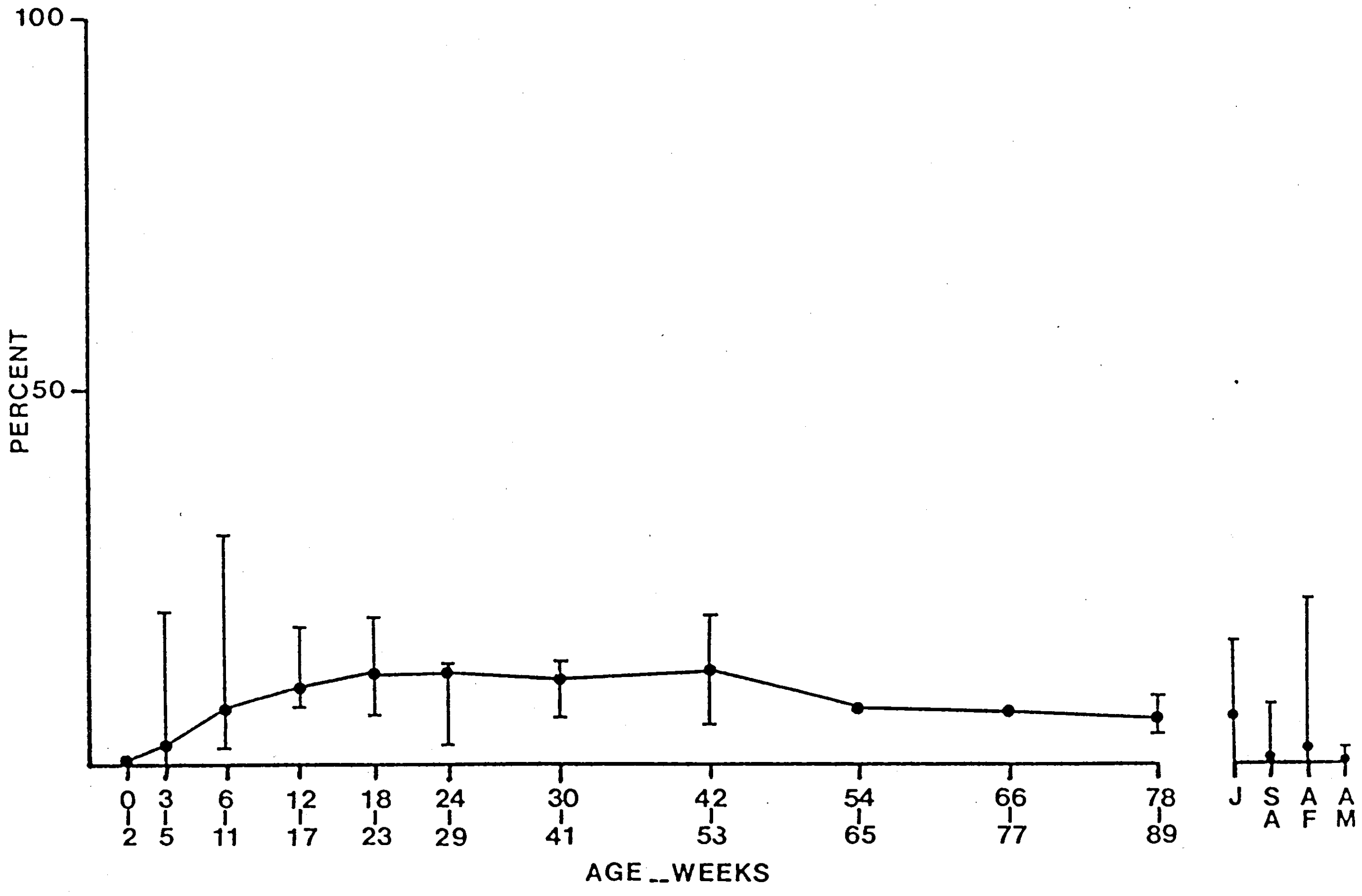


Figure 47. The percentage of off-nipple intervals with long bout mouthing.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

It was suggested earlier that scratch ground usually occurred when subjects were digging for and sorting through solid food. It might therefore be used as a marker of intervals in which subjects were feeding. The positive correlation between its development and that of short bout mouthing together with the negative correlation with on-nipple is evidence to support the notion that short bout mouthing is a measure of feeding frequency. This has to be a tentative suggestion in view of the potential errors described earlier. What is more interesting is the lack of significant correlation between long bout mouthing and scratch ground and the negative correlation with on-nipple. These suggest that long bout mouthing may not necessarily be a measure of feeding frequency. That is, it could be a measure of a type of object manipulation whose function may not only be feeding but also something else.

The limitations of the data prevent further speculation to be made with any confidence. However, the functions of object manipulation which were suggested earlier included investigation and practice. It is reasonable to expect that a strategy of manipulation which provides the greatest opportunity for these would give infants longer rather than shorter contact time with an object. It is possible that long bout mouthing is a measure of such a strategy.

Summary of object manipulation

The major age changes in object manipulation are summarized in Table 19.

Evidence was put forward to suggest that reach, touch and pick-up formed an ontogenetic sequence. Touch remained in the behaviour repertoire even after pick-up was being performed frequently. It is unlikely to have represented failed attempts to pick-up. More likely, it was maintained as a complete and adaptive motor pattern.

Scratching the ground (gathering and sorting small objects) and picking up and mouthing objects increased with age, while the proportion of time on-nipple decreased. This may have indicated an increasing tendency

Table 19. Major age changes in object manipulation

age blocks	0-2	3-5	6-11	12-17	18-23	24-29	30-41	42-53	54-65	66-77	78-89
reach	decreasing										
touch	increasing		maximum frequency	decreasing	constant						
pick-up	increasing most steeply			increasing less steeply							
hold and mouth	increasing most steeply			increasing less steeply							
scratch ground	increasing										
on-nipple	decreasing				plateau		decreasing				
preferred position for object manipulation	in contact with mother		in contact and out of contact with mother			out of contact with mother					
short bout mouthing	increasing most steeply				trough	increasing less steeply					
long bout mouthing	increasing					plateau			decreasing		

to eat solid food. There were no discontinuities which could indicate sudden weaning.

An analysis of positions from which objects were manipulated suggested that infants infrequently manipulated objects when on mother but did so more frequently when not supported by her. No conclusions can be made as to the reason for this tendency, although it is recognised that objects simply may not have been accessible from on the mother. There was evidence for a shift of preferred positions for object manipulation from in contact to out of contact with mother.

Two measures were derived from the data sheets which reflected the tendency to mouth objects for less than or more than 30 seconds. Age changes in these measures suggested that short bout mouthing might have been associated with the tendency to feed on solid food whereas long bout mouthing was less closely associated with this tendency. It was considered reasonable to speculate that the extended contact with an object brought about by long bouts of mouthing provided opportunities for investigation or practice.

Chapter 6. Results: the development of mobile activity

All behaviours in which the subject changed position by at least one body length were classed as mobile activity (see page 55f). The class therefore included all forms of play, non-play and clambering over adults.

The first aim of the chapter is to describe development in terms of age changes in the level of activity, the frequencies of different locomotor patterns and the amount of play. Some developmental changes are put into context by viewing them against other changes in infant life. An attempt is made to identify developmental groups by comparing the development trends of different locomotor patterns.

1. Age changes in mobile activity

Instantaneous samples measured the proportion of time occupied by mobile activity. Figure 48 shows age changes in this measure. Intervals beginning with mobile activity are expressed as a percentage of intervals beginning off-nipple.

Infants of 0-2 weeks spent approximately 2.5% of off-nipple time moving and this proportion increased with age to approximately 30% at 12-17 weeks. The proportion remained fairly constant until 78-89 weeks, although there might have been a slight fall after 42-53 weeks. Older baboons, from juvenile to adult, spent less time moving than did infants.

A second measure was based on one-zero scores. The frequency of intervals in which there was any form of mobile activity was expressed as a percentage of intervals in which infants were off-nipple. Age changes in this measure are shown in Figure 49.

There was a steep rise in frequency to a peak at 12-17 or 18-23 weeks followed by a more gentle decline continuing into adulthood.

Although age changes in these two measures correlate positively and significantly (Spearman rs = +0.93, N = 10, $p<0.01$), the two curves are not parallel. Figure 50 shows weighted means only for ease of comparison. The proportional difference between them appears greater in early weeks than later on. This could mean that the mean duration of bouts of mobile activity increased with age.

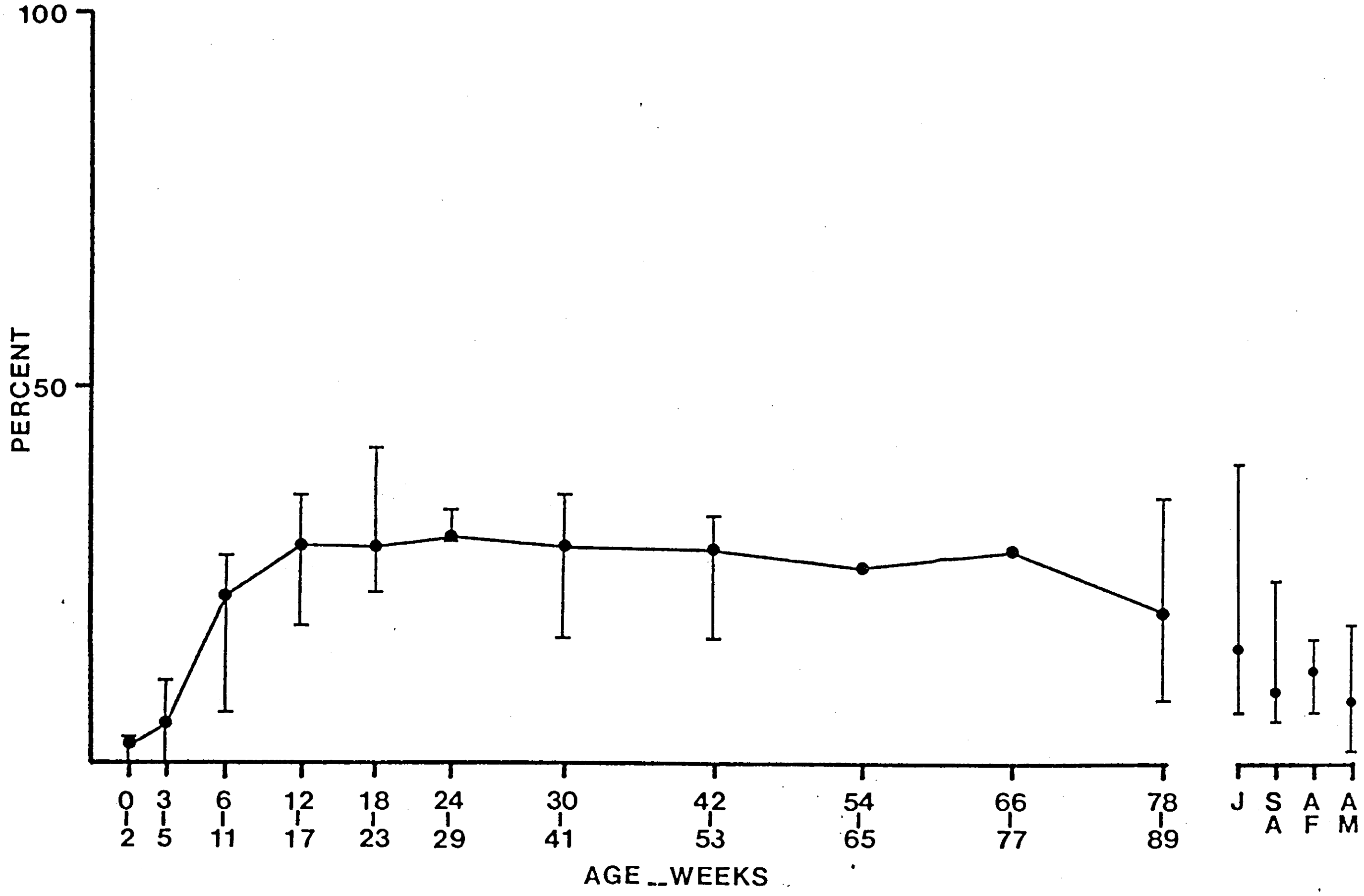


Figure 48. The percentage of 30 second instantaneous samples scoring off-nipple where subjects were engaged in mobile activity.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

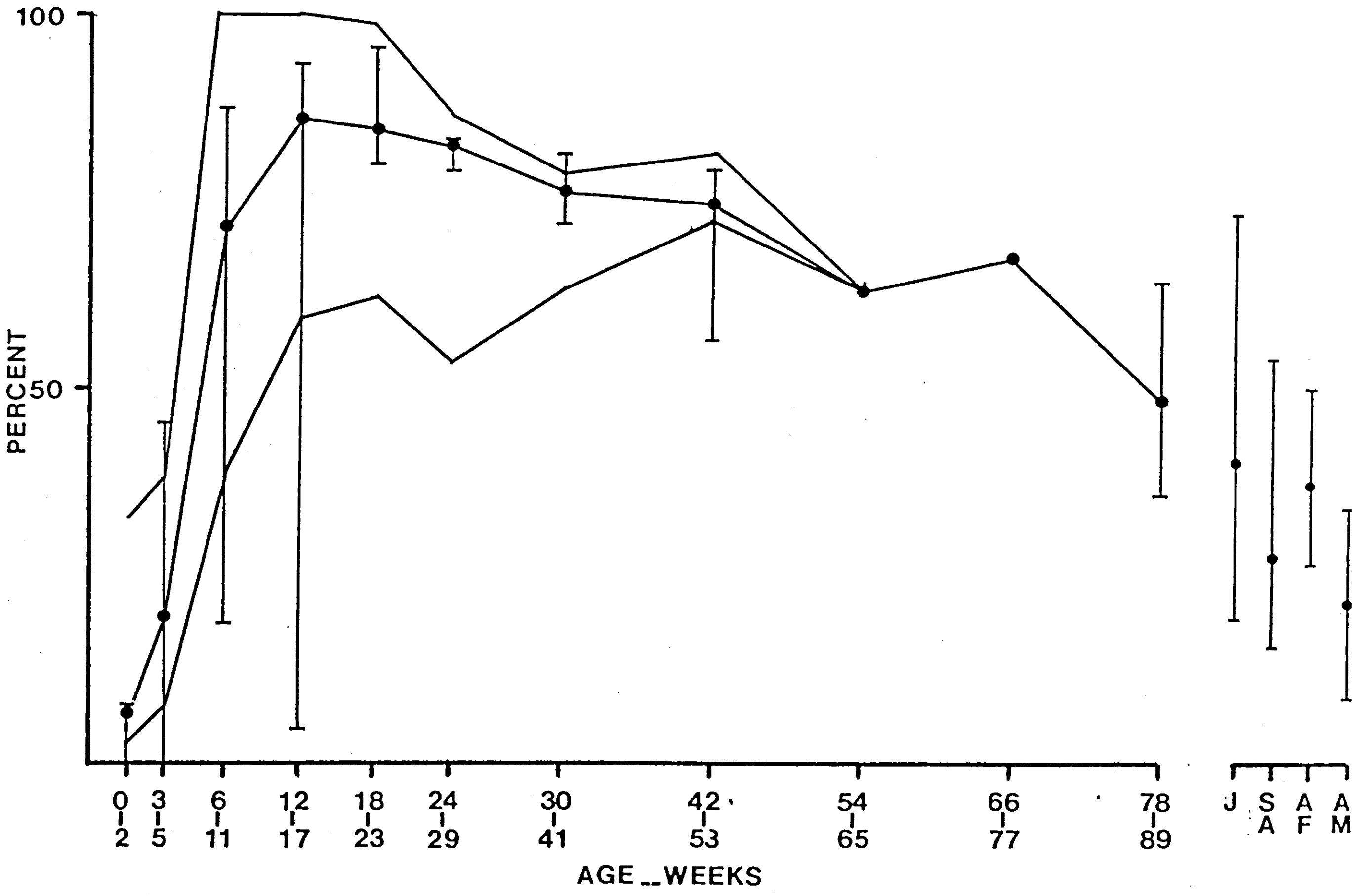


Figure 49. The percentage of off-nipple intervals with mobile activity.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

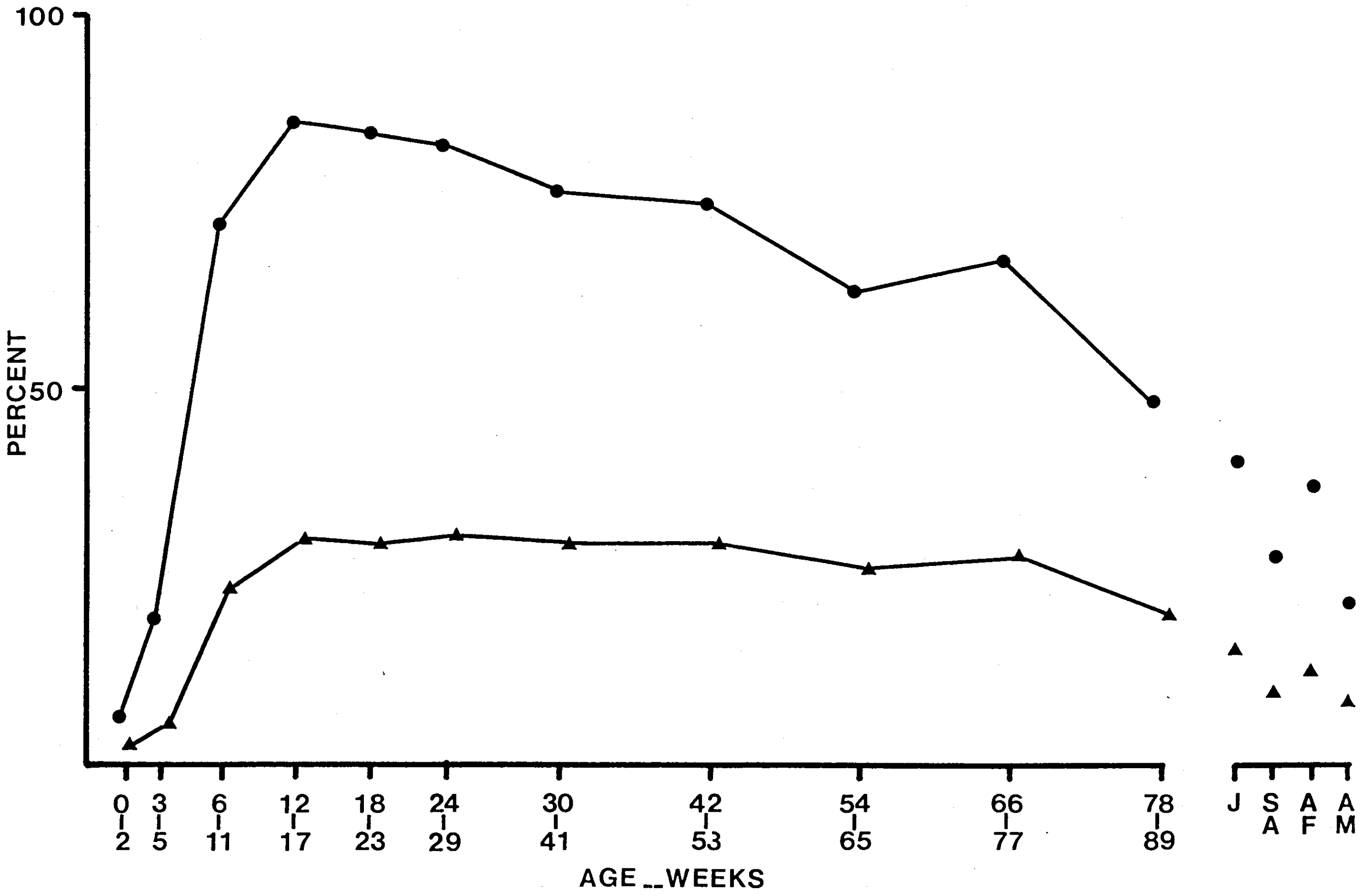


Figure 50. The weighted means from figures 48 and 49.

● one-zero samples (Figure 49)
▲ instantaneous samples (Figure 48)

Discussion

It is interesting to note that infants were most active at around 12-17 and 18-23 weeks when they were most frequently on or in-contact with their mothers (Figure 20) and when the frequency of making and breaking contact with mother was greatest (Figure 11). This would suggest that most activity occurred near the mother and that many of the relatively short bouts of activity consisted of quick sorties away from and back to her. Little of the time out of contact with mother at this age would have been spent stationary.

Mobile activity was, presumably, energy expensive. Its peak occurred during the period in which infants were still associating closely with their mothers and possibly having most of their nutritional needs satisfied by her. After 18-23 weeks the level of activity fell. From Figures 40, 41 and 42 it can be seen that the proportion of off-nipple intervals in which infants picked up and held and mouthed objects and scratched the ground continued to increase. This probably means that after 18-23 weeks they spent an increasing proportion of their time foraging for solid food and so were able to devote less time to, or had less energy available for, other activities.

2. Locomotor patterns contributing to mobile activity

This analysis considers the following Locomotor patterns regardless of play or non-play context.

walk
run
jump
climb-up
climb-down
swing/hang
sloth-like progression

Figures 51 to 57 show age changes in the one-zero frequencies of these behaviours, expressed as percentages of intervals in which subjects

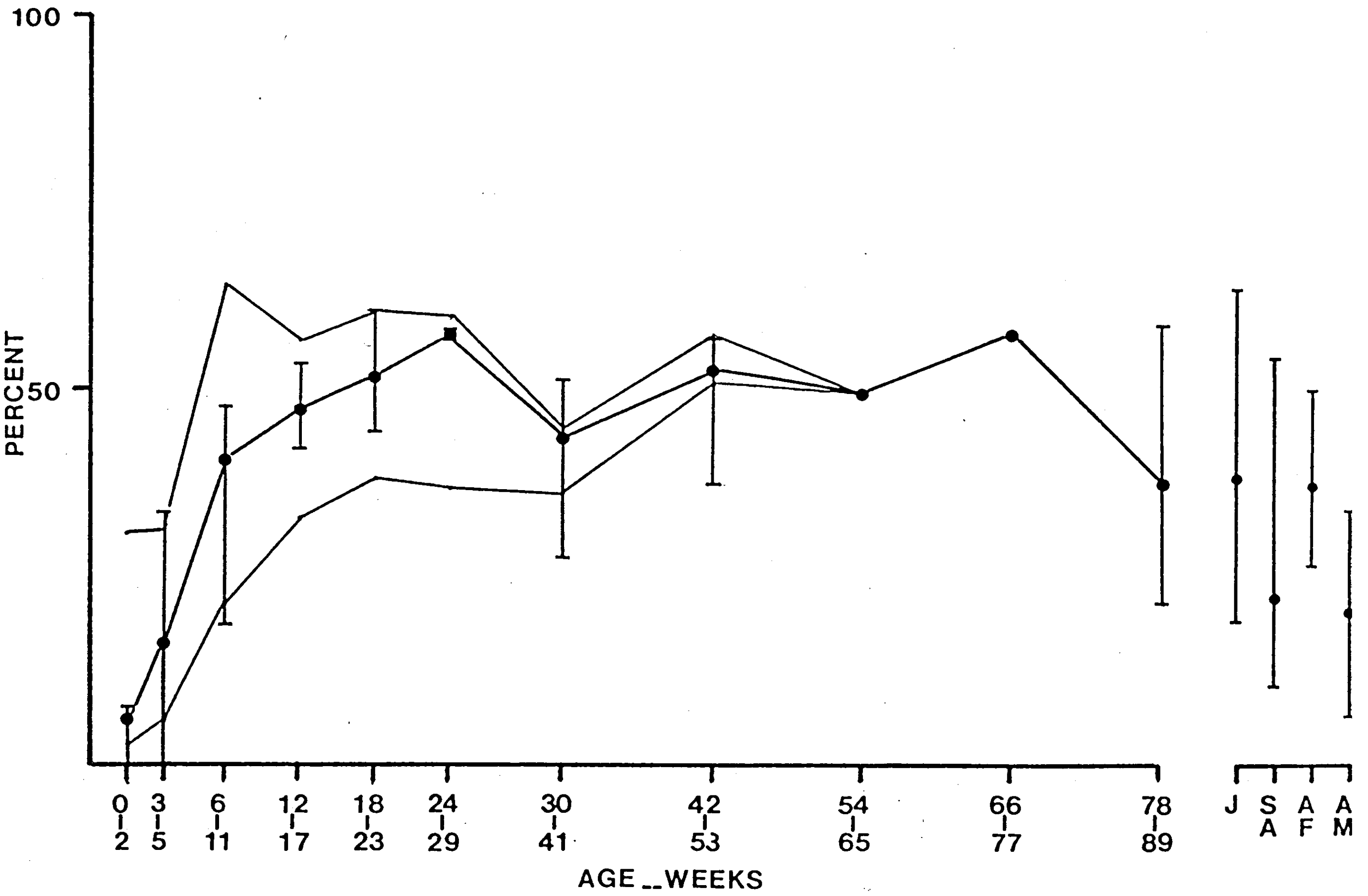


Figure 51. The percentage of off-nipple intervals with walk.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

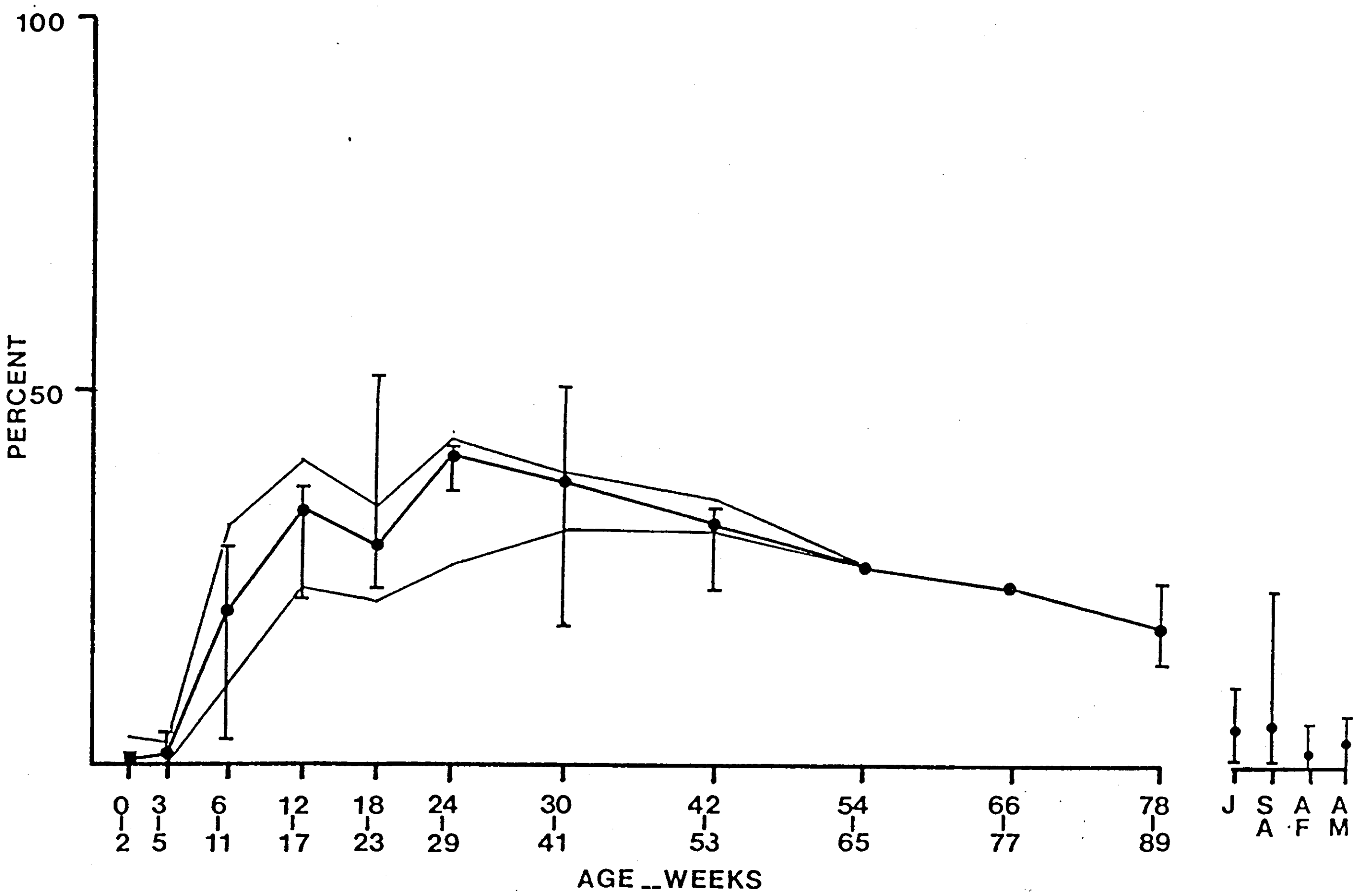


Figure 52. The percentage of off-nipple intervals with run.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

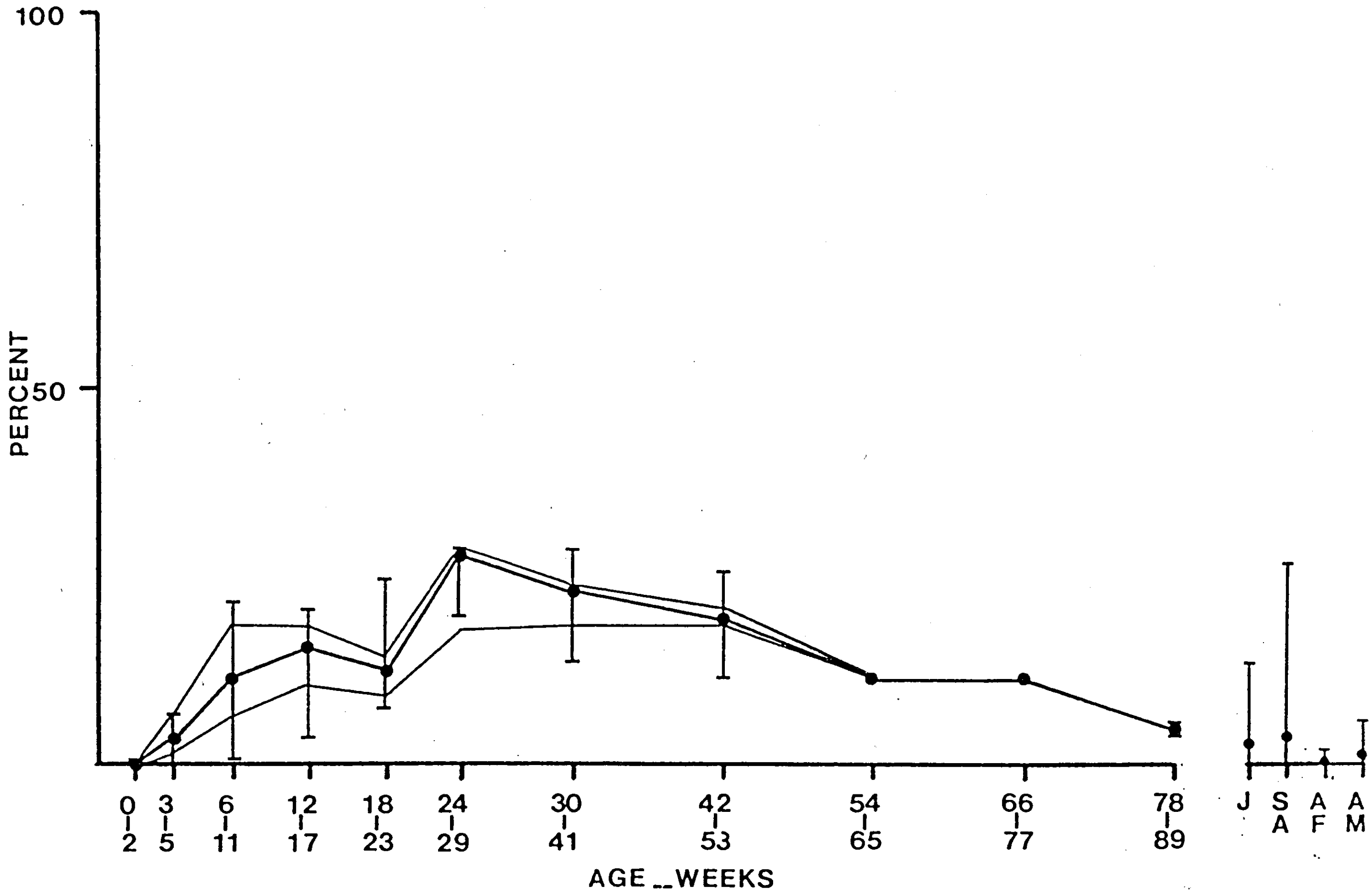


Figure 53. The percentage of off-nipple intervals with jump.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

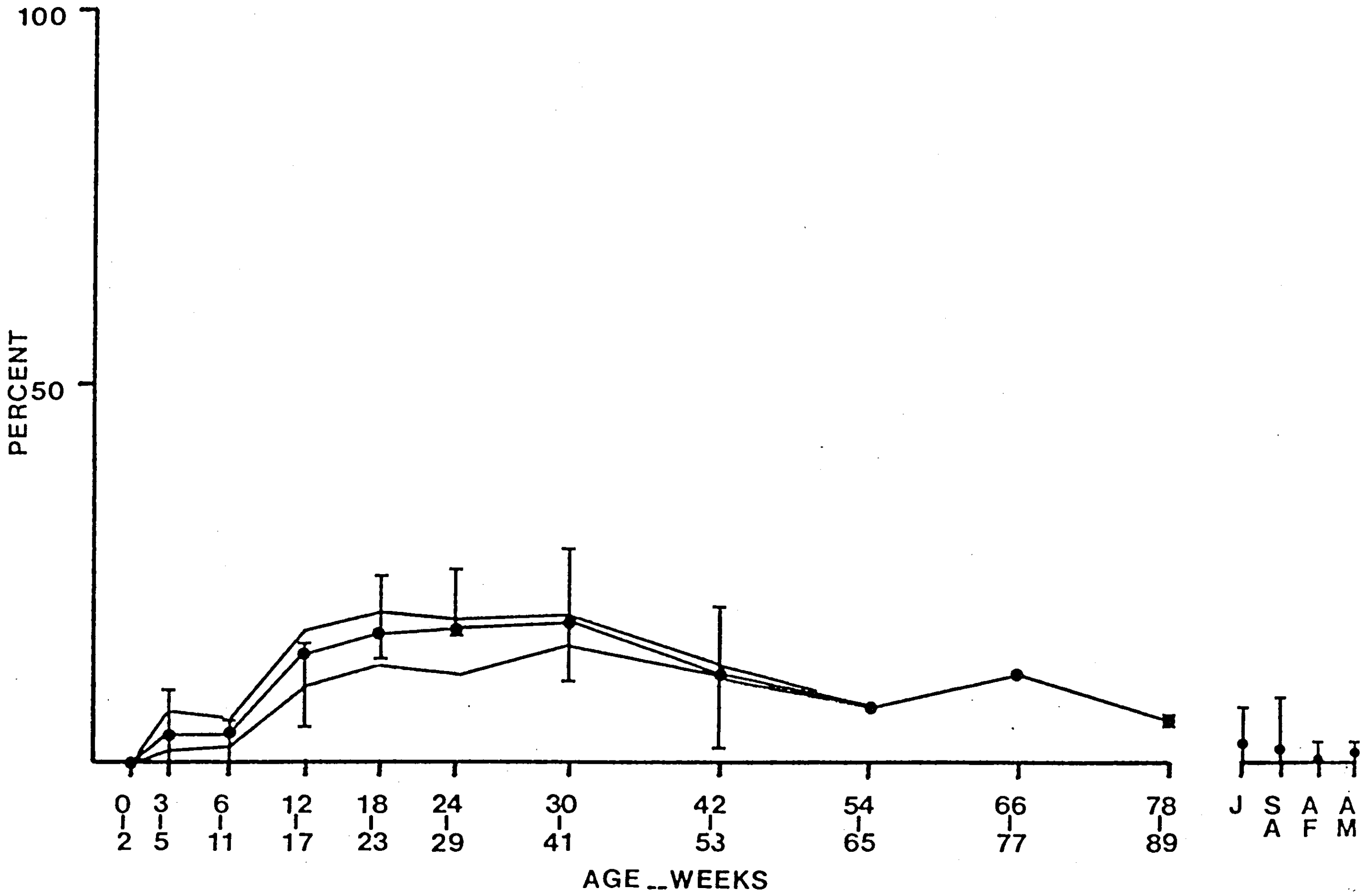


Figure 54. The percentage of off-nipple intervals with climb-up.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

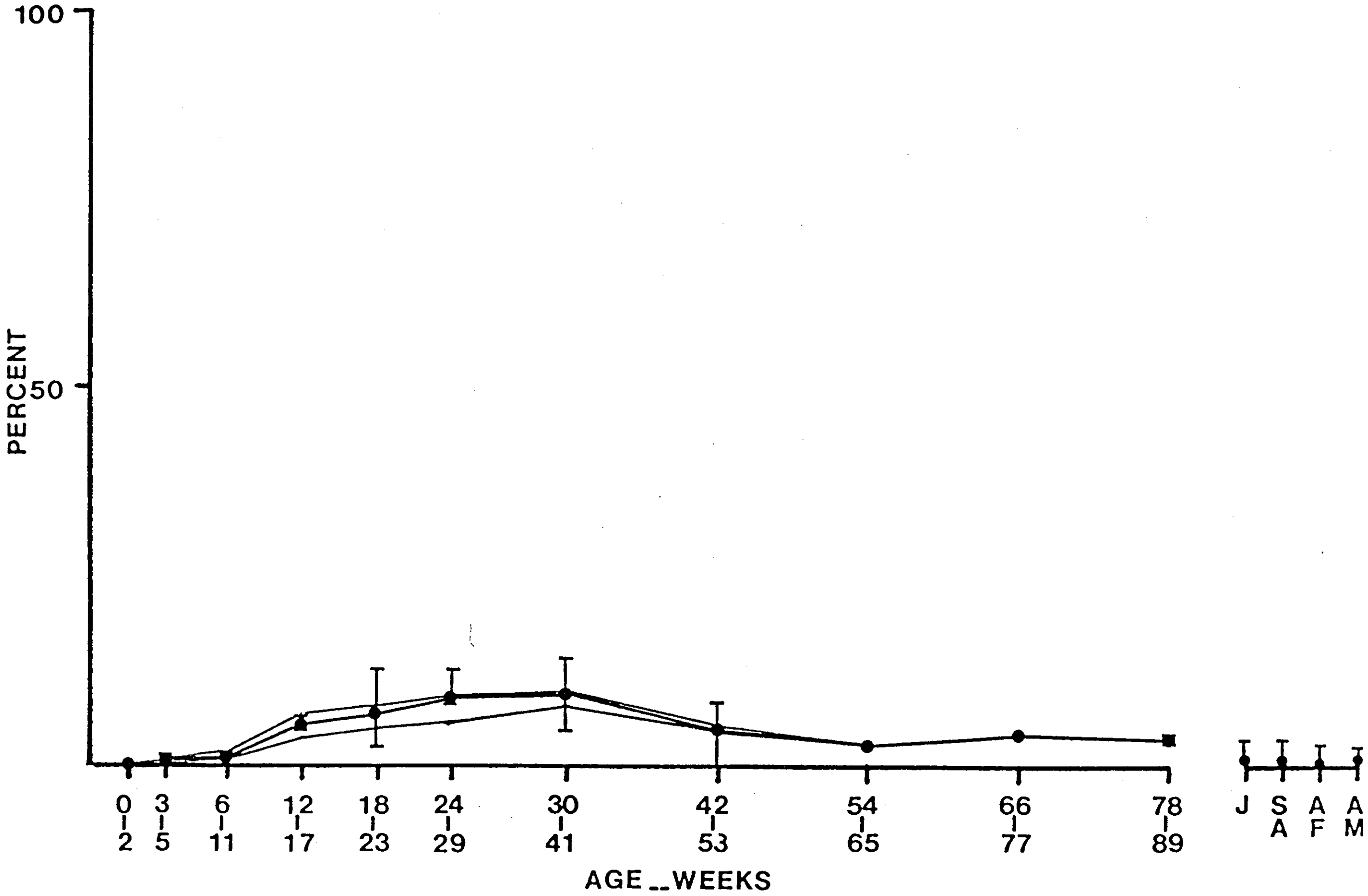


Figure 55. The percentage of off-nipple intervals with climb-down.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

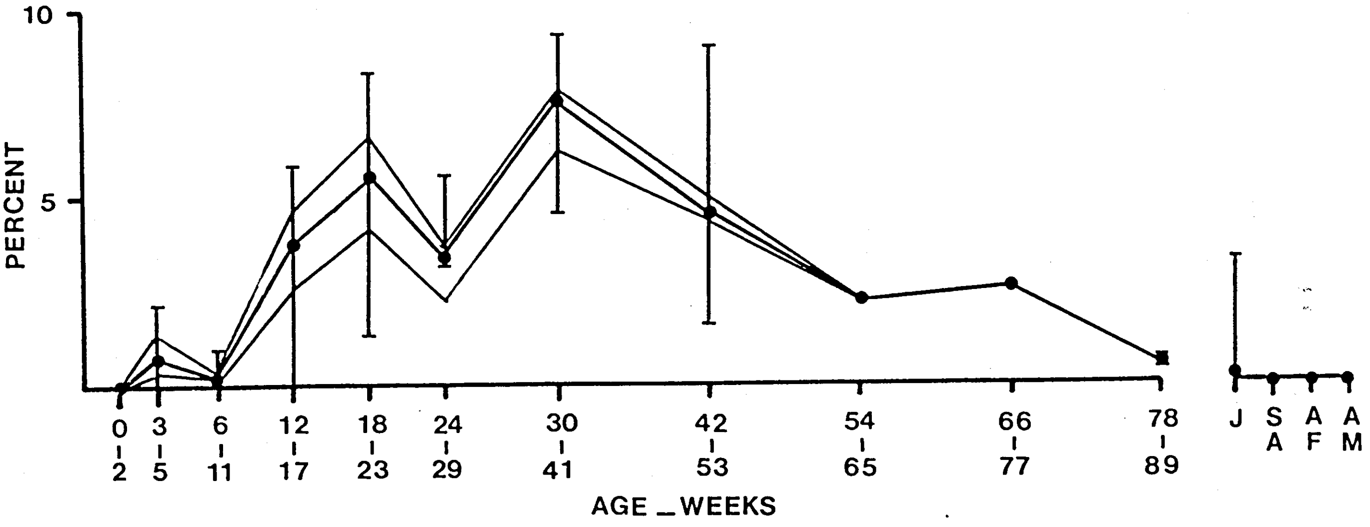


Figure 56. The percentage of off-nipple intervals with swing/hang.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

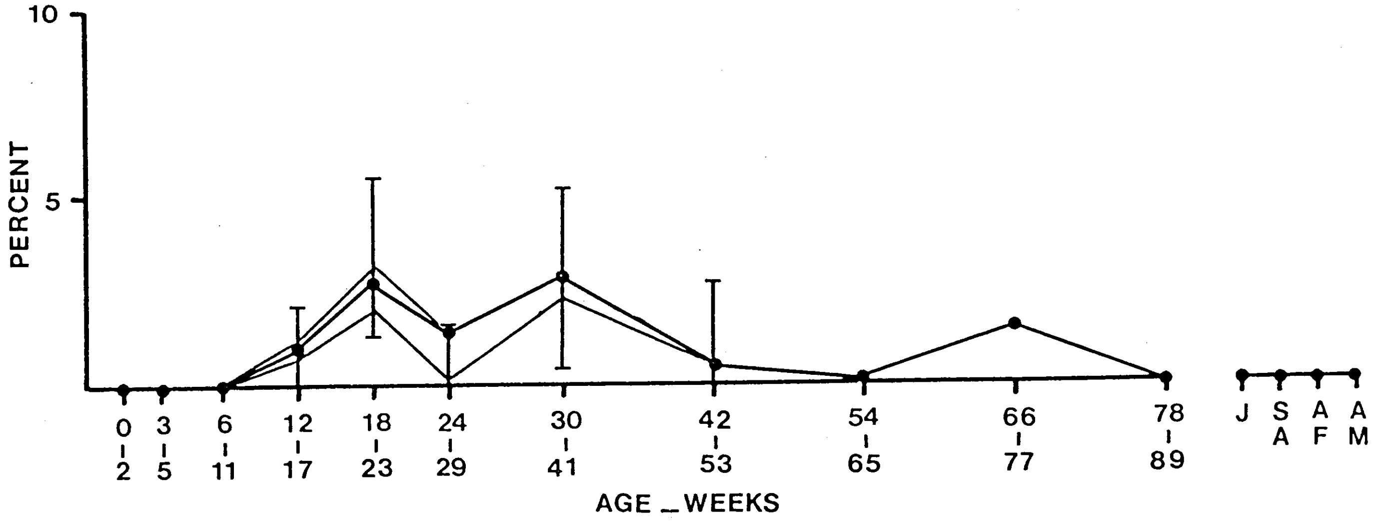


Figure 57. The percentage of off-nipple intervals with sloth-like progression.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

Infants walked, ran and jumped during their first three weeks but not until 3-5 weeks did they show any climbing or acrobatic behaviours. Sloth-like progression began at 6-11 weeks.

Walk, run and jump rose to a peak at 24-29 weeks. Then, run and jump decreased in frequency over the remaining ages while walk remained at around the same frequency. Walk was always more frequent than run or jump. In the early weeks jump was more frequent than run but from 6-11 weeks run was always the more frequent.

The climbing and acrobatic behaviours not only started later but reached maximum frequency later, at 30-41 weeks.

The rank order of frequencies at all ages was climb-up > climb-down > swing > sloth-like progression. Climb-down was less frequent than climb-up because infants did not always climb-down from the positions they climbed to. They sometimes jumped or were retrieved by their mothers. Sloth-like progression was rarely seen, and consequently the small amount of data makes analysis difficult. It is included in later chapters for completeness even though the results are unreliable.

The development trends of the seven locomotor patterns were compared by Spearman rank correlation and the coefficients are shown in Table 20.

The intercorrelations are high because all the trends share a period of increasing frequency up to 24-29 weeks. Walk correlates least well with the rest.

By inspection of the development trends three groups can be identified on the basis of age of first appearance, position of peak frequency and subsequent changes of frequency. The developmental groups are:

1. walk
2. run and jump
3. climb-up, climb-down, swing, sloth-like progression

Comparison with Chalmers (1980, and unpublished results)

Safari park infants appear to lag behind wild infants in development. Chalmers reported that all of his subjects walked, ran, jumped and climbed by 4 weeks of age, but only a few safari park infants were seen to walk,

Table 20. Spearman rank correlation between age changes in the weighted mean on-zero frequencies of locomotor patterns.

N = 10.

	run	jump	climb-up	climb-down	swing/hang	sloth-like progression
walk	+0.71 *	+0.61	+0.72 *	+0.66 *	+0.47	+0.72 *
run		+0.97 ***	+0.94 ***	+0.91 ***	+0.78 *	+0.84 **
jump			+0.90 ***	+0.89 ***	+0.76 *	+0.77 *
climb-up				+0.99 ***	+0.88 ***	+0.94 ***
climb-down					+0.85 *	+0.90 ***
swing/hang						+0.86 **

*	two tailed $p < 0.05$
**	two tailed $p < 0.01$
***	two tailed $p < 0.001$

run and jump so early. Six to eleven weeks was the earliest age block in which safari park infants were all seen to achieve these locomotor patterns. Climbing and acrobatics were only performed by them all from 12-17 weeks. Wild infants reached peak frequency of running, jumping and climbing at around 16 to 20 weeks but the peaks for safari park infants were later, between 24 and 41 weeks depending on the locomotor pattern.

The difference in age of first appearance may have been a result of different watching regimes. In the present study locomotor patterns may have been first performed earlier but only recorded when they became sufficiently frequent to be picked up in short observation sessions.

The relative lateness of safari park infants in achieving peak frequency is more likely to reflect a real difference between the wild and safari park conditions. Safari park infants spent more time on their mothers than similarly aged infants in the "Pumphouse" troop. Their slower development might have been caused by the greater restrictiveness of their mothers.

Chalmers measured the one-zero frequencies of motor patterns in two contexts; during social encounters and during non-encounter time. In both contexts he found that age changes in the frequencies of energetic locomotor patterns (running, jumping, climbing and acrobatics) had high rank correlations with each other but low correlations with age changes in the frequency of walking. In this part of the present study only one context has been considered: the time during which subjects were off-nipple. Some of these findings are therefore consistent with some of Chalmers' findings (inter-correlation of development of energetic locomotor patterns); but since the studies are not directly comparable they are not necessarily contradictory with respect to the correlation of walking with the energetic locomotor patterns.

Discussion

The groups of locomotor patterns suggested above can be distinguished on criteria other than development. Walking can occur in all locomotor situations and is perhaps the least energetic method of locomotion. Running and jumping appear both energetic and conspicuous. They can be performed in most locomotor situations but are more likely to be used in emergencies than walking. Climbing and acrobatics are energetic and might require greater strength and neuro-muscular co-ordination than walking, running and jumping.

Running and jumping need not have been ontogenetic precursors of climbing and acrobatics, in the sense of being the elements from which the more complex motor patterns developed, but the later appearance of climbing and acrobatics probably reflected a later stage of neuro-muscular development. Social factors are also implicated here. Infants of an age when they were most restricted by their mothers had little opportunity for climbing. As they became more independent they were able to climb more. It is relevant that clambering on mother peaked at 6-11 weeks (Figure 27) but climbing on such things as logs, trees and fences became prominent later, 12-17 weeks (Figure 54).

Infants ran, jumped, climbed and performed acrobatics with decreasing frequency after 24-29 weeks or 30-41 weeks whereas they continued to walk with approximately the same frequency. This is consistent with the notion that their behaviour was determined, to some extent, by the availability of two resources, energy and time. It has been suggested that they were spending more time foraging after 24-29 weeks. If it is assumed that this was necessitated by a reduced energy store of mother's milk or of an infant's own fat, then it is reasonable to suppose that the amount of energetic activity including running, jumping, climbing and acrobatics would decrease, but less energetic activity such as walking could remain at the same level. Walking would always be associated with feeding, in moving between food sources, and so would not fall below the minimum frequency which still allowed adequate foraging.

3. Play and non-play

The courses of development of play and non-play (as unitary categories see page 55f for definitions) are shown in Figures 58 and 59. One-zero frequencies are expressed as percentages of intervals in which infants were off-nipple.

Infants were mobile in their earliest weeks (0-2) but only 3 infants played during the first 6 weeks. The majority of infants (4 out of 6) played during the 6-11 week age block and all played at 12-17 weeks.

At all ages it was less common for mobile activity to be play than non-play (Figure 60 for direct comparison). There is a positive correlation between the two trends which is just significant (Spearman $r_s = +0.564$, $N = 10$, $p < 0.05$), but their peaks are at different ages. Non-play activity reached a maximum at 12-17 weeks but play activity did not peak until 24-29 weeks.

These curves suggest that either the proportion of the mobile activity

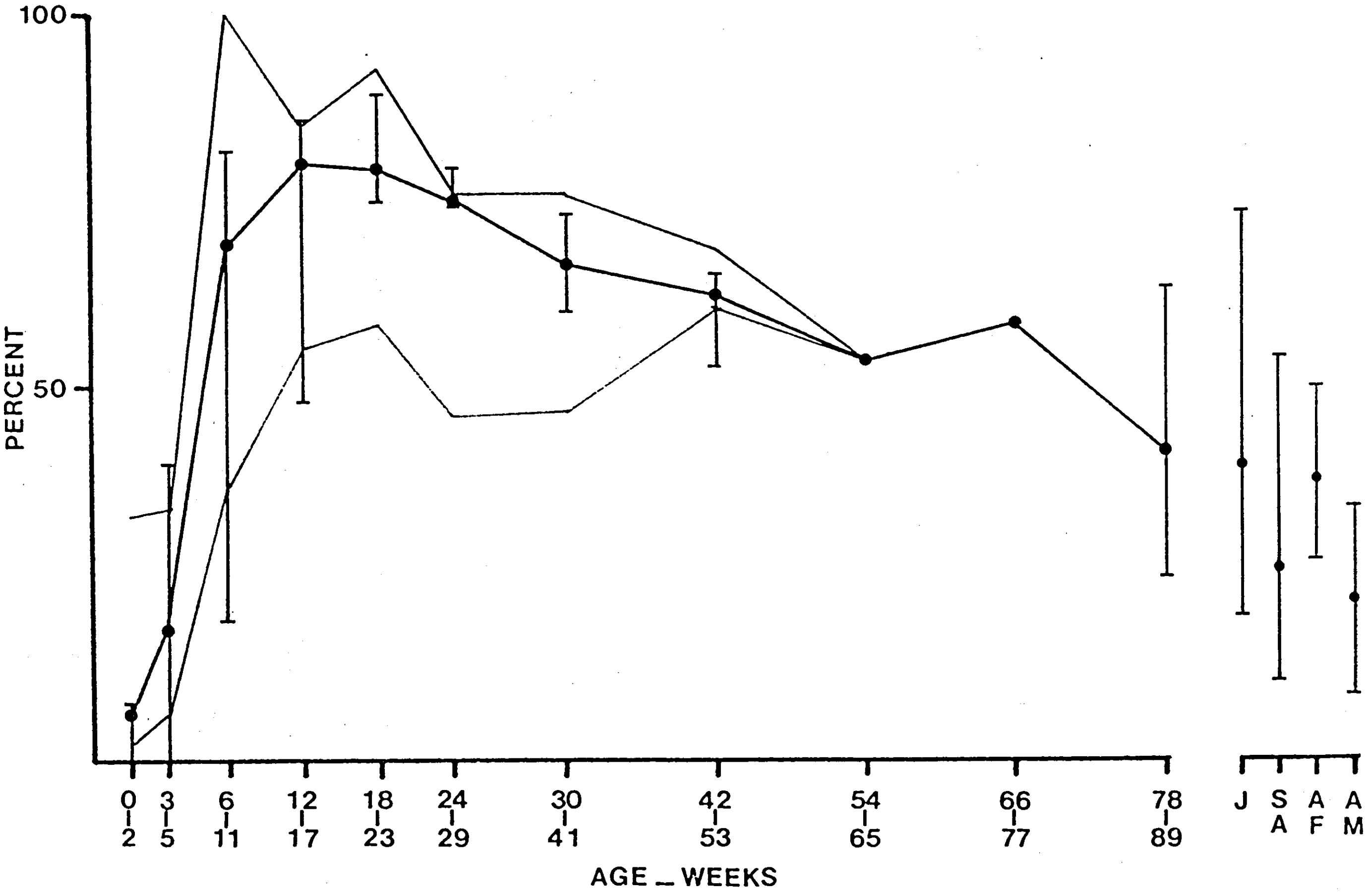


Figure 58. The percentage of off-nipple intervals with non-play.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

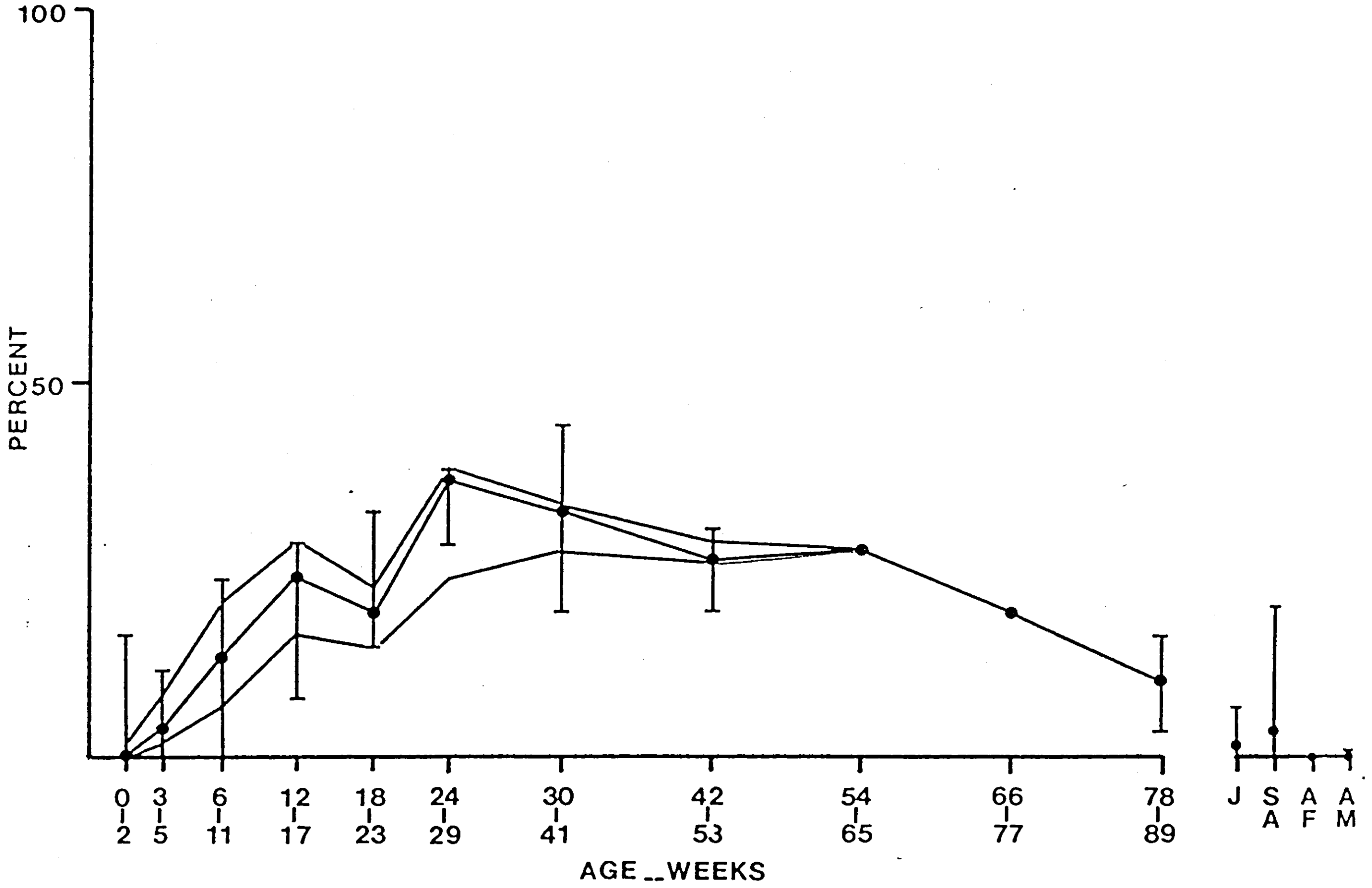


Figure 59. The percentage of off-nipple intervals with play.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

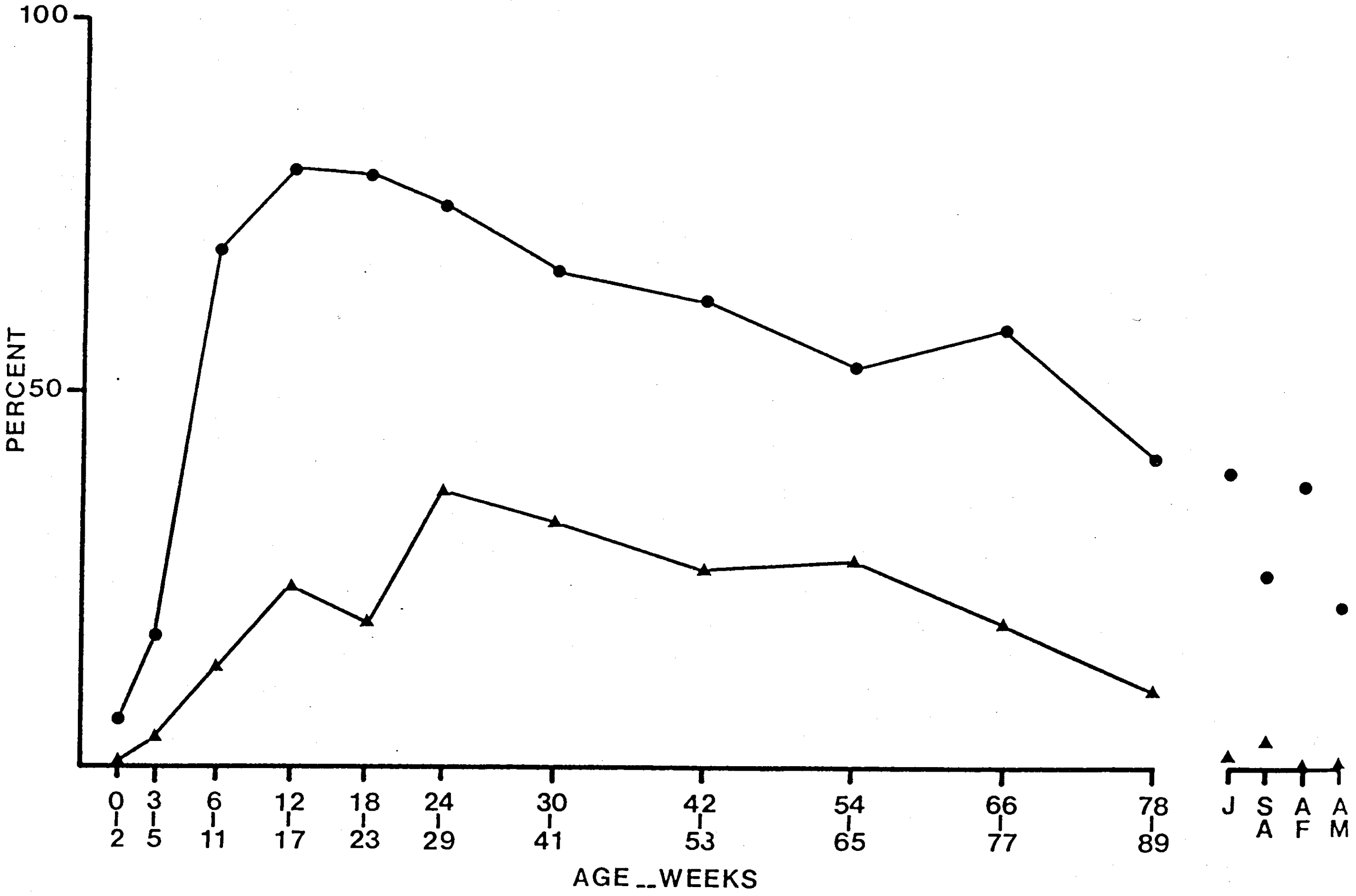


Figure 60. The weighted means from figures 58 and 59.

● non-play (Figure 58)
▲ play (Figure 59)

one-zero measure which was due to play, or that proportion which was due to non-play, changed with age. These proportions are independent because one interval could contain both play and non-play. Figure 61a shows the frequencies of intervals with play and those with non-play expressed as a percentage of intervals with mobile activity.

The proportion of mobile activity which was non-play was always high but fell steadily from 100% to approximately 85% over the infant age range. The proportion which was play changed much more dramatically. It increased from approximately 2% to a peak of 45% at 24-29 weeks, with a major part of that increase occurring between 18-23 and 24-29 weeks. It then decreased to approximately 20% by the end of the infant age range.

Discussion

It is impossible to say whether the later first appearance of play, compared with non-play, was because very young infants failed to signal (if only to this observer) the playful nature of their social behaviour, or because partners were unavailable or inaccessible, or because infants lacked the ability to play.

No record was made of the availability of potential partners. However, infants were off mother hardly more frequently in age block 3-5 weeks than 0-2 weeks so the small increase in play during the first 6 weeks is unlikely to have been due to their coming into contact with more potential partners by virtue of being more independent.

The peak for play came later than the peak for non-play. One explanation could be that there were fewer social interactions before 24-29 weeks, perhaps through lack of potential partners or because of maternal restriction. Play was always social, by the operational definition, and non-play activity could be either social or solitary. Non-play might have had an earlier peak because solitary activity was more frequently possible. Alternatively, the position of the play peak might be more significant. Twenty-four to twenty-nine weeks may have been an appropriate age for maximum social play, that is, the age at which social play gave maximum benefit.

Figure 61a

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

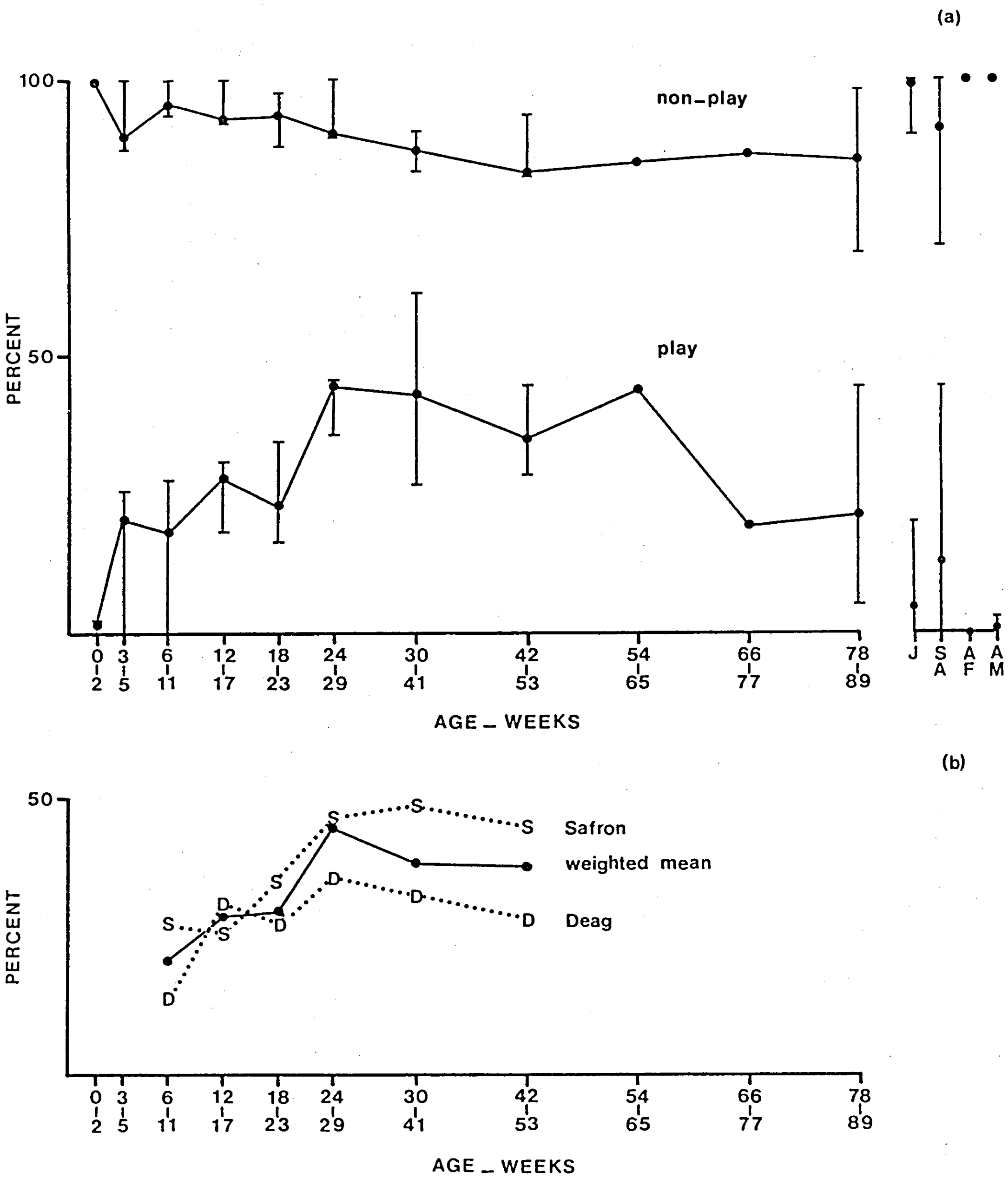


Figure 61

a. The percentage of intervals with mobile activity which contained play and non-play.

b. The percentage of intervals with mobile activity which contained play data from Safron and Deag are shown separately, and the weighted means calculated from those data.

The increase at 24-29 weeks was particularly marked when play was shown as a proportion of mobile activity. This emphasises that the significant question is not only "why was there a peak?" but also "what variables had changed between 18-23 weeks and 24-29 weeks to cause such an increase in the proportion of activity which was playful?"

One possibility which must be considered is that the sharp rise is a sampling artifact. Two subjects contributed to the data at 24-29 weeks whereas 4 contributed to data in the previous and following age blocks. The 2 subjects at 24-29 weeks were the only ones contributing to all 3 sets of data (see Table 21 below).

Table 21: subjects between 18-23 weeks and 30-41 weeks

18-23 weeks	24-29 weeks	30-41 weeks
Safron	Safron	Safron
Deag	Deag	Deag
Gilian		
Kenya		
		Aubrey
		Sigmund

It is a mixture of small longitudinal and cross-sectional samples. We cannot be certain therefore that apparent trends are not the manifestation of individual differences. Figure 61b shows the results calculated only from the data of Safron and Deag, that is, the longitudinal sample. A fairly sharp increase is still apparent between 18-23 weeks and 24-29 weeks. While this does not prove that there is a genuine developmental phenomenon here, it does suggest that the effect should not be simply disregarded as spurious.

Two types of change might have occurred between 18-23 weeks and 24-29 weeks:

1. change in the opportunities for play; and
2. change in the benefits to be gained by behaving playfully.

It is very likely that with their increasing independence infants found themselves with more opportunity for social play. But Figure 8 shows that between these two age blocks there was very little change in the proportion of intervals in which infants were out of contact with their mothers. If there was increased opportunity, it is unlikely to have resulted solely from spending more time away from the mother.

In the next chapter, I shall explore the possibility that at 24-29 weeks it became more beneficial than before to behave playfully.

Summary

Infants were increasingly active through their early weeks, reaching the maximum at 12-17 weeks or 18-23 weeks when most of the activity was around their mothers. The decrease in activity after that age was discussed in relation to infants' increasing need to forage for themselves. Locomotor patterns had highly inter-correlated development trends, but there were sufficient differences in age of first appearance and subsequent age changes to identify three developmental groups. Play was always less frequent than non-play but the proportion of mobile activity that was playful showed greater changes with age than the proportion that was non-playful. The age of greatest change was 18-23 weeks to 24-29 weeks. It was suggested that this was due to increasing opportunity for play or increasing benefits to be gained from playing.

Chapter 7. Results: the development of motor patterns in play and in non-play.

This chapter considers the development of locomotor patterns in the separate contexts of play and non-play. This is to reveal the context in which they first appeared and in which they first became frequent. An attempt is made to relate changes in play and non-play locomotor pattern development to concurrent changes in other aspects of infant life.

The following locomotor patterns are dealt with:

walk
run
jump
climb-up
climb-down
swing/hang
sloth-like progression

Figures 62 to 75 show the development of play and non-play versions of each locomotor pattern. One-zero frequencies are expressed as a percentage of intervals in which infants were off-nipple.

1. First appearance

In every case a locomotor pattern first appeared in non-play before it appeared in play. The play patterns did not all appear for the first time at the same age. Each appeared at the same time as a noteable increase in its non-play frequency. The frequency of the play pattern was always lower than that of the non -play pattern at the age of first appearance in play, and continued to be so throughout the infant age range[1].

---

[1] The only exception to this was "run" at 54-65 weeks. Play run was slightly more frequent than non-play run. This might be best considered a sampling error; there was only one subject at that age. In the age blocks immediately before and after 54-65 weeks, the non-play frequencies were just higher than the play frequencies. It would be reasonable to interpret the results between 42-53 weeks and 66-77 weeks as showing approximately the same decreasing frequencies of play and non-play run.

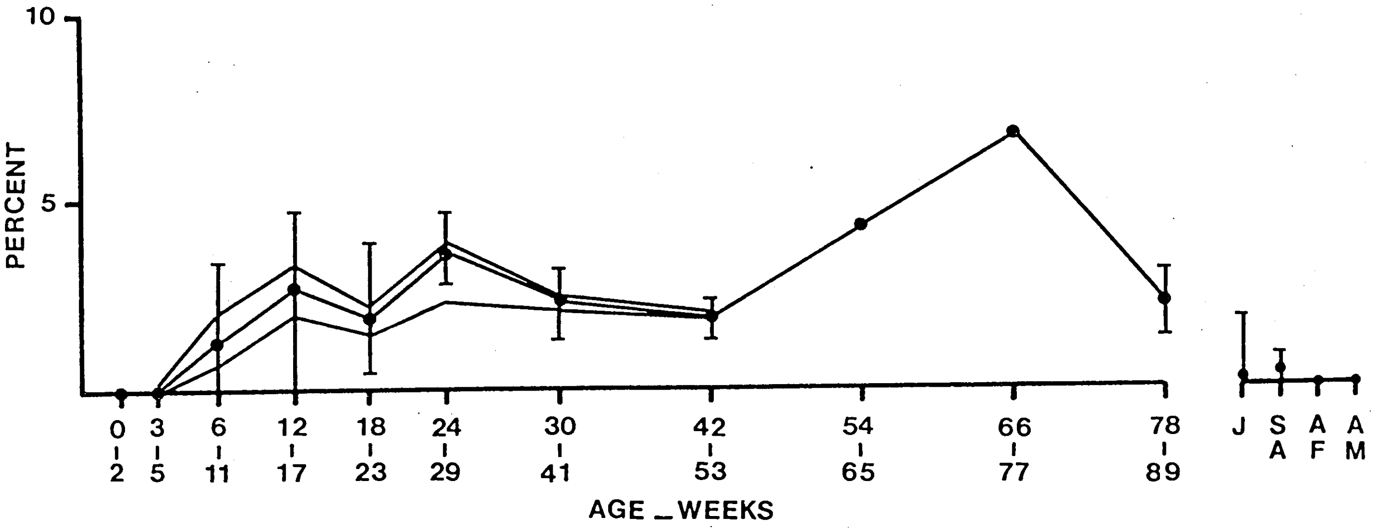


Figure 62. The percentage of off-nipple intervals with play walk.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

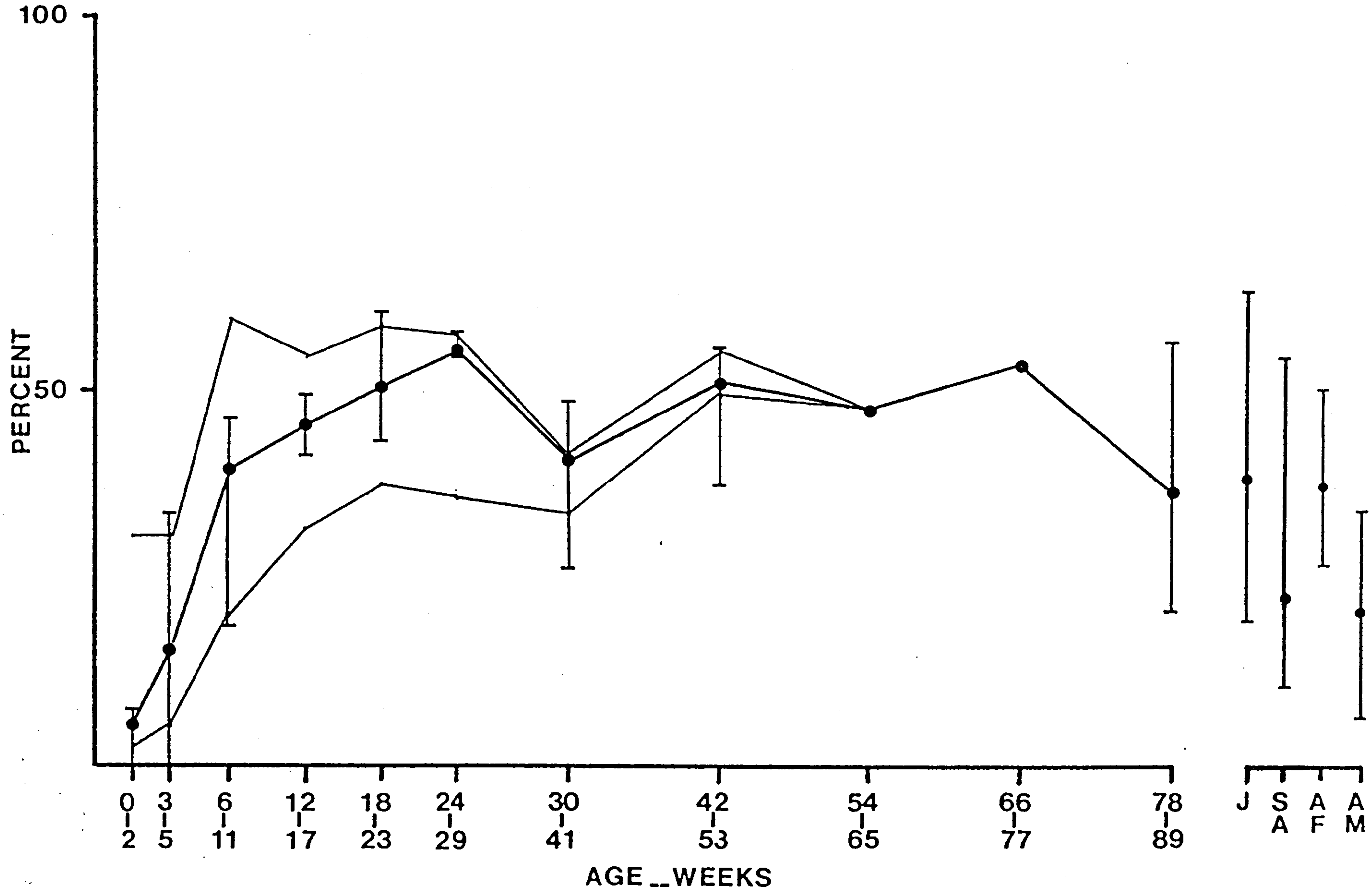


Figure 63. The percentage of off-nipple intervals with non-play walk.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

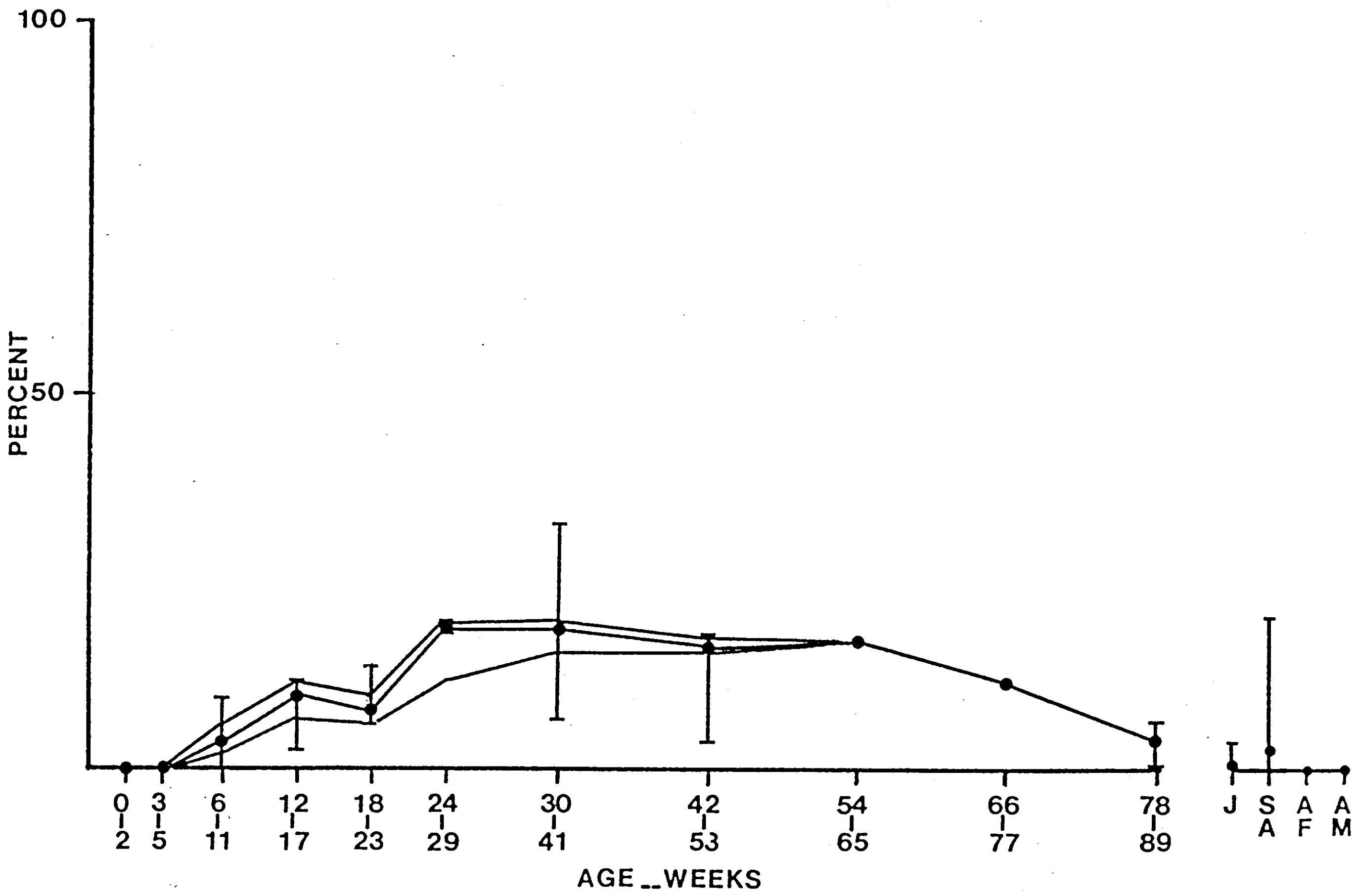


Figure 64. The percentage of off-nipple intervals with play run.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

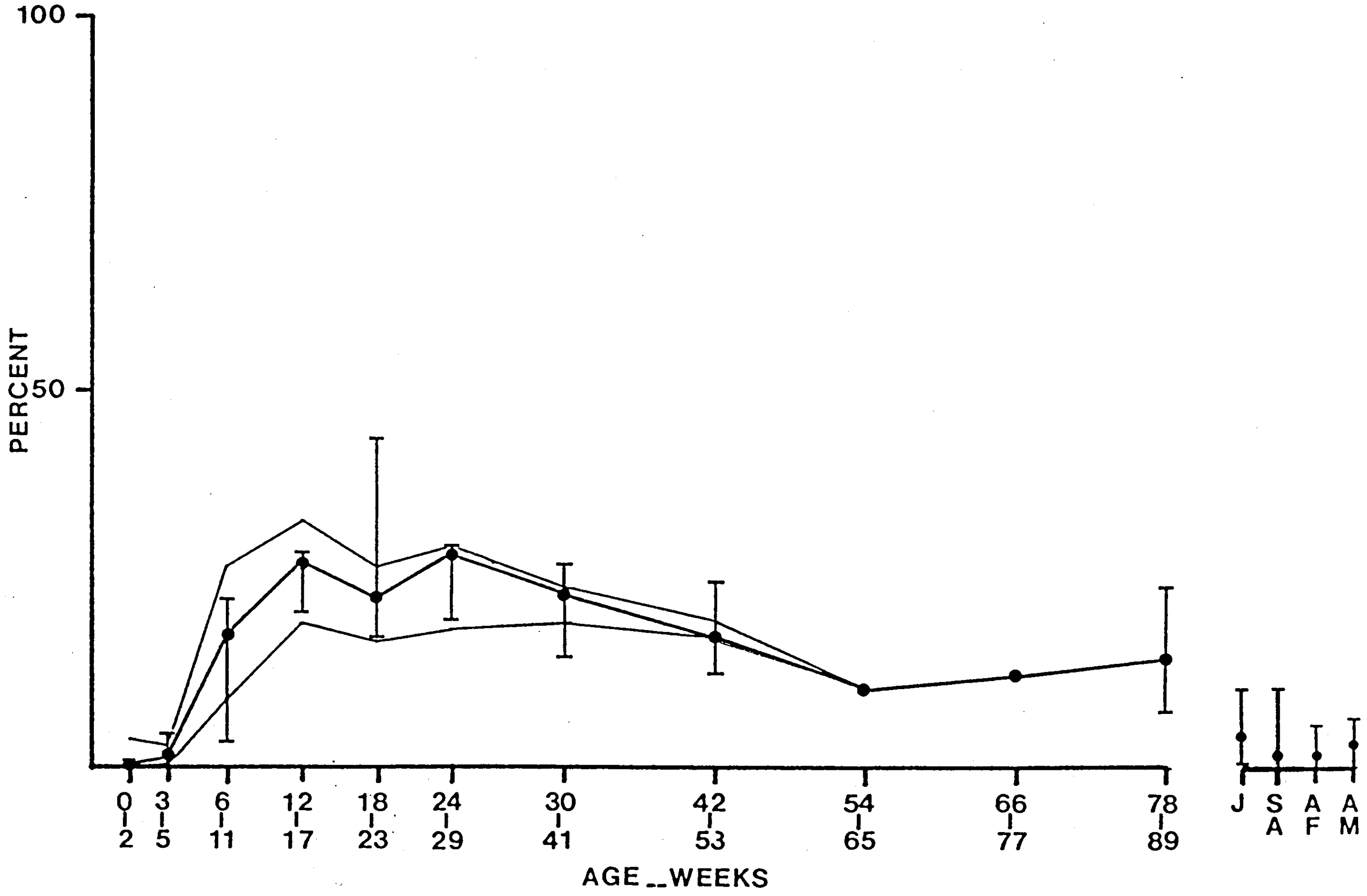


Figure 65. The percentage of off-nipple intervals with non-play run.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

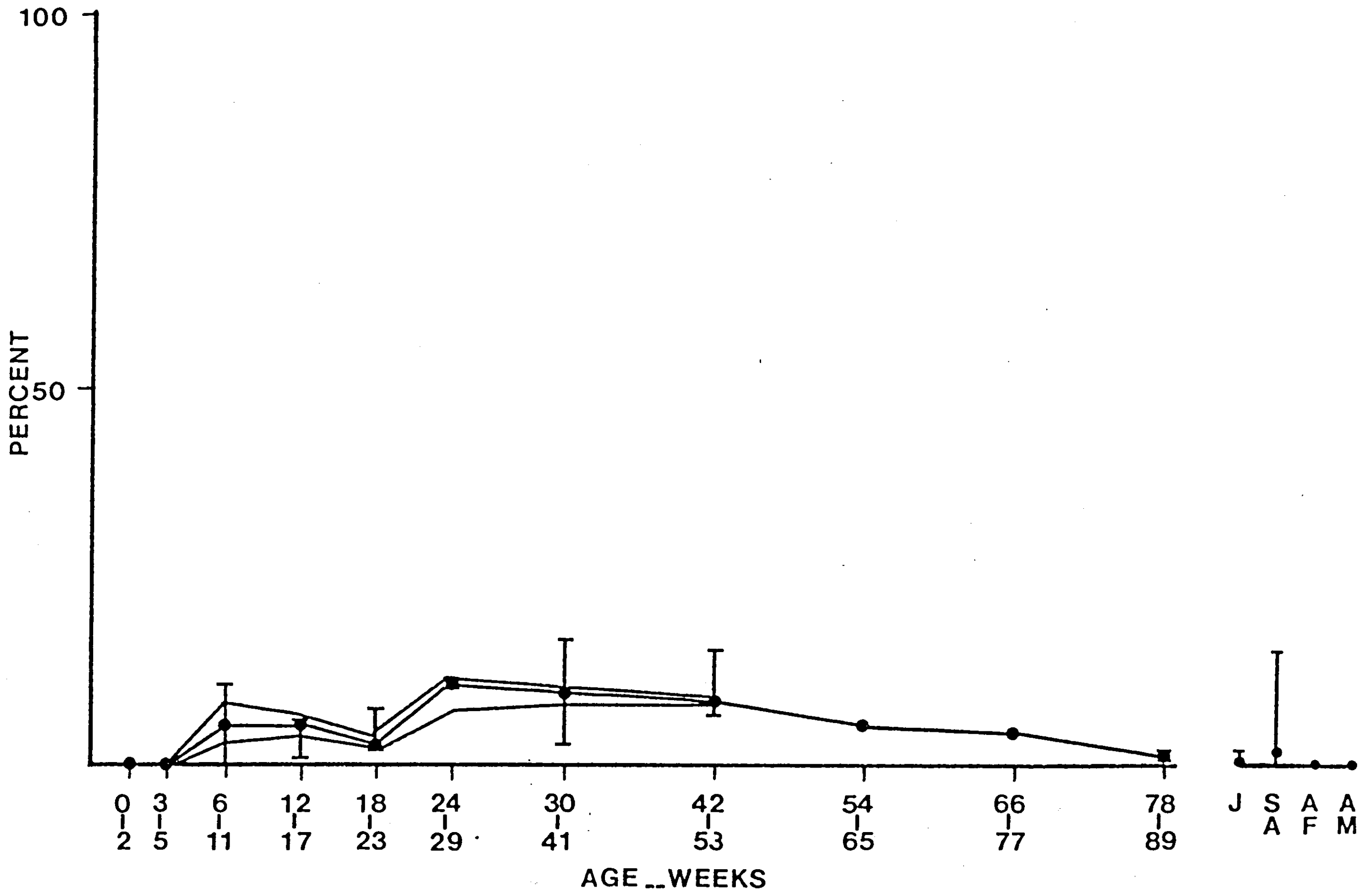


Figure 66. The percentage of off-nipple intervals with play jump.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

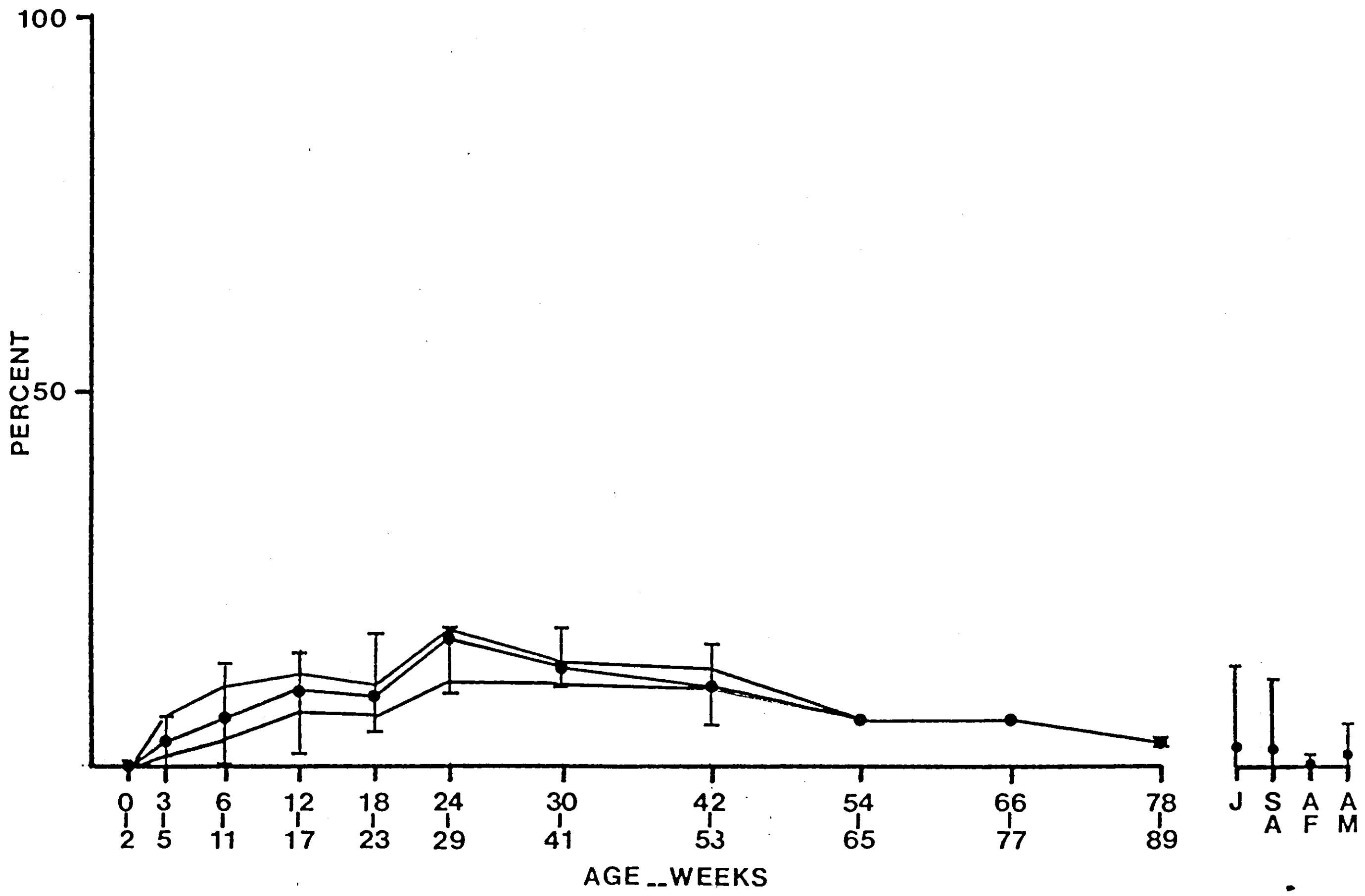


Figure 67. The percentage of off-nipple intervals with non-play jump.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

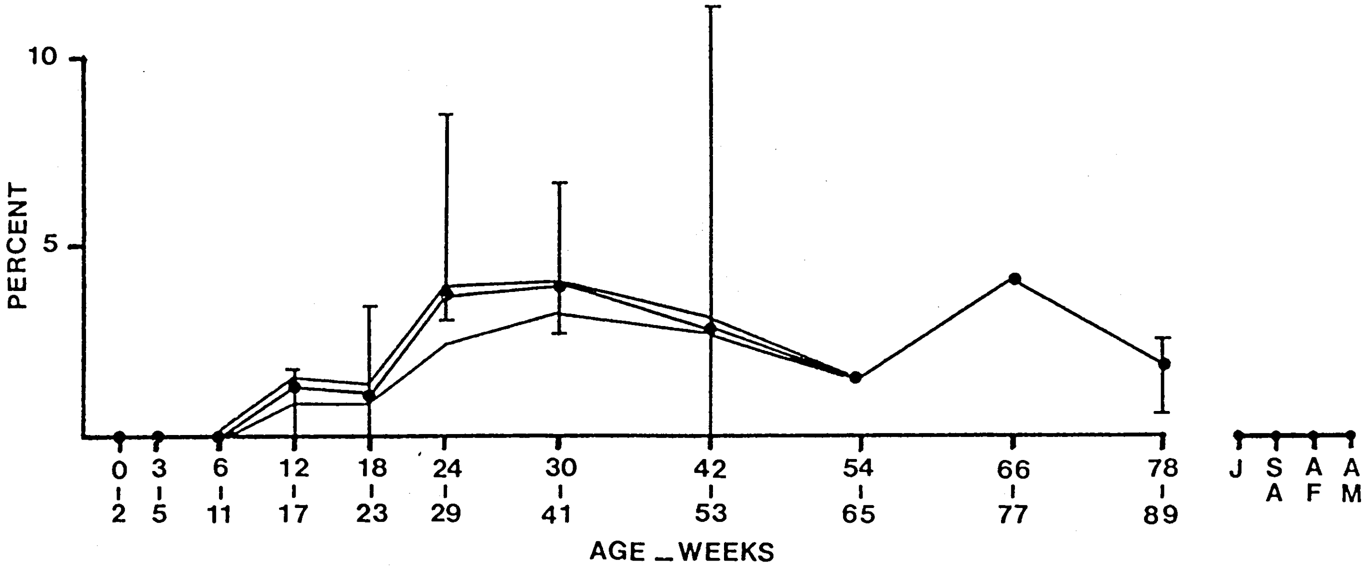


Figure 68. The percentage of off-nipple intervals with play climb-up.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

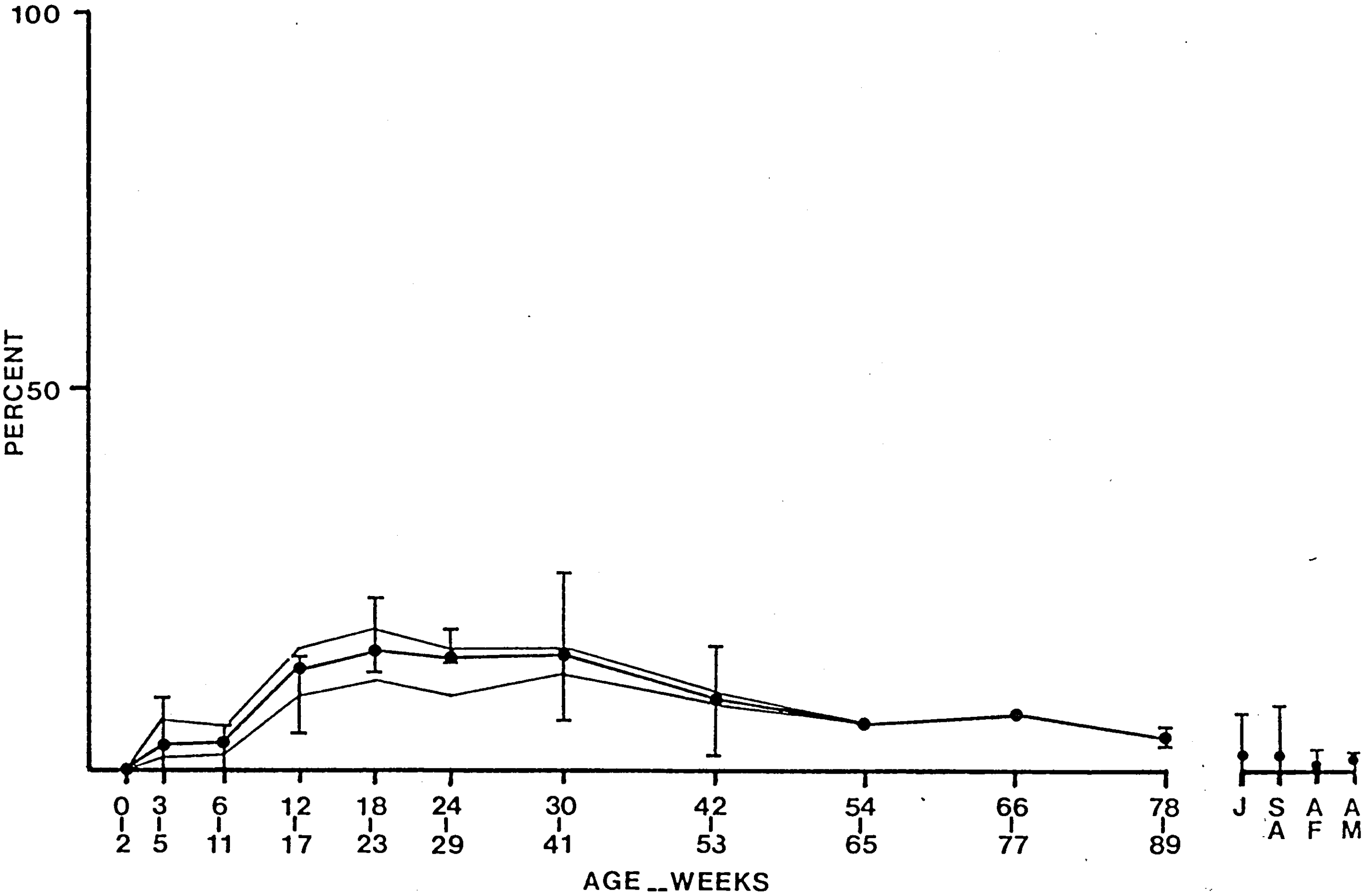


Figure 69. The percentage of off-nipple intervals with non-play climb-up.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

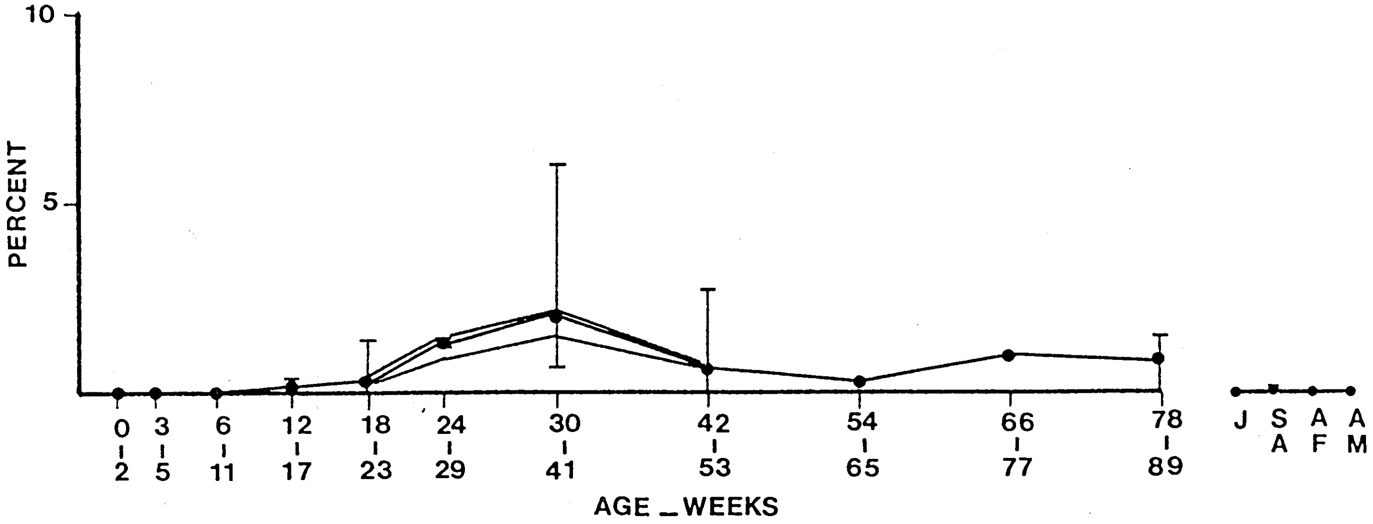


Figure 70. The percentage of off-nipple intervals with play climb-down

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

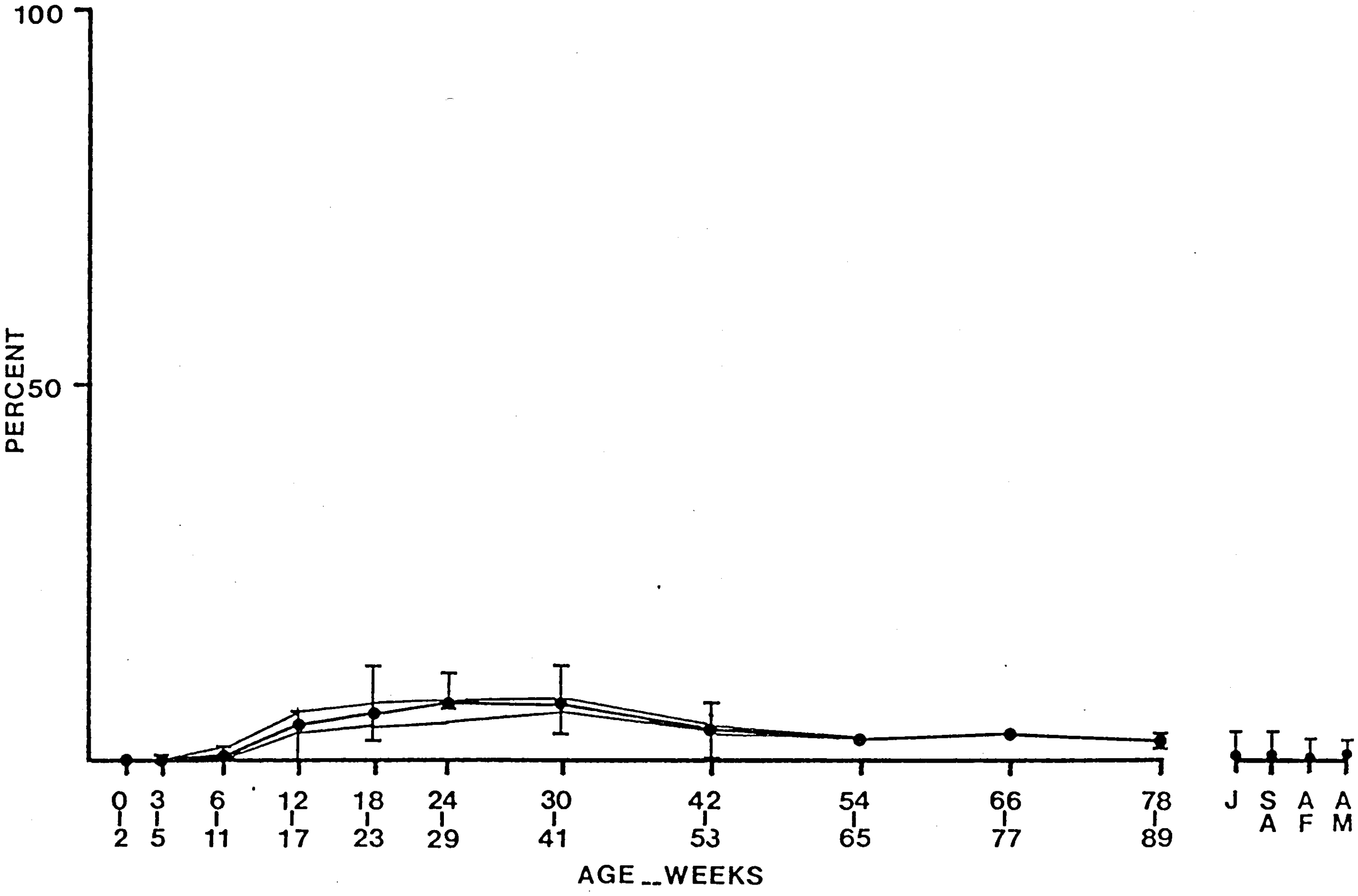


Figure 71. The percentage of off-nipple intervals with non-play climb-down.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

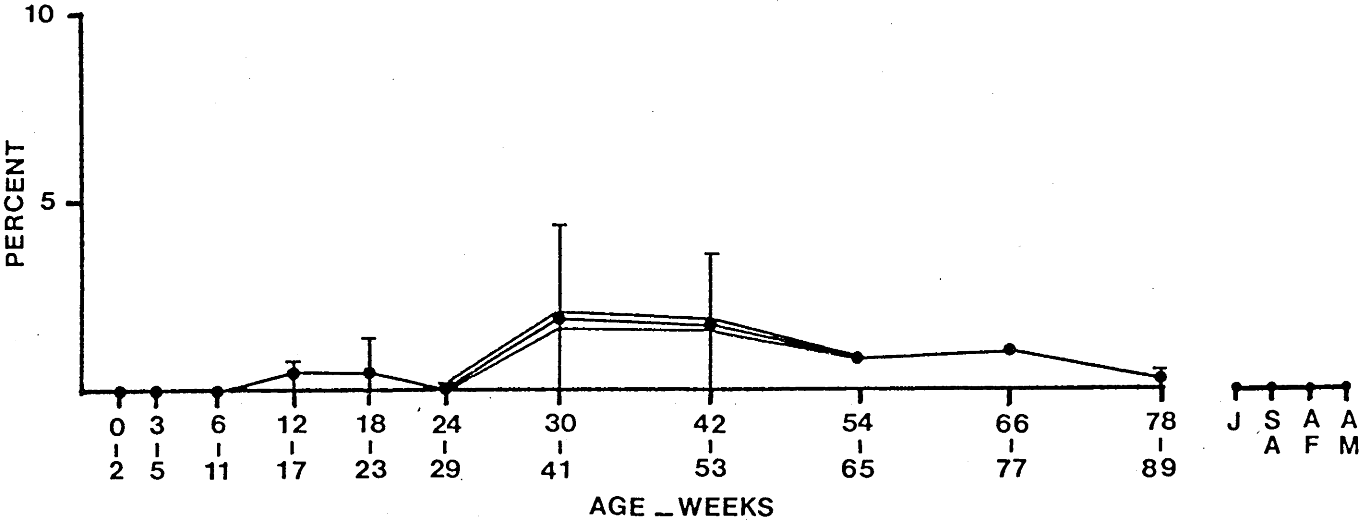


Figure 72. The percentage of off-nipple intervals with play swing.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

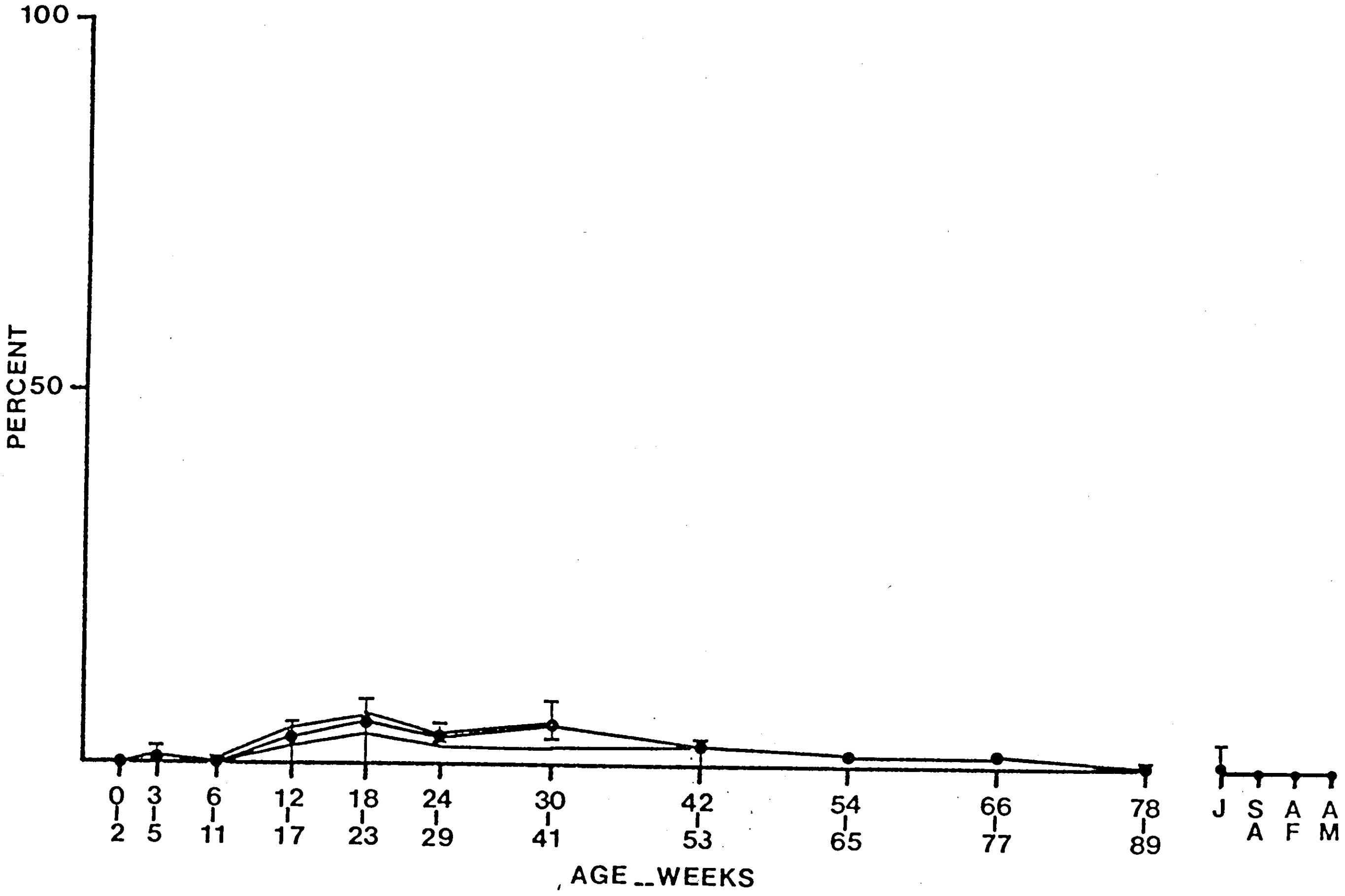


Figure 73. The percentage of off-nipple intervals with non-play swing.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

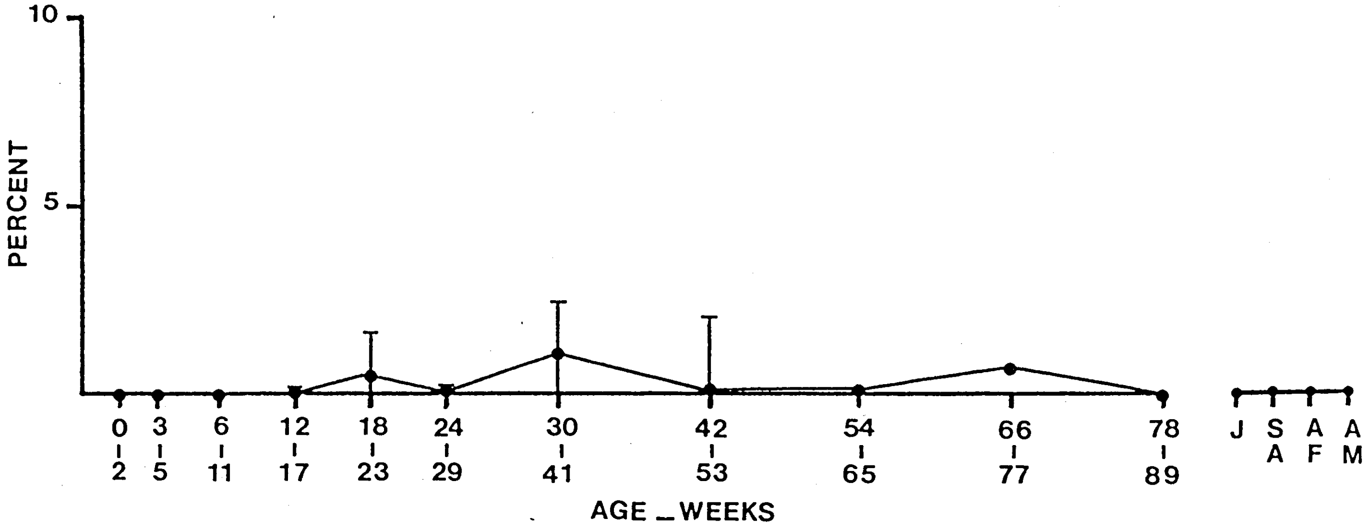


Figure 74. The percentage of off-nipple intervals with play sloth-like progression.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

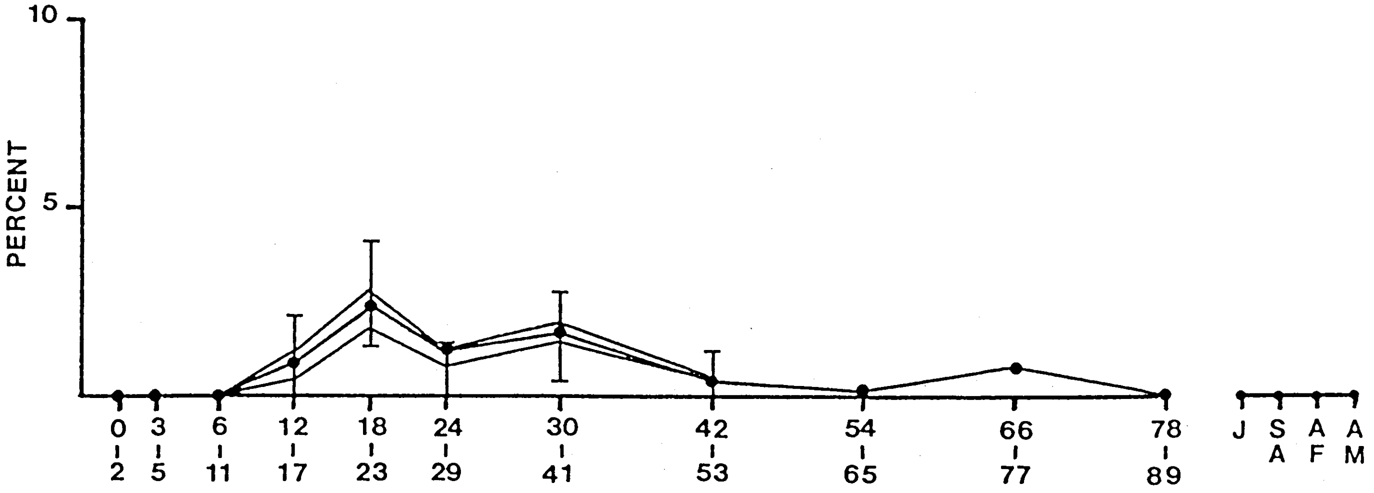


Figure 75. The percentage of off-nipple intervals with non-play sloth-like progression.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

Conclusion

Infants performed in social play those locomotor patterns which were already part of their behaviour repertoire and which they were performing quite frequently in other situations. This result is entirely consistent with Chalmers' (1980a) findings in wild baboons. It is unlikely that social play provided a unique and necessary context for the emergence and practice of locomotor patterns. This supports Fagen's (1976) prediction that behaviour patterns will appear in play after they appear as part of the animal's general behaviour.

2. Comparing frequency changes

Most play locomotor patterns peaked later than their non-play equivalents. Jump was an exception, with both peaks occurring at 24-29 weeks. Play walk did not have an obvious peak. Its frequency was consistently low. The ages at which peaks occurred are shown in Table 22 below.

Table 22: Ages of peak frequency

locomotor-pattern	non-play peak age block	play peak age block
walk	18-23, 24-29	———
run	12-17 24-29	24-29
jump	24-29	24-29
climb-up	18-23	24-29
climb-down	18-23, 24-29	30-41
swing/hang	18-23	30-41
sloth-like	18-23	30-41

With most play locomotor patterns, except climb-down, the increase to peak frequency was quite sudden compared with the preceding trend. Except for jump, a similar step did not occur at the same age in the non-play equivalents. Such a step therefore does not represent a general increase in a locomotor pattern's frequency. It was brought about by a change in the proportion of occurrences which were playful. These changing proportions are seen more easily in Figures 76 to 82 where frequency of intervals with a play locomotor pattern are expressed as a percentage of all intervals with that locomotor pattern.

The same caution should be applied when interpreting these Figures as was applied in the previous chapter to Figure 61a; but the ranges at

24-29 weeks are clearly outside the ranges at 18-23 weeks which supports the claims for sharp increases between these ages.

Walk, Figure 76

The proportion of walking which was in play was always low, although there was a gradual increase over the whole infant age range.

Run, Figure 77

The proportion increased until 54-65 weeks, after which there was a fall. The increase was particularly marked between 18-23 weeks and 24-29 weeks.

Jump, Figure 78

After falling between 6-11 weeks and 18-23 weeks the proportion increased sharply at 24-29 weeks. It continued to rise gently up to 66-77 weeks and then decreased to its lowest level at 78-89 weeks.

Climb-up, Figure 79

Between 12-17 weeks and 18-23 weeks the proportion remained constant and low but there was a prominent increase at 24-29 weeks to a plateau. A further increase occurred at 45-53 weeks.

Climb-down, Figure 80

The same trends are shown as for climb-up except that the increase at 24-29 weeks is less prominent.

Swing /hang and sloth-like progression, Figures 81 and 82

The proportions were low until 24-29 weeks but a major increase occurred at 30-41 weeks which continued less steeply through the rest of the infant age range.

It should be noted, however, that swing/hang and sloth-like progression were rare. Each point in these Figures was calculated from a very small sample and so it is unreliable.

A change of terms

These results can be discussed more easily if I change phraseology slightly. Until now I have referred to locomotor patterns being performed in play or in non-play, and to play and non-play versions of the same loco-

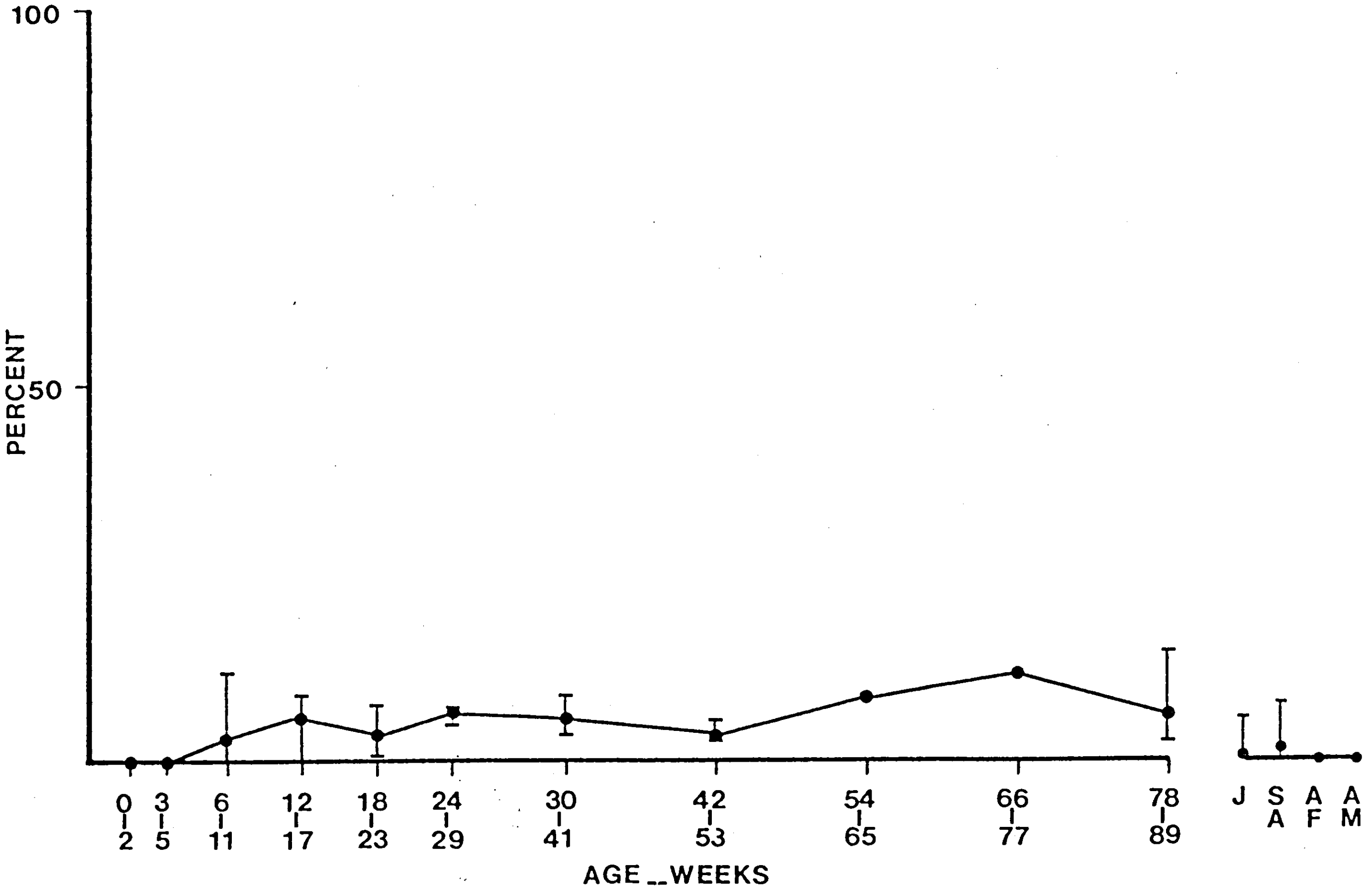


Figure 76. The percentage of intervals with walk which contained play walk.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

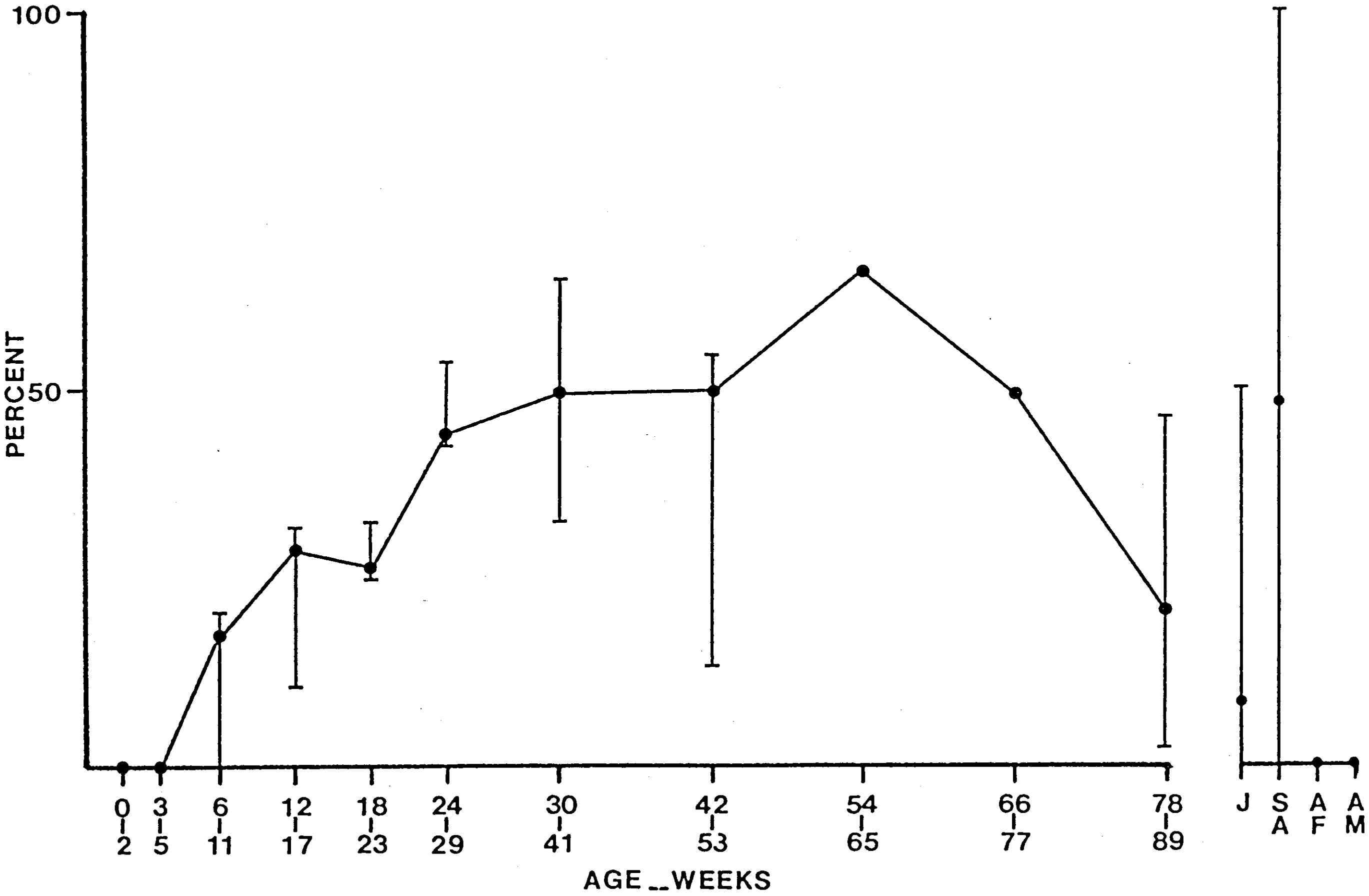


Figure 77. The percentage of intervals with run which contained play run.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

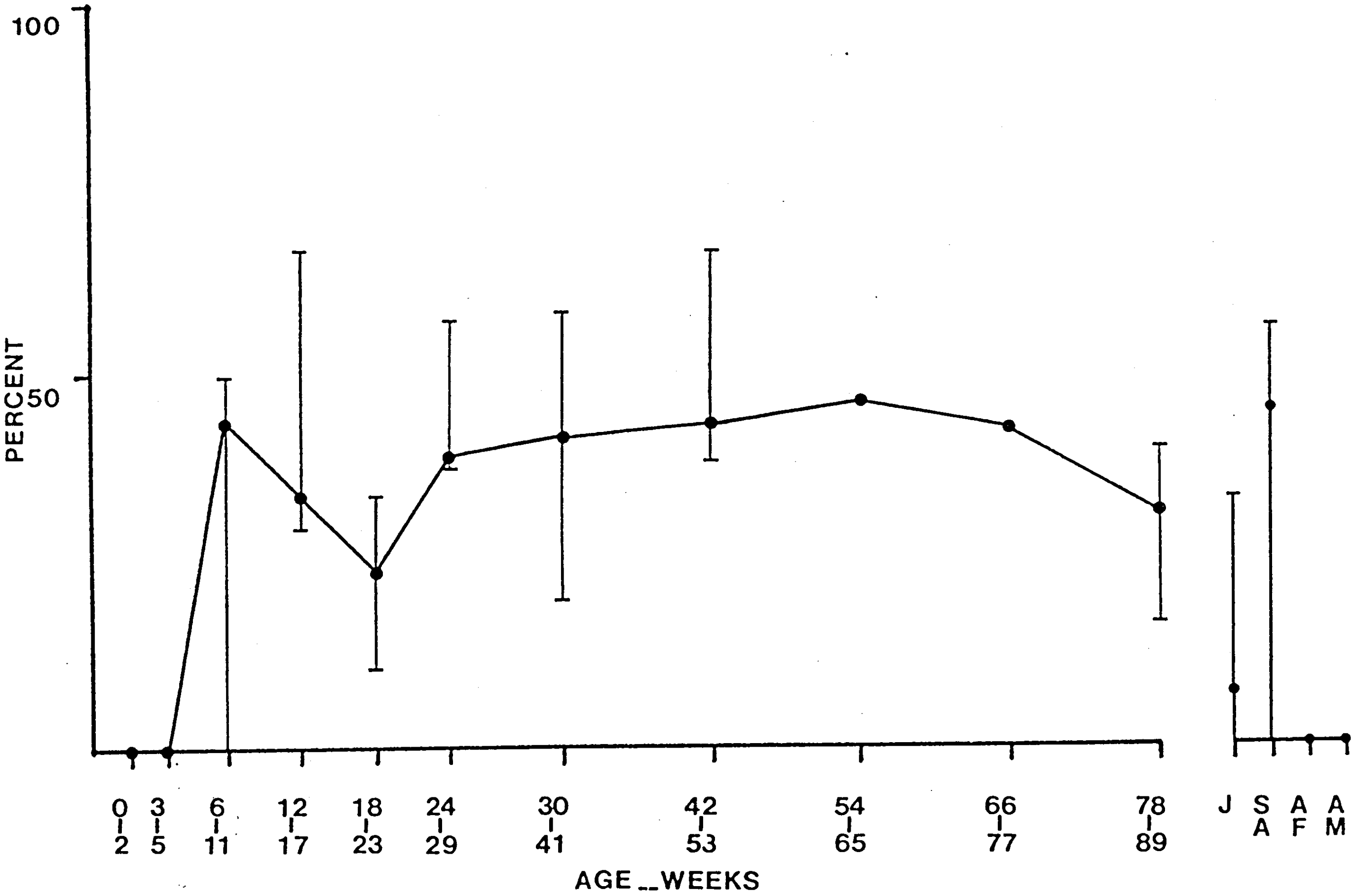


Figure 78. The percentage of intervals with jump which contained play jump.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

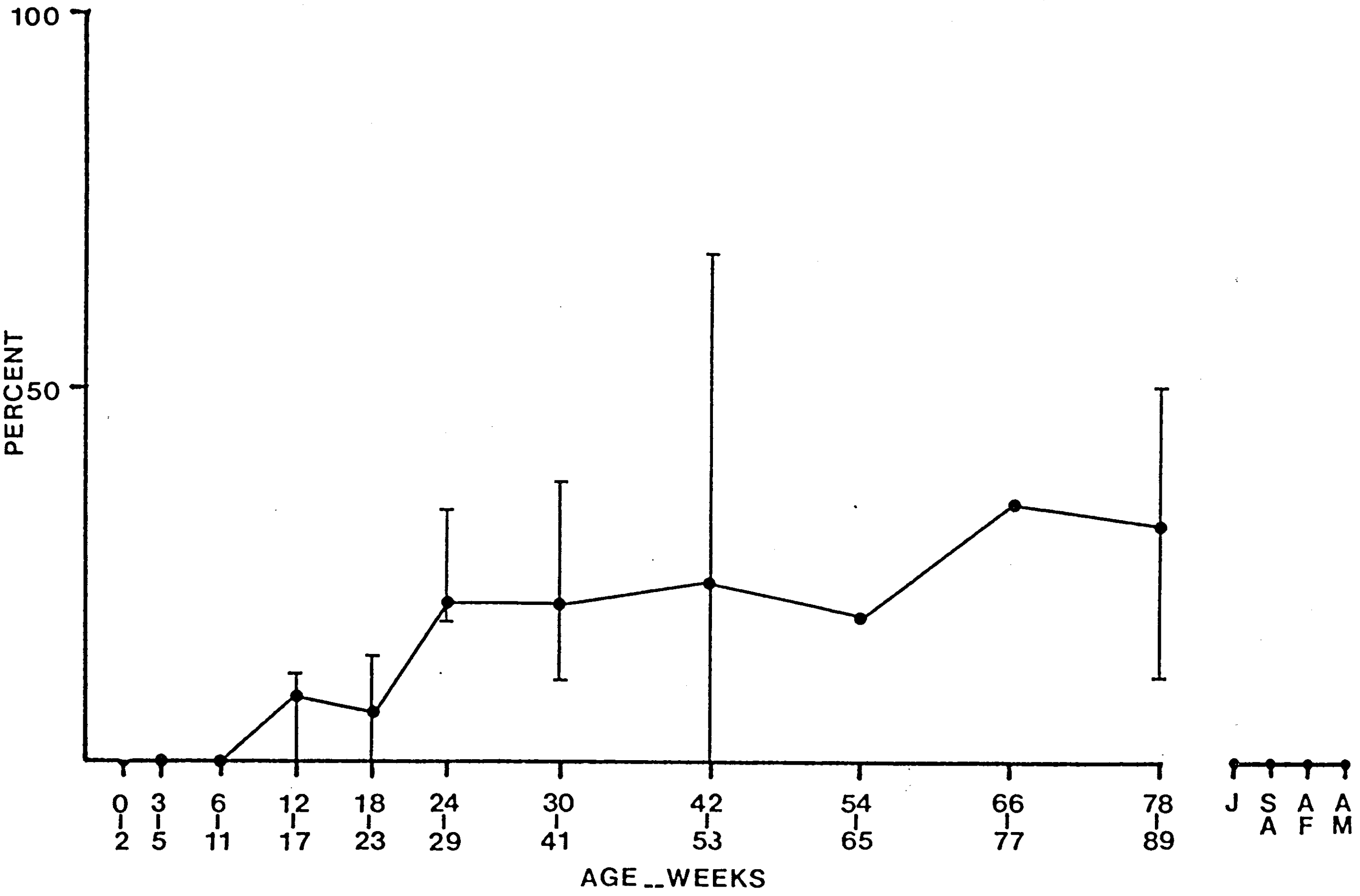


Figure 79. The percentage of intervals with climb-up which contained play climb-up.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

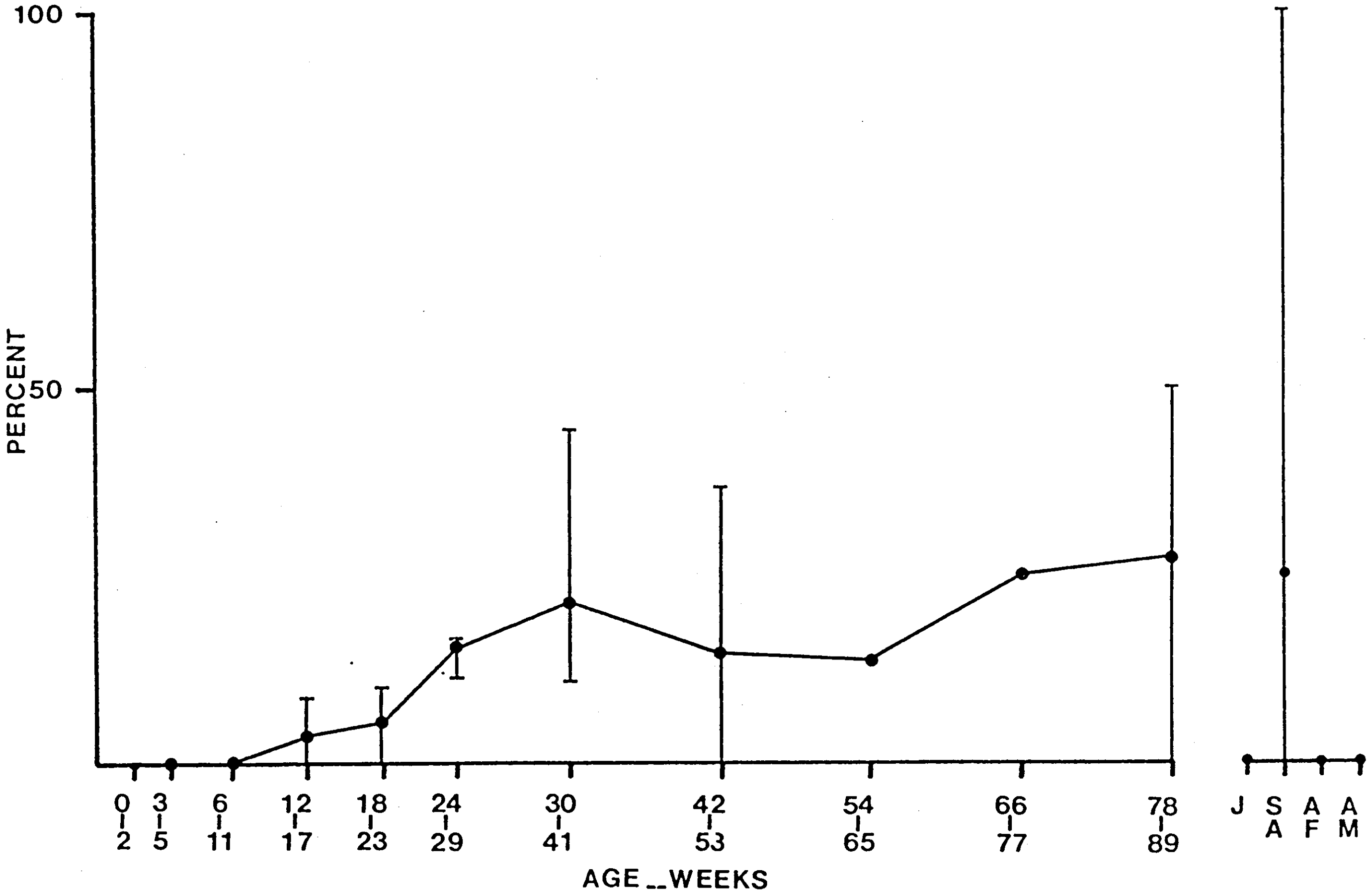


Figure 80. The percentage of intervals with climb-down which contained play climb-down.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

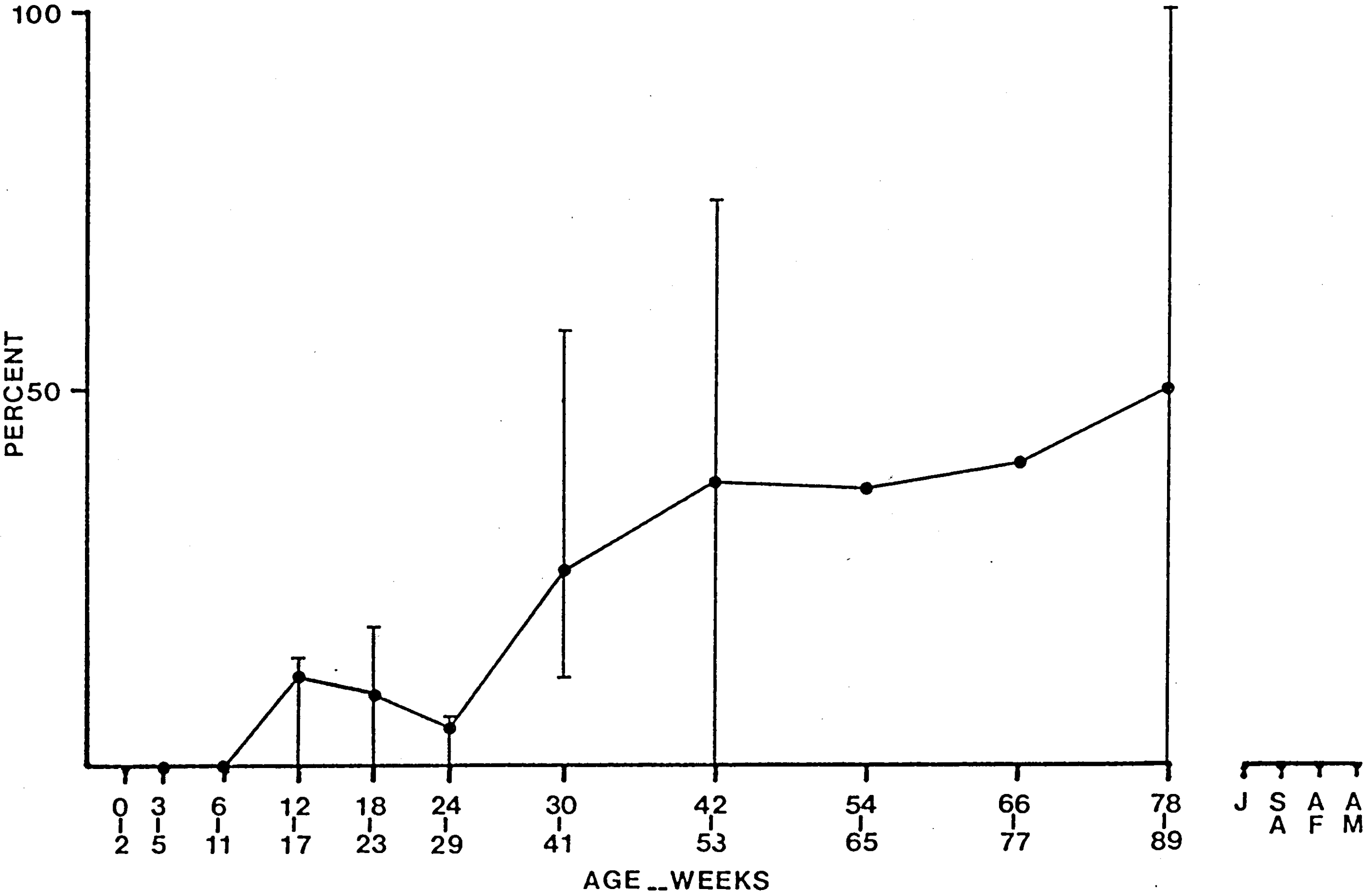


Figure 81. The percentage of intervals with swing/hang which contained play swing/hang.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

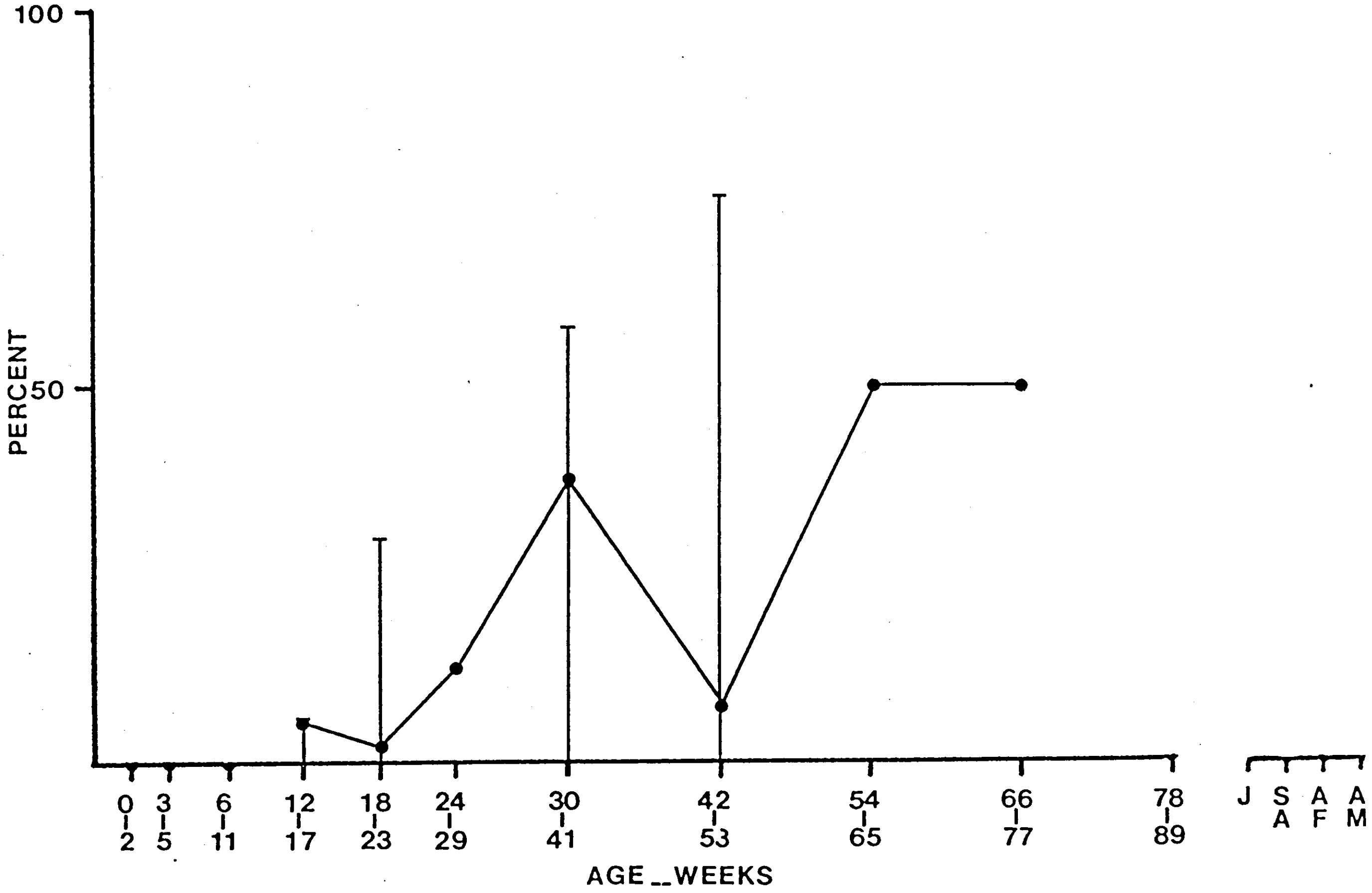


Figure 82. The percentage of intervals with sloth-like progression which contained play sloth-like progression.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

motor patterns. These are conventions which allow sentences to be kept simple, but they do carry certain implications about play. Saying that a locomotor pattern was performed "in play" or "in non-play" might be construed as meaning that play and non-play were distinct motivational states. The terms play locomotor pattern and non-play locomotor pattern suggest that the patterns are essentially different. Both of these implications might be correct but they cannot be substantiated in this study. It would be more helpful to use terms which describe more exactly what the data are. A locomotor pattern was scored as "play locomotor pattern" if the subject performed it at the same time as it performed other actions, signals or postures which met the criteria for play used in this study. That is, the locomotor pattern was performed coincidentally with play signals. I shall therefore refer to "locomotor patterns with or without play signals" to enable an objective statement to be made without overtones of motivation or undefinable differences.

Chalmers (1980a) has used the term "play markers" to denote behavioural components whose presence are sufficient though not necessary for identifying behaviour as playful. I am not adopting his exact term because it included rough and tumble as a marker of a play bout; and that is clearly more than just a signal.

Discussion

All locomotor patterns showed an increase with age in the proportion accompanied by play signals. Chalmers (1980a) described a similar trend in wild baboons, although it was measured differently. He found that locomotor patterns, particularly jumping, climbing and "run-to" (running towards another baboon) became increasingly more frequent in social encounters containing play markers compared with encounters without play markers. This effect was most marked with run-to between 16 weeks and 28 weeks of age.

In the present study the increase was gradual with walk; but run, jump, climb-up, climb-down, swing/hang and sloth-like progression each had a conspicuous step-up in their proportion with play markers. With run, jump, climb-up and climb-down the increase happened at 24-29 weeks. With swing/hang and sloth-like progression it was in the next age block, 30-41 weeks, although those results must be considered unreliable.

The following questions are raised: can any significance be attached to the age 24-29 weeks such that infants performed play signals more frequently then, with certain locomotor patterns, than they did before? What benefits could be gained from this? Why should run, jump, and climbing show a relatively sharp increase and not walk?

Consider some other changes which were particularly noticeable at 24-29 weeks (see Tables 17 and 19).

1. Black natal coat had disappeared. This was the first age block in which infants were completely brown.
2. For the first time infants were supported by their mothers (on mother) in less than 50% of intervals and out of contact with her in more than 50% of intervals; although the latter measure had changed very little since the previous age block.
3. Contact makes and breaks became less frequent and there was a sharp increase in the length of time infants spent off mother in each bout.
4. Clambering on mother or other adults became very infrequent.
5. There may have been more dorsal riding, or infants may have moved independently of their mothers when the mothers changed position; but these are conjectures.
6. Objects were manipulated preferentially out of contact with mother.
7. Long bout mouthing of objects reached a plateau.

Numbers 2,3,4 and 5 are associated with increasing independence from mother. Number 6 may be associated with increasing dependence on solid food. Number 7 might also be associated with changing diet although in Chapter 5 it was argued that long bout mouthing was only weakly associated with feeding.

Infants might have performed play signals with locomotor patterns more at 24-29 weeks because there were increased opportunities for social play as a result of greater independence. Increasing use of solid food could also have lead to more play opportunities as infants came into contact with others when foraging. But these do not account for the differential performance of play signals with walk and the other locomotor patterns.

I should like to examine the possibility that the increase was associated with the completion of the colour change from black to brown at 24-29 weeks. Safron was recorded "completely yellow/brown" at 25 weeks and Deag was "completely brown" at 28 weeks. Their individual results (Figure 61b) are consistent with the notion that the behaviour change was associated with the colour change.

Brown infants may have derived more benefit by giving play signals when running, jumping, climbing and swinging or hanging than they had done while they still had black natal coats. Benefit to be gained from giving play signals with walking may not have increased in the same way.

Running, jumping, climbing and acrobatics are more vigorous and conspicuous than walking, and it is likely that they are important components of physical training. Such vigorous activity might therefore be beneficial. On the other hand, it could be socially disruptive. From casual observation of older baboons, I gained the impression that when individuals were suddenly very active in the vicinity of others, say, chasing or being chased in an aggressive encounter, the others became agitated themselves, perhaps joining the chase, threatening others or simply moving away. Young baboons live within a social group whose continued integrity and cohesion is in their own survival interests. It is surely maladaptive to engage frequently in behaviour which stimulates unfruitful aggression from and among other group members or which causes unprofitable activity, and hence energy wastage, by others. Thus vigorous activity may have disadvantages as well as advantages.

It is likely that there are strategies which minimize the disadvantageous effects and allow benefits to be gained. Possession of a black natal coat may be one such strategy; giving play signals may be another.

I suggest that when a black infant runs and leaps among a group of older baboons, either in solo activity or in a social encounter, its black coat inhibits negative social responses from them. When the natal coat is completely replaced by brown that inhibitory signal is lost and a running and leaping brown infant then becomes disruptive. In order to continue physical training the infant performs play signals, at least in social encounters, such as the play-face and locomotor rotational movement, and these signals transmit the same inhibitory message as did the black natal coat. Walking may be less disruptive in all contexts and at all ages than the more vigorous locomotor patterns. The need to inhibit reactions from others when walking may not change so much when the colour changes.

The same principle might apply to a social dyad. When a black infant and an older baboon engage in a social encounter incorporating vigorous running, jumping and climbing, the black infant is clearly not a threat to its partner and its black colour proclaims a message to that effect. Two brown baboons engaged in similar vigorous social activity may need to transmit special signals of "good will" such as the play-face and locomotor rotational movements in order to maintain the interaction. This is the metacommunication thesis of Bateson (1955). Once more, vigorous activity in social interactions would be accompanied by play signals more frequently after the colour change.

This hypothetical model is falsifiable because it generates predictions which can be tested, though not with data from this study.

A brown infant should give play signals in vigorous social encounters relatively more frequently than does a black infant.

If a brown infant does not give play signals in a vigorous encounter with another brown baboon, then the partner should be more likely to terminate the interaction than if play signals are given. However, if a black infant fails to give play signals in such an encounter, then the partner should be no more likely to terminate the interaction.

Black infants should be more likely to perform vigorous solo activity in the presence of older baboons than are brown infants. If brown infants do perform vigorous solo activity near others then, unless it is emergency behaviour such as escape or appetitive behaviour with a goal, it is likely to be accompanied by some form of signal such as locomotor rotational movement.

Oates (1982) has described juvenile and adult Nilgiri langurs (Presbytis johnii) with aberrant coat colours. In these individuals the natal brown colouration continued into later life. They did not develop the mature black, silver and brown colouring. Provided it could be shown that normal coloured individuals increasingly accompanied vigorous activity with play signals at the age of colour change (and Poirier, 1969, has stated that infants spend much time playing at that age) a langur group containing one or more aberrant specimens could provide a natural experiment for investigating the influence of coat colour. The hypothesis predicts that an infant which retains its natal colour longer than normal will cause less disruption of its group by vigorous solo or social activity than its normal coloured age mates.

Summary

It was concluded that social play did not provide the necessary context for practising locomotor patterns prior to becoming part of the general repertoire. On the contrary, infants used in play locomotor patterns which were already well established in their behaviour repertoires.

The probability that a locomotor pattern would be accompanied by play signals increased through the infant age range and for the more energetic and conspicuous locomotor patterns that increase was most marked at 24-29 weeks. The increasing frequency of play might have been due to greater independence and therefore greater opportunity, but that does not account for the difference between changes in energetic locomotor patterns and walking. A hypothetical model was suggested in which the infant colour change at 24-29 weeks was important. Infants may have been more likely to perform play signals while engaging in energetic and potentially socially disruptive locomotor patterns during social encounters, thereby reducing their disruptive effect. Some suggestions were put forward of observations which could be made in future studies of social behaviour which would test this hypothesis.

Chapter 8. Results: further measures of play development; sex differences and effects of play partners' ages

The development of play, as a unitary category, is given in terms of the proportion of total time (i.e. total observation intervals) devoted to it. This is different from previous chapters where frequencies were expressed as proportions of off-nipple intervals. It allows comparisons to be made with Owens' (1975a) and Cheney's (1978) findings on age changes in time spent playing by wild baboons.

The form of play is described using the categories: contact and non-contact play, which Harlow's school has used and which are equivalent to the "rough and tumble" and "approach-withdrawal" used by Hinde's school. Contact play is sub-divided into: close-contact wrestling, little-contact wrestling and poke/touch (see page 55f for definitions). The latter three terms are not found in other studies, but close- and little-contact wrestling are equivalent to two of the categories used by Owens (1975a).

Other points of comparison with Owens' and Cheney's studies are provided by the analysis of sex differences in amount and form of play and of the effects of age differences within play dyads.

1. Age at first play

Table 23 gives details of the earliest records of play for 6 infants born during the study period. The earliest age at which play was observed (although this was not necessarily the first instance of play) was 18 days. Five out of the 6 infants observed at 6-11 weeks played during or before that age and by 12-17 weeks all of them had played.

2. Development trends

Age changes in the proportion of total time given to play are shown in Figure 83. Intervals in which play occurred are expressed as a percentage of total observation intervals. There appear to be two phases of increasing frequency: firstly, from 0-2 weeks to 12-17 weeks, which is followed by a period with no change extending through 18-23 weeks, and secondly a gradual rise to a plateau at about 30-41 weeks. The frequency fell once more after about 42-53 weeks.

Table 23. Records of early play

RECORDS OF EARLY PLAY

		POKE/ TOUCH CONTACT PLAY	CLOSE-CONTACT WRESTLE	LITTLE-CONTACT WRESTLE	NON-CONTACT PLAY
BOOBY ANUBIS FEMALE	AGE OF FIRST RECORD	18 days			
	PARTNER	BLACK INFANT			
	COMMENTS	SUBJECT WAS ON MOTHER			
KENYA ANUBIS FEMALE	AGE OF FIRST RECORD	48 days	19 days	49 days	49 days
	PARTNER	BLACK INFANT	MOTHER	BLACK INFANT	BLACK INFANT
	COMMENTS			Recorded during same play bout	WALKING
GILIAN ANUBIS FEMALE	AGE OF FIRST RECORD	102 days			103 days
	PARTNER	NOT RECORDED			
	COMMENTS	RECORDED ONLY AS CONTACT PLAY			RUNNING
DEAG ANUBIS FEMALE	AGE OF FIRST RECORD	61 days			61 days
	PARTNER	NOT RECORDED			JUMPING
	COMMENTS	RECORDED ONLY AS CONTACT PLAY			ALSO SAME DAY: RUNNING WALKING
SAFRON CYNOCEPHALUS MALE	AGE OF FIRST RECORD	45 days			45 days
	PARTNER	NOT RECORDED			
	COMMENTS	RECORDED ONLY AS CONTACT PLAY			JUMP AND WALK
GUSH CYNOCEPHALUS MALE	AGE OF FIRST RECORD		79 days		
	PARTNER		BROWN INFANT		
	COMMENT		SUBJECT WAS ON MOTHER		

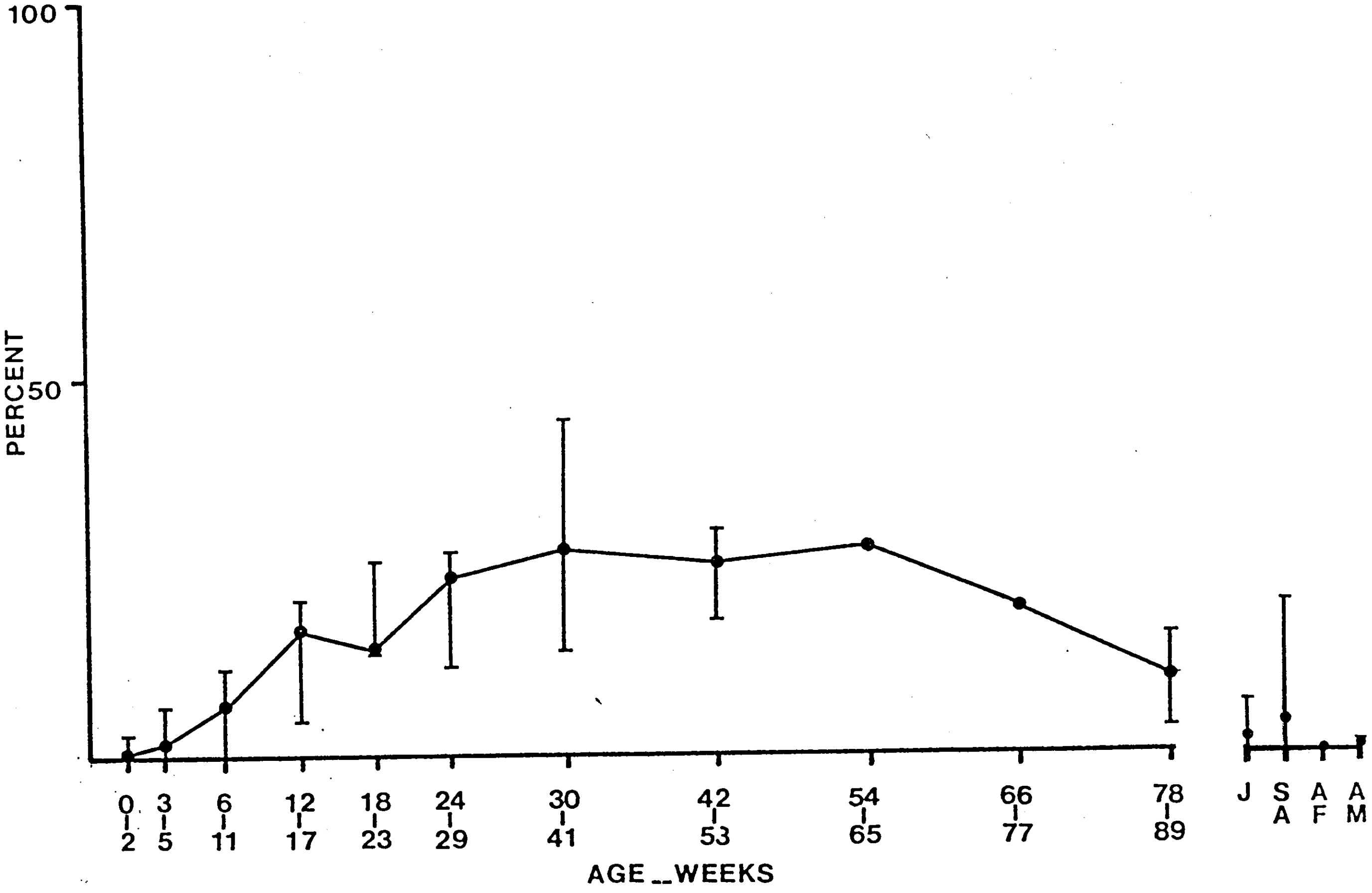


Figure 83. The percentage of total intervals which contained play.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

For comparison, age changes in the percentage of total intervals containing non-play are shown in Figure 84. Clambering on mother has been excluded from the non-play activity score so that the resulting measure is independent of measures of behaviour on mother. This allows the discussion to consider the age changes in relation to quite separatebehaviour on mother.

As with play, the non-play frequency increased between 0-2 weeks and 12-17 weeks, but the period with little change extended further to 24-29 weeks. The frequency then increased to a maximum at 42-53 weeks.

3. Sex differences in the amount of play

It has not been possible to analyse the data rigorously for sex differences. There were too few subjects to provide enough pairs matched for age. Some data are presented here although no firm conclusions can be made. Two age ranges were defined (6-23 weeks and 24-53 weeks) and the data within them analysed separately. This was an attempt to separate age effects from sex differences, but it is not satisfactory. Samples have become very small and there are still big age differences within each age range. Data have been lumped to give one measure per subject per age range. The measure is the percentage of total intervals in which play occurred. The results are shown in Tables 24 and 25. Inspection reveals no sex differences. In order to increase the sample size the two age ranges have been combined, but at the price of possibly increasing the effects of age differences. Table 26 shows that there are no clear sex differences within this enlarged group (Mann Whitney $U = 8$, $p = 0.36$).

4. Changes in the form of play

Contact and non-contact play

In this analysis changes in the form of play are described in terms of contact and non-contact between partners.

Figure 85 shows changes in the proportion of off-nipple intervals which contained contact and non-contact play.

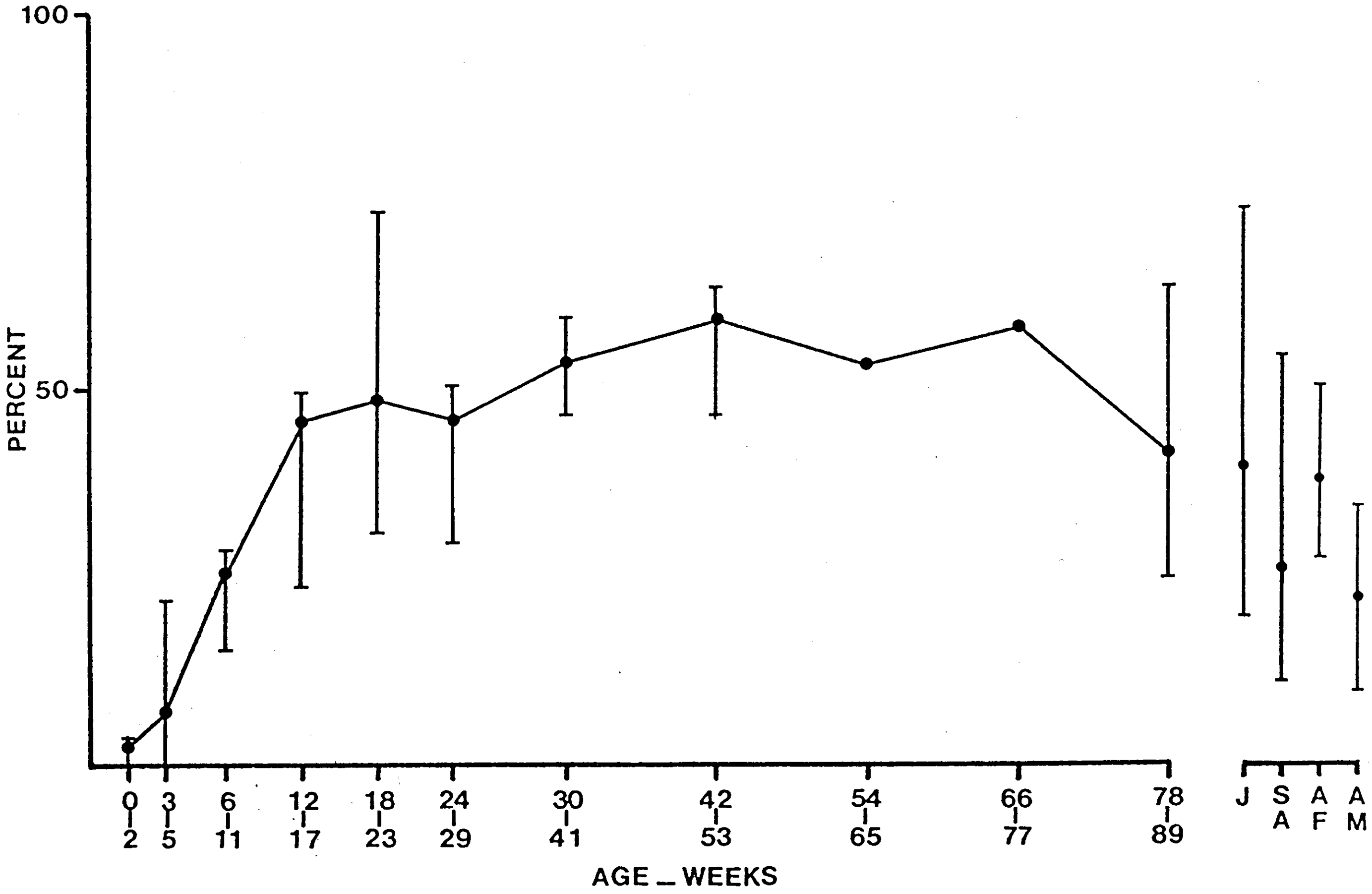


Figure 84. The percentage of total intervals which contained non-play excluding clambering on mother.

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

Comparison between sexes in the proportion of 30-second intervals containing play

Table 24

Percentage of total intervals in which play occurred between 6 and 23 weeks.

	male	rank	female	rank
Safron	13.26	4		
Gush	5.13	1		
Gilian			6.52	2
Deag			13.31	5
Kenya			11.39	3

Table 25

Percentage of total intervals in which play occurred between 24 and 53 weeks.

	male	rank	female	rank
Safron	29.79	5		
Aubrey	30.63	6		
Sigmund	13.75	1		
Capone	19.61	3		
Deag			17.18	2
Viola			19.66	4

Comparison between sexes in the proportion of 30-second intervals containing play

Table 26

	male	rank	female	rank
Safron	18.35	6		
Gush	5.12	1		
Sigmund	13.75	4		
Capone	19.61	7		
Aubrey	30.63	9		
Gilian			6.52	2
Deag			14.31	5
Kenya			11.39	3
Viola			19.66	8

Percentage of total intervals in which play occurred between 6 and 53 weeks.

Mann Whitney U for difference between sexes = 8.

$n_1 = 4$

$n_2 = 5$

$p = 0.365$
not significant.

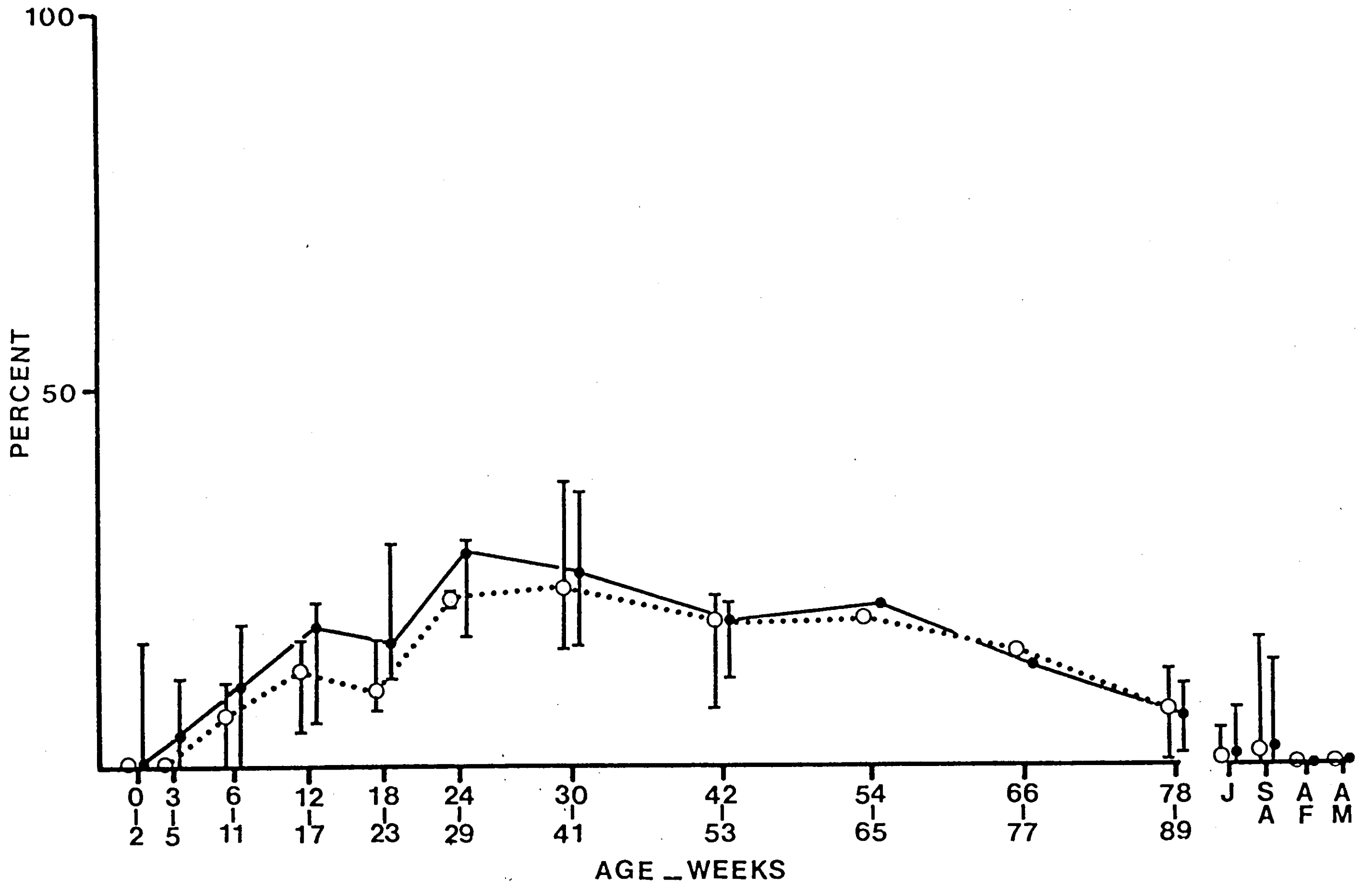


Figure 85. The percentage of off-nipple intervals which contained contact play and non-contact play.

see ●——● contact play
○·····○ non-contact play

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominators of weighted means.

There are three points to be made:

(1) contact play appeared earlier than non-contact play 0-2 weeks versus 6-11 weeks);

(2) the two development trends are very similar (Spearman $r_s = +0.97$, $N = 10$, $p < 0.001$);

(3) the weighted mean percentage of contact play is higher

than the weighted mean precentage of non-contact play until 30-41 weeks. After that age the weighted mean percentages are approximately equal.

Despite the weighted means remaining separate up to and including 30-41 weeks, the ranges overlap. Therefore it is not possible to conclude that contact-play and non-contact play had different frequencies.

The data from individual subjects were examined. Two age ranges were defined, 6-41 weeks and 42-89 weeks, and within each range the data from each subject were lumped. Two hypotheses were tested using the Wilcoxon matched-pair signed-ranks test:

(1) in the age range 6-41 weeks the percentage frequencies of contact play are higher than those of non-contact play;

(2) in the age range 42-89 weeks there is no difference between the frequencies of contact play and non-contact play.

The data for these tests are given in Table 27. Both hypotheses are supported.

Changes in the relative proportion of the two types of play are made more apparent in Figure 86, where intervals with each type of play are expressed as percentages of intervals with any play. Until 3-5 weeks contact play was the only form. When non-contact play began at 6-11 weeks there was a corresponding fall in the proportion of play that was contact play. After that age this proportion decreased only very slightly over the rest of the infant age range. During that time non-contact play increased in its proportional contribution to play. Most of this increase happened through 24-29 weeks to 30-41 weeks.

Types of contact play

Three styles of contact play were recognized:

close-contact wrestling;
little-contact wrestling;
poke/touch

Age changes in their frequency are shown in Figures 87 to 89 where

Table 27a and b - Wilcoxon matched-pairs signed-ranks test of the difference between the frequency of non-contact and of contact play (frequency = % off-nipple intervals)

Table 27a

Age range 6-41 weeks

N = 7

	non-contact %	contact %	d	rank of d
Safron	14.8	23.0	-8.2	-7
Aubrey	37.7	36.0	+1.7	+2
Gush	3.4	6.7	-3.3	-5
Gilian	6.0	9.0	-3.0	-3
Sigmund	15.5	15.9	-0.4	-1
Deag	13.1	16.3	-3.2	-4
Kenya	7.8	12.4	-4.6	-6

positive sum +2

negative sum -26

H_1 - % contact play $\neq$ % non-contact play

Two-tail test T = 2 $p < 0.05$

Table 27b

Age range 42-89 weeks

N = 6

	non-contact %	contact %	d	rank of d
Safron	22.7	21.4	+1.3	+3
Aubrey	19.0	19.71	-0.71	-2
Capone	7.5	11.3	-3.8	-5
Rover	0.6	1.3	-0.7	-1
Deag	13.4	11.3	+2.1	+4
Viola	19.4	14.0	+5.4	+6

positive sum +13

negative sum -8

H_1 - % contact play $\neq$ % non-contact play

Two tail test T = 8 $p > 0.05$

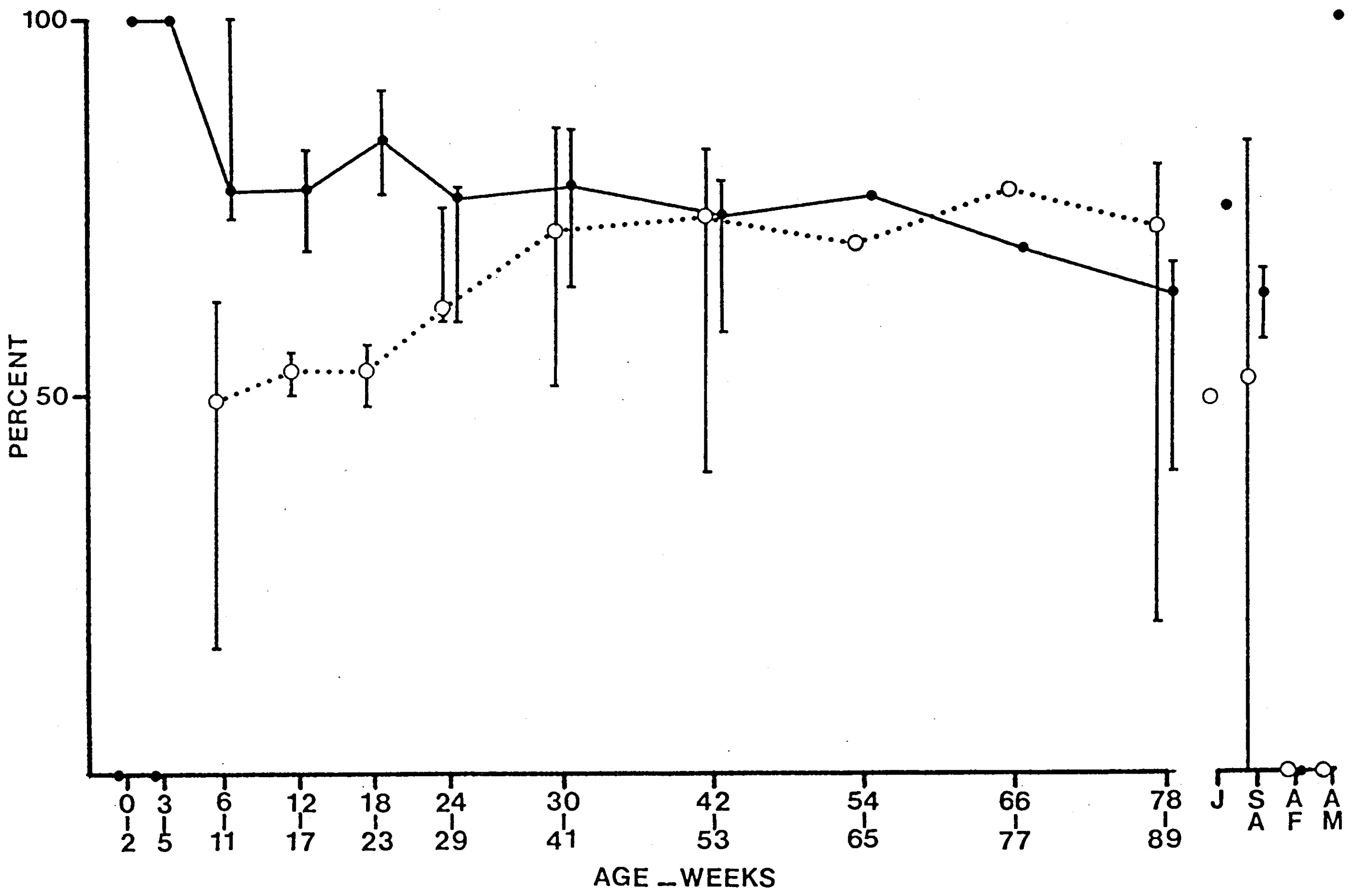


Figure 86. The percentage of intervals with play which contained contact play and non-contact play.

●——● contact play
○•••••○ non-contact play

For key to symbols see Appendix I.

Sample sizes:

see Appendix II for the number of subjects at each age;
see Appendix III, Table A, for the denominator of weighted means.

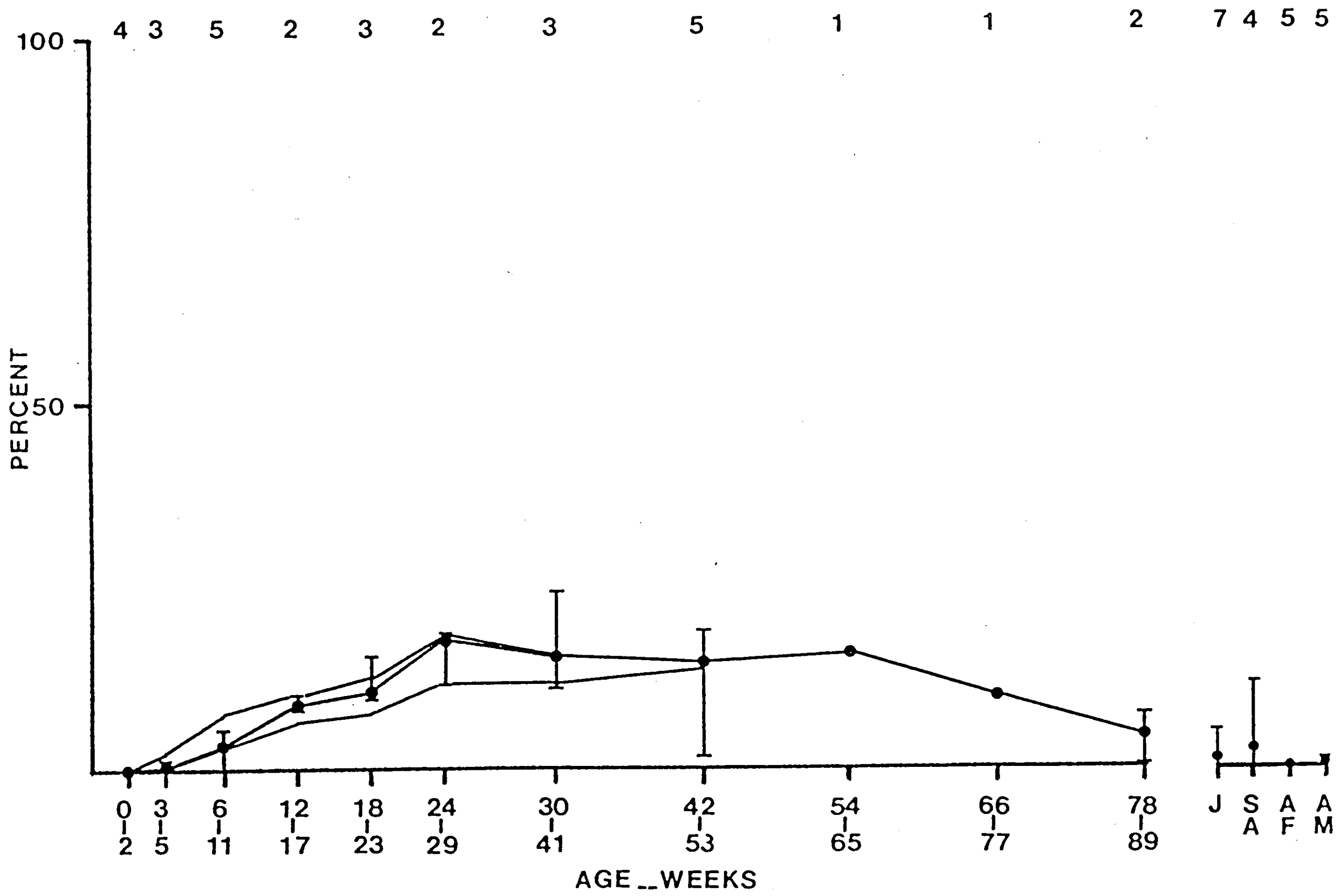


Figure 87. The percentage of off-nipple intervals which contained close-contact wrestling.

For key to symbols see Appendix I.

Sample sizes:

the number of subjects at each age is shown above the figure;
see Appendix III, Table A, for the denominators of weighted means.

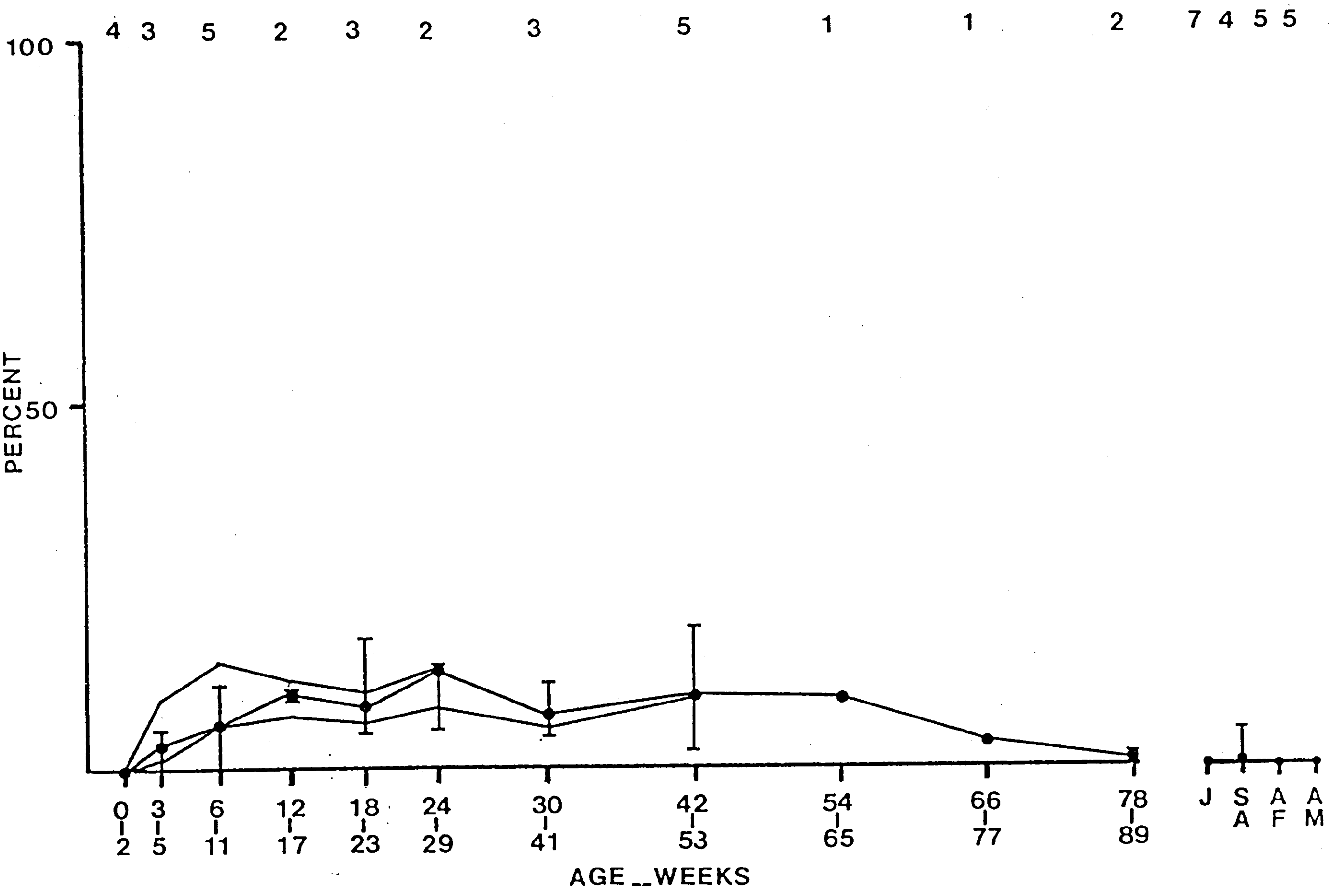


Figure 88. The percentage of off-nipple intervals which contained little-contact wrestling.

For key to symbols see Appendix I.

Sample sizes:

the number of subjects at each age is shown above the figure;
see Appendix III, Table A, for the denominators of weighted means.

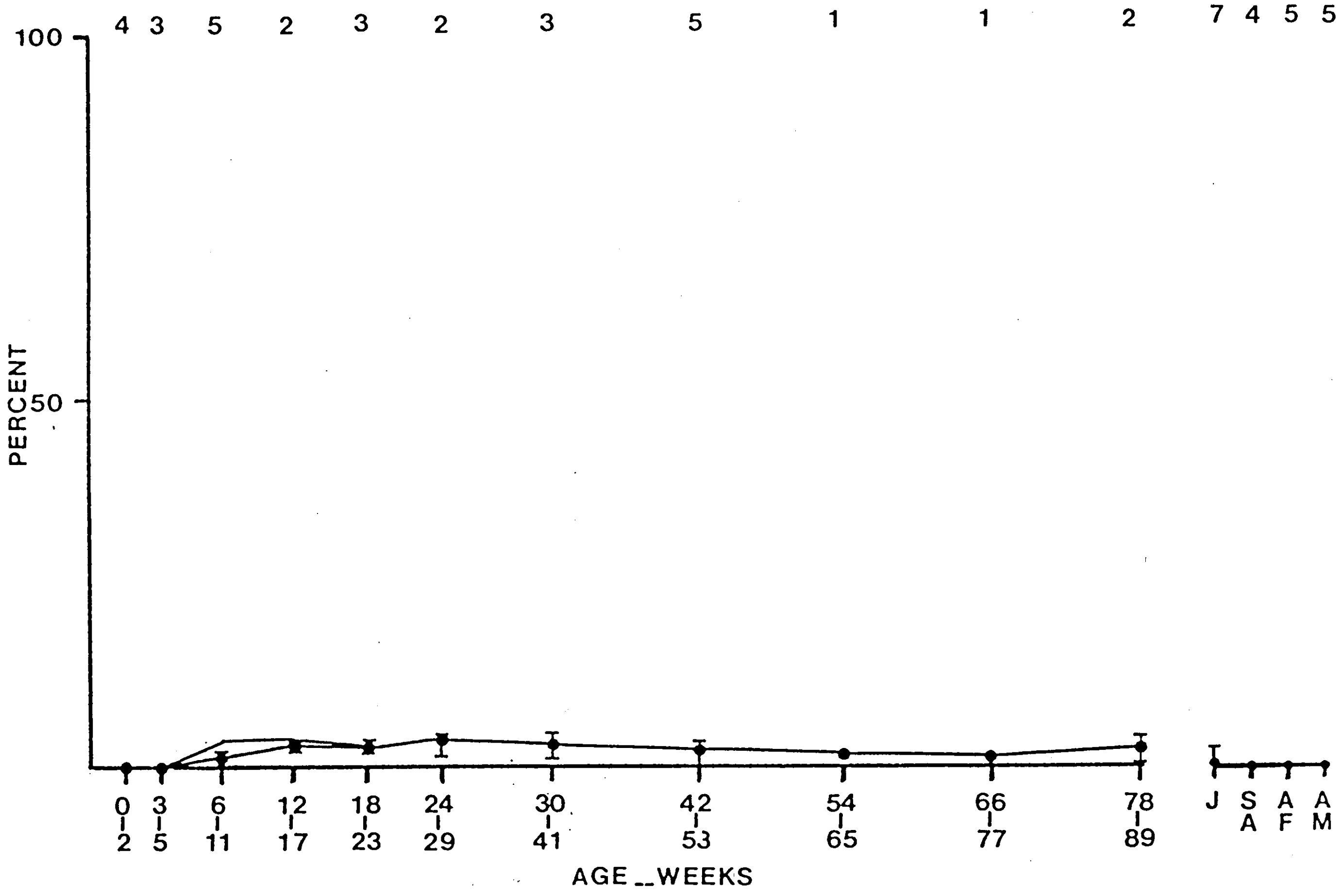


Figure 89. The percentage of off-nipple intervals which contained poke/touch.

For key to symbols see Appendix I.

Sample sizes:

the number of subjects at each age is shown above the figure;
see Appendix III, Table A, for the denominators of weighted means.

one-zero frequencies are expressed as percentages of intervals in which infants were off-nipple.

Close-contact and little-contact wrestling were first seen at 3-5 weeks but poke/touch did not appear until 6-11 weeks. Close-contact was more frequent than little-contact up to 6-11 weeks but at 12-17 weeks and 18-23 weeks they were equally frequent. From 24-29 weeks onwards little-contact was the more frequent. At all ages except 78-89 weeks poke/touch occurred least frequently, but in that final age block close-contact became the least frequent.

The relative frequency changes are shown more clearly in Figure 90 where frequencies are expressed as percentages of intervals with any contact play. It can now be seen that close-contact decreased proportionately throughout the infant age range while little-contact increased. Poke/touch remained fairly constant except for a sharp rise at 78-89 weeks.

5. Sex differences in contact and non-contact play

The data were examined for sex differences in the proportional contributions of contact and non-contact play to all play. The same caveats apply to the interpretation of this analysis as applied to the analysis above of sex differences in the frequency of play. Only the complete sample was used, that is, all subjects within the ages 6-53 weeks.

Three hypotheses were tested:

(1) that the play of one sex contained a greater proportion of contact than the play of the other sex;

(2) that the play of one sex contained a greater proportion of non-contact than the play of the other;

(3) that one sex had proportionately more of one type of play than of the other type.

Tables 28 and 29 show data relevant to hypotheses 1 and 2 respectively. Table 28 shows, for each subject, the percentage of play intervals which contained contact play. Table 29 shows the percentage of play intervals containing non-contact play. For each table the Mann Whitney U test was used to compare percentages between the sexes. Neither case showed

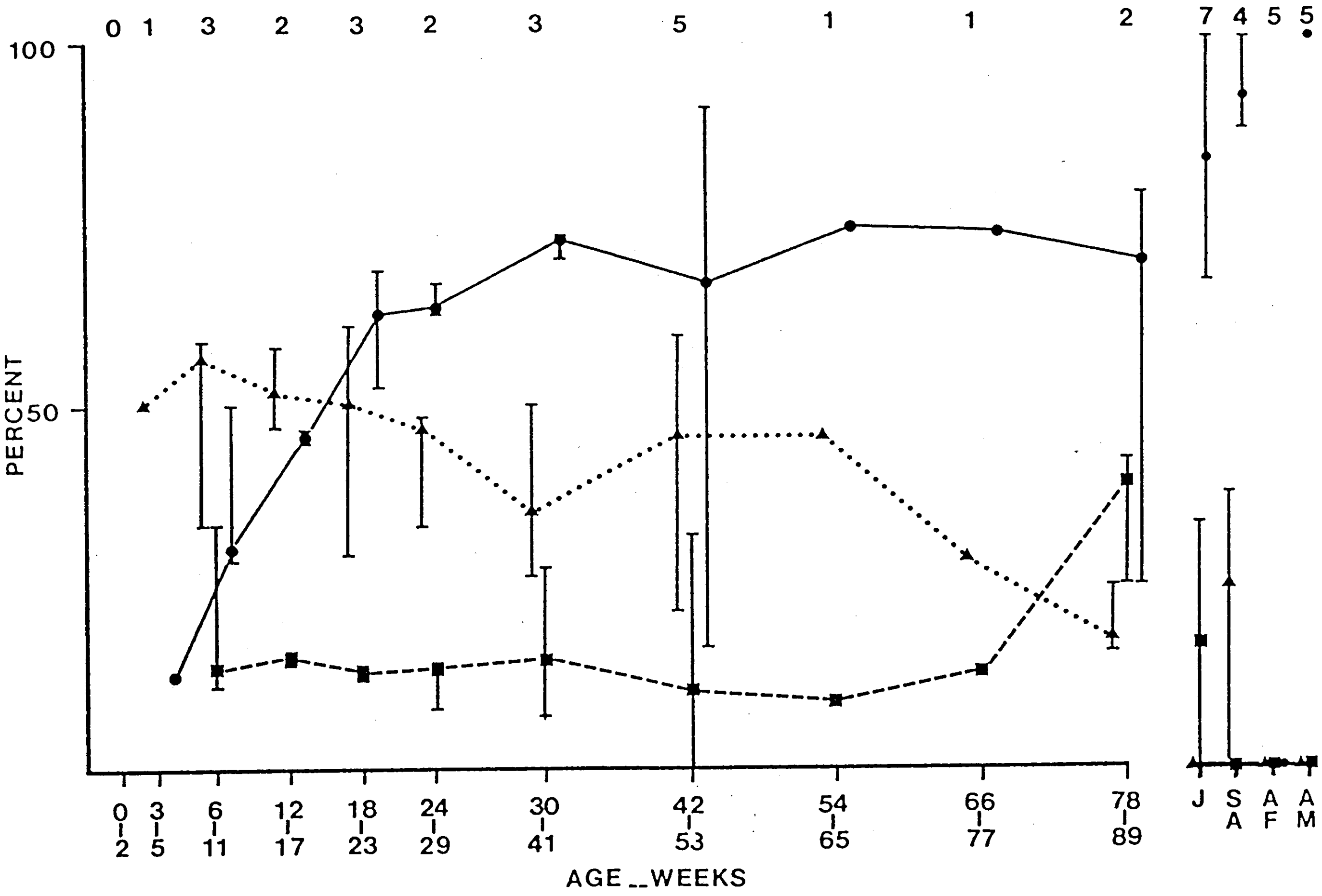


Figure 90. The percentage of intervals with wrestling which contained close-contact, little-contact and poke/touch.

▲······▲ close-contact wrestle
●——● little-contact wrestle
■----■ poke/touch

For key to symbols see Appendix I.

Sample sizes:

the number of subjects at each age is shown above the figure;
see Appendix III, Table A, for the denominators of weighted means.

Comparison between sexes in the composition of play

Table 28

	male	rank	female	rank
Safron	79.86	6		
Gush	100	9		
Sigmund	83.33	7		
Capone	60.00	1.5		
Aubrey	79.42	5		
Gilian			75.0	4
Deag			71.45	3
Kenya			88.31	8
Viola			60.00	1.5

Percentage of intervals with play which contained contact play between 6 and 53 weeks.

Mann Whitney U for difference between sexes = 6.

$n_1 = 4$

$n_2 = 5$

$p = 0.206$
not significant

Comparison between sexes in the composition of play

Table 29

	male	rank	female	rank
Safron	55.10	4		
Gush	50.00	2.5		
Sigmund	81.25	8		
Capone	40.00	1		
Aubrey	77.99	7		
Gilian			50.00	2.5
Deag			59.22	6
Kenya			55.19	5
Viola			82.86	9

Percentage of intervals with play which contained non-contact play between 6 and 53 weeks.

Mann Whitney U for difference between sexes = 7.

$n_1 = 4$

$n_2 = 5$

$p = 0.278$
not significant

significant sex differences.

Table 30 shows data relevant to hypothesis 3. For each subject the relative contribution to play of contact compared with non-contact is expressed as the difference between their proportions (contact as percentage of all play minus non-contact as percentage of all play). These differences were compared between sexes using the Mann Whitney U test. There was no significant difference. No evidence was found to support any of the hypotheses regarding sex differences in the form of play.

6. The effect of partners' relative ages on the form of play

Play partners were frequently of very different ages. It was thought that the age difference might have influenced the proportions of contact and non-contact in play.

Three infant age ranges were defined: 6-23 weeks, 24-29 weeks and 50-89 weeks. These ranges were meaningful in that 23 weeks marked the end of colour transition and 49 weeks was the last age that any infant was recorded on-mother. What is more, the data fell easily into three blocks. Data from several subjects were combined in each block: 6-23 weeks, 3 subjects; 24-29, 4 subjects; 50-89, 4 subjects. The partnerships analysed were those in which the subject animal was within one of these three age blocks and the partner was 6-23 weeks, 24-29 weeks, 50-89 weeks, juvenile, sub-adult, adult or the mother. No data were available for subjects of 24-49 weeks playing with partners of 6-23 weeks. The percentage of play intervals containing non-contact and the percentage containing contact play are compared in Figure 91 for different age pairs.

Play contained similar proportions of non-contact and contact when it was between similarly aged partners. This is particularly noticeable when the subjects were 6-23 weeks or 24-49 (Figures 91a and b respectively). As the age difference becomes greater there appears to be a greater difference between the proportions of contact and non-contact such that non-contact decreases while contact increases. This pattern is shown more

Comparison between sexes in the composition of play

Table 30

	male	rank	female	rank
Safron	+24.7	6		
Gush	+50.0	9		
Sigmund	+2.1	3		
Capone	+20.0	5		
Aubrey	+1.4	2		
Gilian			+25.0	7
Deag			+12.2	4
Kenya			+33.1	8
Viola			-22.9	1

Difference between the percentage of contact play in play and the percentage of non-contact play in play, age 6 to 23 weeks.

Mann Whitney U for difference between sexes = 10

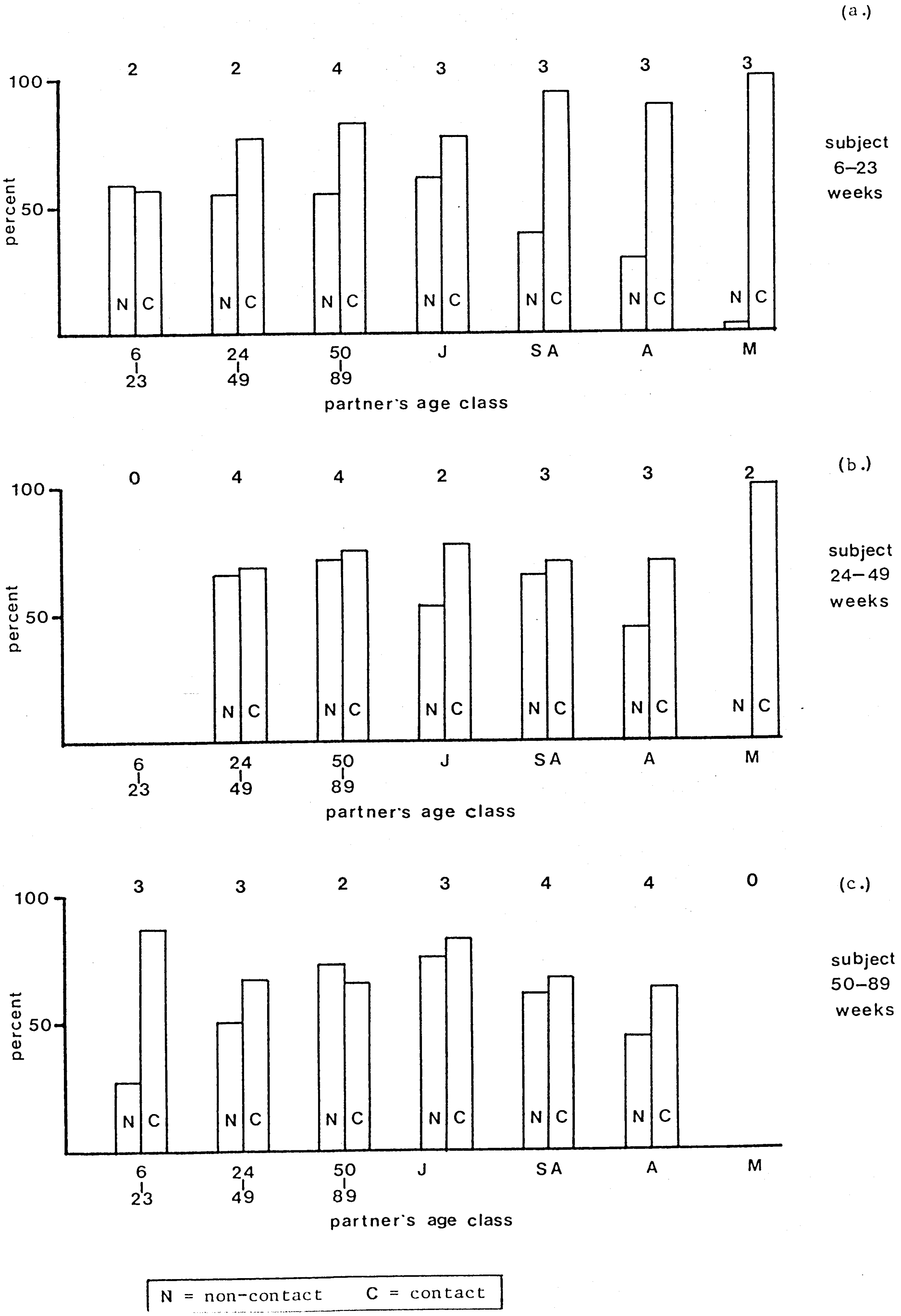
$n_1 = 4$

$n_2 = 5$

$p = 0.55$

not significant

Figure 91. The proportions of non-contact and contact in play between different age pairs.



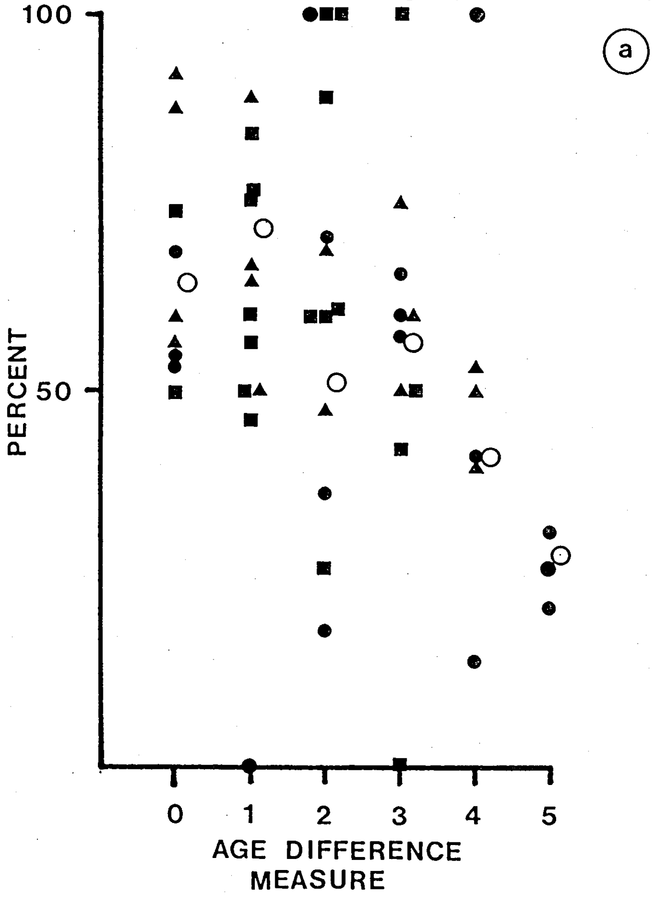
clearly by the scattergrams in Figure 92. Values have been assigned to the age classes: 6-23 = 1; 24-49 = 2; 50-89 = 3; juvenile = 4; subadult = 5; adult = 6. Age differences between partners are expressed as the differences between those values. For example, same aged partners give a difference of 0. A partnership between 24-49 weeks and a juvenile gives a difference of 2-4 = 2 as does that between 50-89 weeks and 6-23 weeks (3-1 = 2). The scattergrams show the percentage of non-contact and contact play plotted against the age difference values. Each point represents one subject at one age. Both trends are significant by the Spearman rank correlation test. As the age difference tends to increase the proportion of non-contact in play tends to decrease and the proportion of contact in play tends to increase.

During observation an impression was gained that the type of wrestling was influenced by the relative ages,or rather sizes,of the partners. It appeared that small infants tended to perform little-contact wrestling with similarly sized partners but did more close-contact wrestling with larger partners. On the other hand, larger infants and older baboons seemed to do more little-contact wrestling with all partners. The data were analysed for evidence to test this hypothesis.

Figure 93 shows the proportion of close-contact and little-contact wrestling in contact-play between different age pairs. Percentages were calculated from combined data as in Figure 91. As before, there were no data for subjects of 24-49 weeks with partners of 6-23 weeks.

The results support the hypothesis. Young infants of 6-23 weeks wrestled mostly using the little-contact style with partners who were also 6-23 weeks but with all other partners they wrestled mostly with close-contact or with approximately equal proportions of little- and close-contact. In all other partnerships there was a greater proportion of little-contact than close-contact wrestling.

Figure 92. Scattergrams showing correlation between the age difference of play partners and the percentage of non-contact (a) and contact (b) in the play of the subject animal



Closed symbols: one subject playing with one age group.

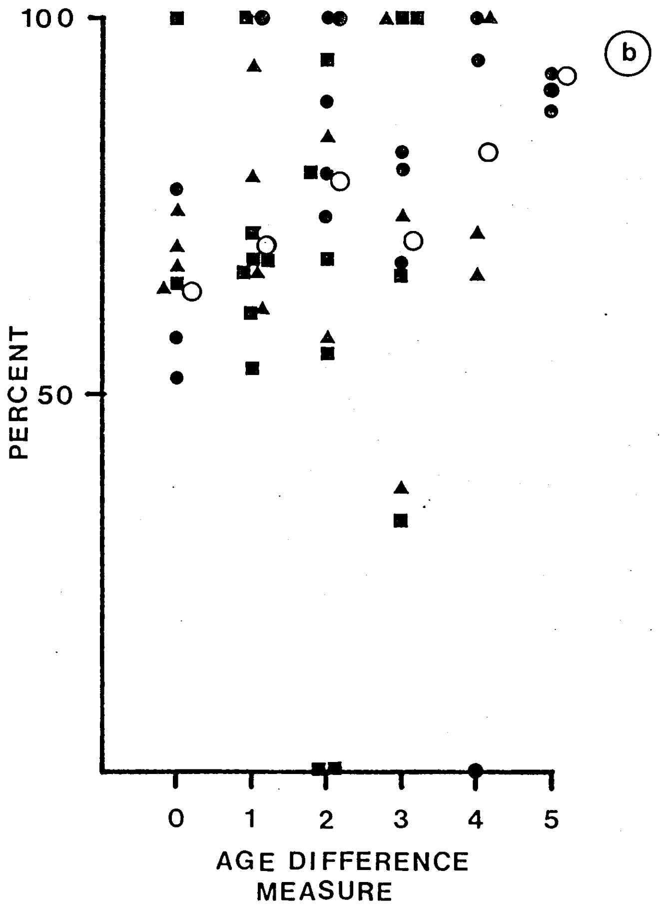
● Subject aged 6-23 weeks.

▲ Subject aged 29-50 weeks.

■ Subject aged 50-89 weeks.

Open symbol.

○ Weighted mean percentage calculated from the data at each age difference.



Spearman Rank Correlation

Weighted mean percentage correlated against age difference.

a) Non-contact play

$r_s = -0.89$

$p < 0.05$

$N = 6$

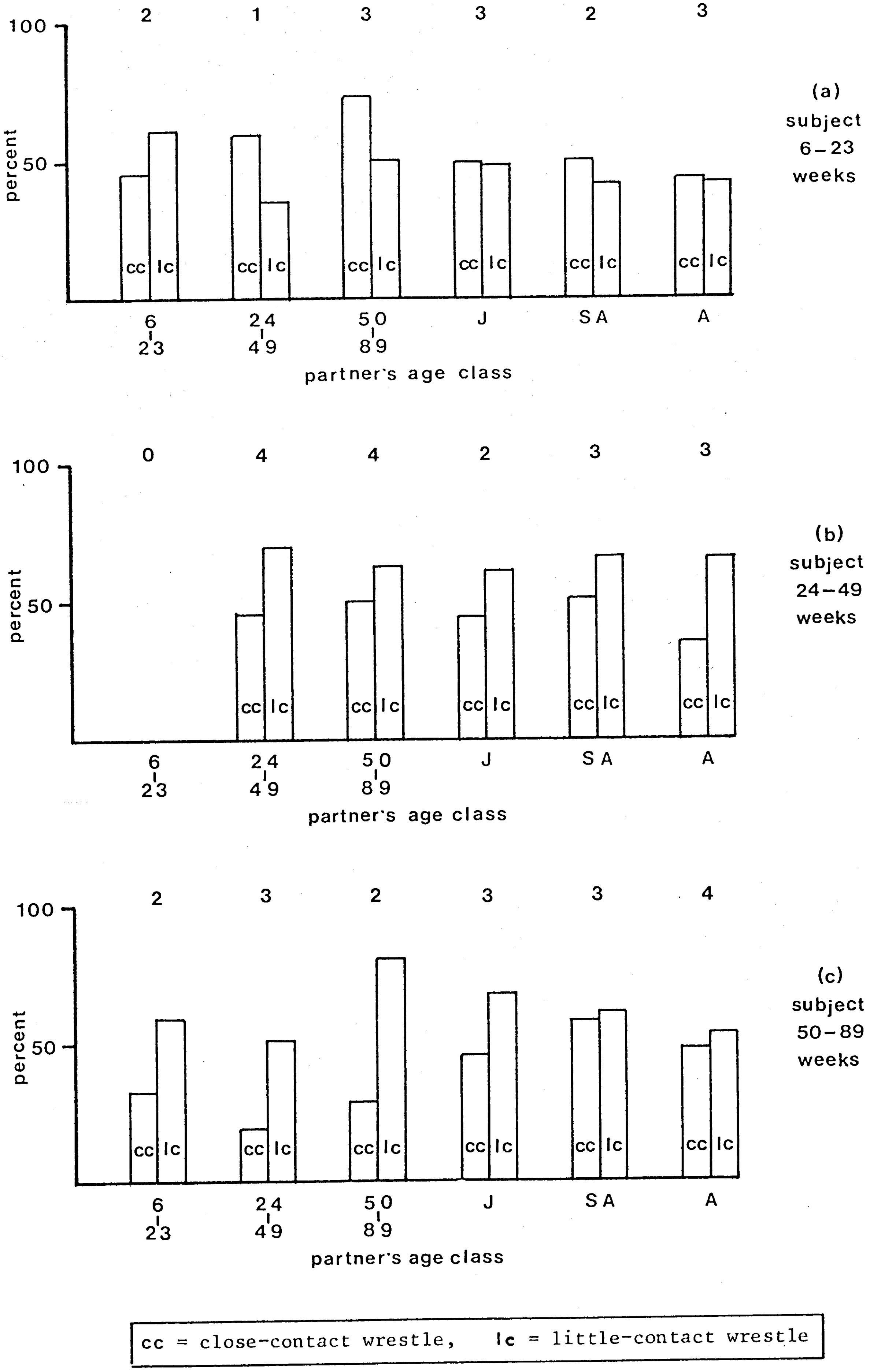
b) Contact play

$r_s = +0.943$

$p < 0.01$

$N = 6$

Figure 93. The proportions of close-contact wrestling and little-contact wrestling in contact play between different age pairs



Discussion

Development

Safari park baboons began playing at approximately the same age as wild baboons. Owens (1975a) and Cheney (1978) reported that play was first recorded at 2 or 3 weeks and Owens noted that all infants were playing by 6 weeks.

The play of safari park infants went through two phases of increasing frequency, the first ending at 12-17 weeks and the second ending at 30-41 weeks. It would be an over-interpretation of the data to claim that play peaked at these ages but it is interesting that both Owens and Cheney found two frequency peaks. Owens' initial peak (for males) was at about 18 weeks with a trough at about 34 weeks followed by a second, higher peak at 56 weeks. In Cheney's study the first peak and trough were at 27-30 weeks and 39-46 weeks, later than Owens'; but the second peak was at 51-59 weeks which includes the age given by Owens.

Cheney asked whether the trough in her study was associated with weaning. Perhaps infants were preoccupied with the changing relationship with their mothers and consequently spent less time playing? But she found no correlation between the frequency of play and the frequency of weaning tantrums or the resumption of the mothers' sexual cycles. In the present study the period when play frequency changed very little, 18-23 weeks, coincided with peaks in both the frequency of making and breaking contact with mother and of the proportion of time spent in contact with mother (Table 17). This is consistent with infants spending an increased proportion of their time attempting to stay in contact with the mother and so not having time available to increase the amount of play. There is other evidence that 18-23 weeks marked the end of one phase of the infant-mother relationship. It preceded a sharp drop in the proportion of time on mother spent performing certain behaviours (grip fur, rooting and clambering on mother). It also preceded a sharp increase in the proportion of time with mother spent on the nipple. While these results do not explain the trends in the same way as Cheney attempted, they do support the idea that play does not increase while infants are experiencing certain changes in the relationship with their mothers.

It was not only play whose frequency underwent little change at 18-23 weeks. Figure 84 shows that the frequency of non-play activity also changed very little. However, when play increased once more at 24-29 weeks it was not merely because of an increase in general activity since non-play decreased slightly at that age. The opposite movement is reflected in the sharp increase in the proportional contribution of play to mobile activity which was discussed in Chapter 6. The fact that non-play decreased slightly while play increased supports the hypothesis put forward in Chapter 7 that in some circumstances there was more advantage in being active playfully (with play signals) than in being active non-playfully (without play signals).

The sub-categories of play used in this study were similar to those used by Owens. Contact-play can be considered equivalent to Owens' "rough and tumble", and non-contact-play equivalent to "approach-withdrawal". Both close-contact and little-contact wrestling were embraced by Owens' "wrestling" category and little-contact wrestling was the same in all respects as his "sparring".

The first appearance of contact-play before non-contact-play and its consistently higher frequency during the first year of life agrees with Owens' observations. It is also in accord with Hinde and Spencer-Booth's (1967) results with captive rhesus. During the safari park infants' first year the proportion of non-contact in play increased while the proportion of contact changed very little. This is also what Owens found in baboons, but is different from the development of play in captive rhesus. Hinde and Spencer-Booth (1967) showed rough and tumble increasing relative to approach-withdrawal during the first year.

In the safari park infants, increasing frequency of non-contact play seems to have been a reflection of increasing mobility generally, since non-contact play first appeared at the same age, 6-11 weeks, as the first big increase in non-play activity (Figure 84).

Contact-play was sub-divided. Close-contact and little-contact wrestling were distinguished mainly by the criterion of distance between the subject's torso and its partner. That criterion was chosen because it created objective, easily scored categories; but it was possible that those categories had no other meaning.

The results suggest that close-contact and little-contact wrestling were not spurious categories. If they had been random divisions of a wrestling continuum then the data would not have produced the clear development trends shown in Figures 87, 88 and 90.

Changes in the style of contact-play for safari park infants are similar to the changes reported by Owens. His "sparring" and my little-contact wrestling increased in relative proportion to other types to become the most frequent form. Owens' "wrestling" category changed very little in its proportional contribution to play, and my data would probably have given the same result if close-contact and little-contact wrestling had been combined into one category; the increase in one would have cancelled the decrease in the other.

The proportion of little-contact wrestling in safari park infant play increased with age. Owens showed the same trend in wild baboons and also demonstrated that in this respect play-fighting became more like adult aggressive fighting. Adult fighting had a much higher proportion of sparring than of close wrestling. He suggested that sparring represented a higher level of fear than close wrestling, and that an increasing level of sparring showed that infants became more fearful with age during bouts of rough and tumble.

The changing proportion of little-contact can be looked at from another viewpoint. Contact-play changed from a predominantly clinging form to a predominantly manipulative form between 3-5 weeks and 18-23 weeks. It was the more manipulative little-contact wrestling which changed by becoming more frequent than the more clinging close-contact wrestling. Such increased performance of a manipulative skill might have been a result of improved sensori-motor coordination during that period. There is other evidence of increasing manipulative ability at that time in that the frequency of the more skilful types of object manipulation (pick-up and hold and mouth) increased most rapidly from 0-2 weeks to 12-17 weeks. Perhaps the frequency of little-contact wrestling and the frequency of successful attempts at picking up and holding and mouthing objects depended on similar levels of sensori-motor coordination. It must be said, though, that during this period mobile activity was also increasing in frequency and so to claim a particular relationship only between wrestling and object manipulation would be special pleading. Improvements in neuromuscular coordination are likely to have resulted in higher frequencies of a great many behaviours.

The changing form of play can be interpreted from the point of view of function. Fagen (1976) argued that if play functions as a strategy for providing physical training then in order to be efficient it should offer a regime of three types of activity: prolonged bouts of low intensity endurance exercise, brief high intensity overload or isometric exercise that are punctuated by frequent rest periods and longer bouts of lower intensity overload exercise. He suggested that locomotor play (non-contact play) could provide the endurance exercise and that rough and tumble, with partners pulling and pushing against each other, could give both types of overload. I think it would be fruitful to consider close-contact and little-contact wrestling as distinct exercise patterns which infants could use to satisfy their requirements for overload exercises. Close-contact might be equivalent to the intense, isometric form and little-contact equivalent to the less intense form.

This hypothesis could be tested, although not with the present data. Fagen predicted not only the effects of playful exercise but also the relative durations of the different behaviour patterns. From those predictions, young baboons should perform close-contact wrestling in shorter bouts than little-contact wrestling and should rest for short periods between those bouts. The duration of non-contact locomotor play bouts should be greater than those of either type of wrestling.

If it is the case that baboons can derive different physiological benefits from these two types of wrestling then age changes in their relative frequencies might point up phases in development when particular exercise regimes are appropriate.

Sex differences

There was no evidence of sex differences in the play of safari park baboons, either in its frequency or in the relative proportions of contact and non-contact. The number of subjects and their age distribution within the sample do not allow a more confident statement to be made.

Cheney found no sex differences in the amount of play, but Owens demonstrated differences both in the amount of play and in its form. Males played more, and with more wrestling, than females. Also, until 5 months males showed proportionately more approach-withdrawal than females, but after 10 months females showed the greater proportion of approach-withdrawal.

Cheney was able to demonstrate that the type of partner available dictated to a large extent the amount of play. She pointed out that her troop was small compared with that of Owens and that the relative lack of partner choice resulted in each infant having similar play experiences, which eclipsed sex differences. The sample of infants in the present study included 6 at Blair Drummond and varied between 2 and 8 at Woburn. These numbers are more similar to Cheney's sample (6 juveniles, 8 infants) than to Owens' (20 infants). If safari park males and females really did play as much, and in the same way, as each other it may have been because they had only a small choice of partners.

The effects of partners' ages

Play between similarly aged partners contained similar proportions of contact and non-contact, but the wider the age gap, the smaller was the proportion of non-contact and the larger the proportion of contact. The effect on non-contact was the greater. When very young, and therefore small, infants wrestled with older, larger partners they used more close-contact than little-contact. In all other partnerships, even when older infants were wrestling with very young infants, little-contact was the predominant type.

Owens (1975a) observed that when baboon play partners were of very different ages, and hence different sizes, play bouts tended to be shorter. This was because in chases the smaller partner was soon caught or could not catch the other; and in rough and tumble the smaller one retired early because its larger partner was too rough.

If imbalance between partners had the same effect on both contact and non-contact play such that both were likely to be cut short, the resulting proportions of contact and non-contact in what remained of play might have stayed constant. But the data from safari park baboons show that the proportions did change. It is reasonable to conclude that, if Owens' explanation is accepted, the tendency to cut short non-contact play was greater than the tendency to cut short contact play.

Another explanation might be that unmatched pairs tended to engage in proportionately fewer bouts of non-contact play chasing compared with contact play. Altmann (1962) and Fady (1969) suggested that play between unmatched pairs is made "fair" and therefore kept going, by means of restraint and self-handicapping by the superior partner. If, as the present results suggest, with unmatched pairs contact play kept going longer or was entered into more frequently than non-contact play, then it is possible that contact play was the more easily inhibited form of play. This could be tested, but not with the present data. If the hypothesis is correct, then the probability of a play bout between unmatched partners breaking up, escalating into aggressive fighting or being interrupted by a non-playing adult would be greater during a period of non-contact than

The age, or more likely size, of partner had quite a subtle effect on the wrestling style of very young infants. A small infant was more likely to engage in close-contact wrestling, that is, pressing its body close to its partner, when the partner was larger than when it was of similar size to itself.

The simplest interpretation of this is a physical one. The larger partner could keep the smaller one at a distance from its body by means of its longer and stronger limbs. In response the small infant could only cling to the forelimbs or shoulders of its larger partner. Thus the small partner would be recorded wrestling with close-contact while the large partner was wrestling with little-contact.

Young infants might have derived benefit from this situation if, as was suggested earlier, close-contact wrestling represented a form of high intensity overload exercise. That sort of exercise would be achieved if work was done against a body with high inertia; and a larger, heavier partner might have provided such a body.

Summary

The age at which play was first seen was consistent with observations of wild baboons. The frequency of play increased in two phases, with a period of no change from 12-17 weeks to 24-29 weeks. Comparisons were made between the pattern of development and the bimodal patterns described in studies of wild baboons. The "flat" phase corresponded with events in infant-mother behaviour development which suggested that it represented a change in infant time budgeting.

The earliest form of play was contact play. Non-contact-play first appeared a few weeks later. Contact play was slightly more frequent than non-contact until 30-41 weeks, after which they had similar frequencies.

The form of wrestling changed from predominantly close-contact to predominantly little-contact. The significance of there being two forms was discussed with regard to possible cause and function. It was suggested that they might represent different degrees of manipulative skill and also satisfy different requirements for exercise.

Evidence was given which suggested that some aspects of a subject's play depended on the relative age or size of its partner. The proportion of contact play increased and that of non-contact play decreased with the age difference, and very young infants engaged in close-contact wrestling more with older infant partners. It was suggested that play between unmatched partners may have been in greater danger of failing than that between matched partners, and that of the two categories of play, contact play may have been the one in which self-handicapping was easier. When the size difference was great the smaller infant tended to cling to its partner's forelimbs and that qualified as close-contact wrestling. The large partner may have provided a good object against which a small infant could perform overload exercise.

No evidence was found of sex differences in the amount or form of play but the small number of subjects in the sample and their age distribution made such analyses unreliable. However, it may have been significant that a wild population with approximately the same number of young baboons as in the present study has been reported not to have sex differences. It is possible that in small populations all infants have similar play experiences because of the narrow range of partners.

Chapter 9. Results: analysis of developmental and temporal associations

These analyses were carried out to identify groups of motor patterns which followed similar courses of development or tended to be performed close together in time.

1. Developmental groups

Development trends have been compared already in previous results chapters but only within behaviour categories which were defined externally, that is, within the previously defined categories of object manipulation, mobile activity, non-play locomotion and play. In this section the development trends are allowed to "speak for themselves". The analysis is based on rank correlations between trends. The motor patterns are those which were not of necessity performed on or in contact with the mother and all frequencies are expressed as a percentage of off-nipple intervals. Thus, motor patterns were not automatically intercorrelated by virtue of increasing time spent off-nipple and off mother.

Two rare motor patterns, sloth-like progression and play walk, have been excluded because with their very low frequencies small sampling errors could have had large effects on rank orders, making correlations unreliable.

The Spearman rank correlation coefficient was calculated for each pair of motor pattern development trends (ages 0-2 weeks to 78-89 weeks, N = 10) and the results are shown in Table 31. The same information is summarized in Figure 94 in the form of a single link hierarchical cluster dendrogram (Dawkins, 1976; Colgan, 1978). Pairs of motor patterns are linked at the level corresponding to their rank correlation coefficient value provided it is the highest correlation that either of the pair enters into. A motor pattern is linked to an existing cluster at the level of the highest correlation that it has with any member of that cluster. Two clusters are linked at the level of the highest correlation between any pair of motor patterns within those clusters.

Table 31. Spearman rank correlation between age changes in weighted mean one-zero frequencies of object manipulation, non-play and play motor patterns. Only high coefficients are shown (rs > 0.7). N = 10

							NON-PLAY					
		pick-up	hold and mouth	scratch ground	short bout mouth	long bout mouth	walk	run	jump	climb-up	climb-down	swing/hang
	touch											
	pick-up		+1.00	+0.90	+0.99							
	hold and mouth			+0.90	+0.99							
	scratch ground				+0.99							
	short bout mouth											
	long bout mouth						+0.90	+0.82	+0.90	+0.81	+0.83	
NON-PLAY	walk								+0.79	+0.76	+0.81	
	run								+0.90	+0.86	+0.91	+0.77
	jump									+0.79	+0.89	+0.72
	climb-up										+0.95	+0.95
	climb-down											+0.88
	swing/hang											
PLAY	walk											
	run											
	jump											
	climb-up											
	climb-down											
	swing/hang											
	little-contact											
	close-contact											

Table 31 continued

		PLAY								
		walk	run	jump	climb-up	climb-down	swing/hang	little-contact wrestle	close-contact wrestle	poke-touch
	touch									
	pick-up									
	hold and mouth									
	scratch ground									
	short bout mouth									
	long bout mouth		+0.78	+0.83				+0.83	+0.84	
NON-PLAY	walk		+0.77					+0.85	+0.91	
	run			+0.85				+0.74	+0.84	
	jump		+0.86	+0.94				+0.87	+0.84	
	climb-up		+0.78					+0.81		
	climb-down		+0.87	+0.81	+0.78	+0.75		+0.90	+0.81	
	swing/hang							+0.71		
PLAY	walk									
	run			+0.89	+0.95	+0.85	+0.79	+0.97		
	jump				+0.78			+0.86	+0.77	
	climb-up					+0.95	+0.76	+0.93		
	climb-down							+0.85		
	swing/hang									
	little-contact								+0.76	+0.80
	close-contact									

The 0.001 significance level is used as a first, arbitrary criterion for identifying groups. It cuts off five groups: two major ones and three individual motor patterns whose trends are unlike any others. These are given in Table 32.

Group 1 consists mostly of motor patterns which made up mobile activity. The exception is long bout mouthing. These patterns are intercorrelated because their development followed "humped" trends, with a rise phase to a peak or plateau at about 18-23 or 30-41 weeks followed by a fall or a continuation of the plateau.

Group 2 comprises object manipulation patterns whose frequencies increased throughout the infant age range.

Group 3 is "play swing/hang". It should be noted that it correlates with other mobile activity (Group 1) at a lower level of significance (0.01).

Group 4 is "clamber on other". It was only seen at all frequently between 6-11 weeks and 18-23 weeks.

Group 5 is "touch". Its peak was earlier than that of any other motor pattern, at 6-11 weeks.

Trends in the mobile activity group (Group 1) have the same general shape with at least one quite long horizontal, or near horizontal, portion. Small sampling errors can give rise to significant ranking differences in such trends. This means that sub-divisions within this group might be spurious unless the value of r_s chosen as the criterion is sufficiently high; the higher the value, the smaller the chance of a spurious result.

Inspection of Figure 94 reveals that in Group 1, the sub-group with the highest value of r_s, and therefore the one least likely to be due to sampling error, contains two play motor patterns: play run and little-contact wrestle. In other words, the development trends of play run and little-contact wrestle were more similar to one another than to those of any other motor patterns, and no other two motor patterns shared such similar development trends.

Table 32. The major correlation clusters derived from Figure 94

group	motor pattern		
1	non-play swing/hang		separate above rs = 0.88
	non-play climb-up		
	non-play climb-down		
	non-play run		
	little-contact wrestle	separate above rs = 0.97	
	play run		
	play climb-up		
	play climb-down		
	play jump		
	non-play jump		
	close-contact wrestle		
	non-play walk		
	long bout mouthing		
2	pick-up		
	hold and mouth		
	short bout mouthing		
	scratch ground		
3	play swing/hang		
4	clamber on other		
5	touch		

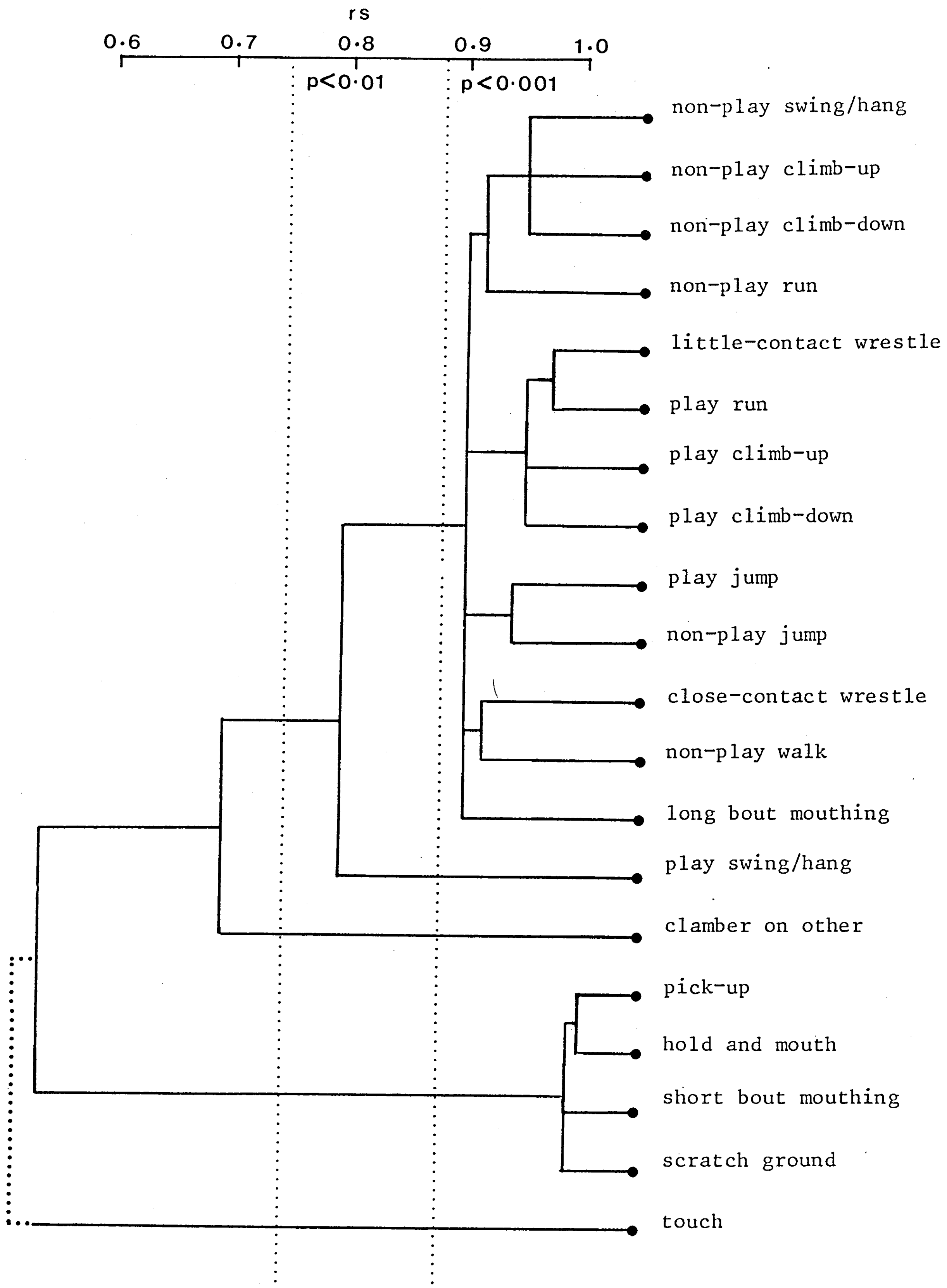


Figure 94. Dendogram showing correlations between development trends, based on Spearman rank correlation coefficients

By reducing the criterion value of r_s a new sub-group appears, comprising non-play patterns: swing/hang, climb-up and climb-down. The group of play patterns becomes enlarged with the addition of play climb-up and play climb-down.

Further reduction of the criterion brings play and non-play patterns together in the same groups. Play jump and non-play jump form a sub-group as do close-contact wrestle and non-play walk. Non-play run joins the group of other non-play patterns, climbing and acrobatics.

Less confidence can be had in the validity of these later sub-groups than in the first play run/little-contact wrestle sub-group. There is a greater probability that these component patterns had similar development trends by chance.

2. Temporal associations

Cluster analysis

This analysis was based on two assumptions: that it was possible for any two motor patterns in the behaviour catalogue to occur during the same 30 second observation interval and that motor patterns which shared some aspect of causation or function would occur together more frequently than would be expected by chance. The first of these assumptions did not seem unreasonable from the impression gained during data collection.

The probability of two motor patterns arriving in the same interval by chance would be the product of their individual probabilities of having arrived there. Expected frequencies were calculated for all pairs of motor patterns. The statistic chi-square was chosen to measure the strength of association between pairs of motor patterns.

Data from three subjects were used:

Kenya:	anubis female from Woburn
Deag :	anubis female from Woburn
Safron:	cynocephalus male from Woburn.

These were chosen because they were the only subjects with sufficient data covering a wide age range and encompassing all the behaviours in the catalogue. It was unfortunate that Deag and Safron were not matched for species and sex. The age ranges were:

Kenya	6-12 weeks
Deag	12-53 weeks
Safron	10-52 weeks

The data from Deag and Safron fell naturally into two smaller age blocks:

Deag	12-24 weeks and 29-53 weeks
Safron	10-21 weeks and 25-52 weeks

They were analysed separately in case associations between motor patterns changed over time.

The behaviour catalogue contained 31 motor patterns. Chi-square was calculated for every possible non-similar pair (465 pairs) in the same way as reported by Blurton Jones (1967) with a 2 x 2 contingency table for each pair and applying Yates' correction for continuity. Yates' correction was used because many of the expected frequencies were less than 5 (following Cochran's (1954) recommendation)[1]. Calculations were carried out, and the resulting matrix printed,by computer.

Published levels of significance for chi-square would only be valid criteria for non-random associations if the data recorded in a 30 second interval were independent of those in other intervals. The data sheets were records of continuous behaviour so it was not reasonable to assume that the data in one interval were independent of those in the previous interval. Two strategies were adopted in an attempt to permit the use of published significance levels:

1. the data analysed were a sample of the total data from each subject. Every fifth interval was sampled.[2] This did not guarantee that the resulting sample contained fully independent data (behaviours scored in an interval might still

---

[1] My matrices probably had a smaller proportion of low expected frequencies than Blurton Jones' (1967). In the sample he published, 82% of the cells (64 out of 78) had $E<5$. In my matrix for Safron aged 10-21 weeks there were 70% (227 out of 325) cells with $E<5$.

[2] Dunbar (1974) found that in the gelada baboon a sampling interval of between 2 and 4 minutes provided reasonably independent data. The probability of successive samples coming from the same bout of activity was less than 0.05.

have depended on the behaviour performed five intervals earlier) but it provided a greater likelihood of independence;

2. a high significance level ($p<0.001$) was chosen as the criterion for non-random association. Even with data which were not independent, and even with the effects of low expected frequencies, this improved the chance of making a correct decision (i.e. reduced the chance of a type 1 error, according to Siegel (1956)).

Some pairings gave a high chi-square which was misleading because the observed frequency was very low. These rare pairings with inflated chi-square values were disregarded and the analysis continued with the common pairings, whose observed frequencies were 5 or more.

For each subject at each age a single link hierarchical cluster analysis dendrogram was constructed. These dendrograms are shown in Figures 95 to 99. The clusters which exist below $p = 0.001$ are shown in Table 33.

It is possible that some motor patterns have arrived in a cluster by chance, despite the measures taken to avoid it. Associations are less likely to be spurious if they occur in more than one subject. Table 33 also shows those clusters which are common to both Safron and Deag at each age.

Description of clusters

Motor patterns performed on mother

Rooting and shift position was a cluster common to all subjects at all ages. They were two of the most frequent motor patterns performed on-mother and were associated because of the situation they were performed in; in ventro-ventral contact with the mother, gaining or maintaining a hold on the nipple.

The number of motor patterns within the on mother cluster becomes smaller with age. This reflects the tendency reported in Chapter 4 for infants to spend less of the time in which they were on mother in activities other than suckling. The persistence of rooting and shift position is consistent with that tendency because an infant could perform both

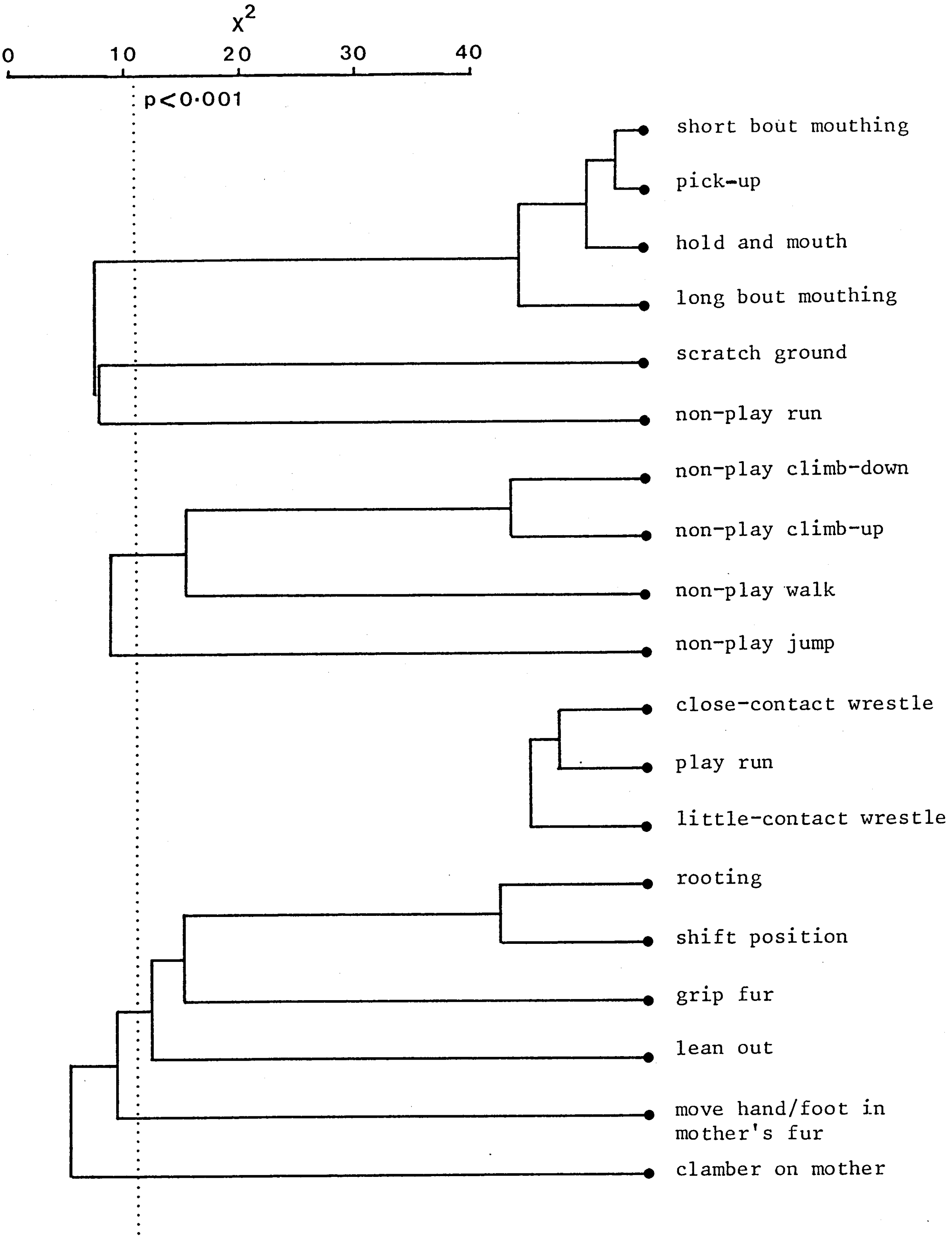


Figure 95. Dendrogram showing the strength of temporal association between motor patterns, based on chi-square with Yates' correction. The results are only for those pairings of motor patterns with an observed frequency of at least 5.

Kenya, 6-12 weeks.

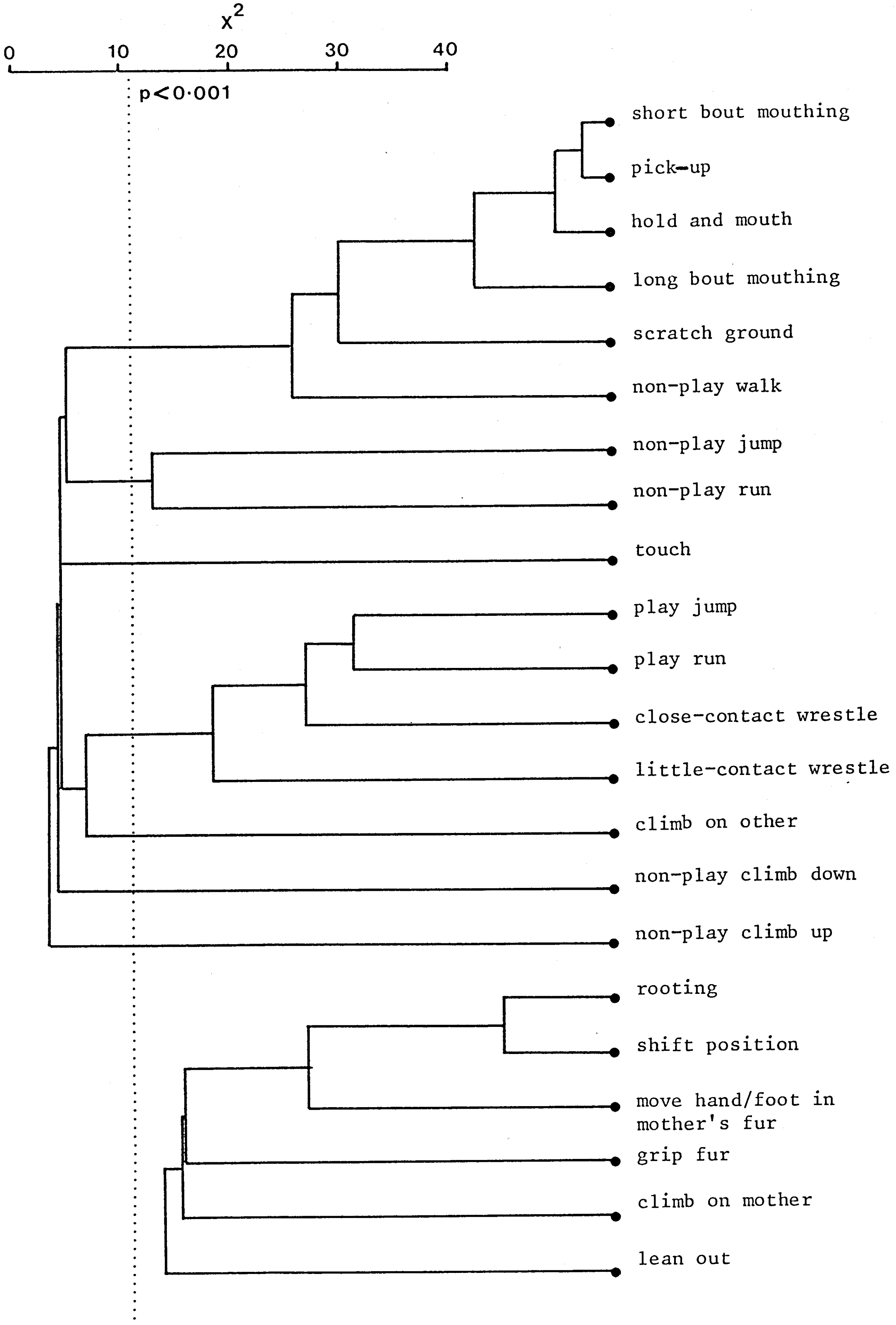


Figure 96. Dendrogram showing the strength of temporal association between motor patterns, based on chi-square with Yates' correction. The results are only for those pairings of motor patterns with an observed frequency of at least 5.
Safron, 10-21 weeks

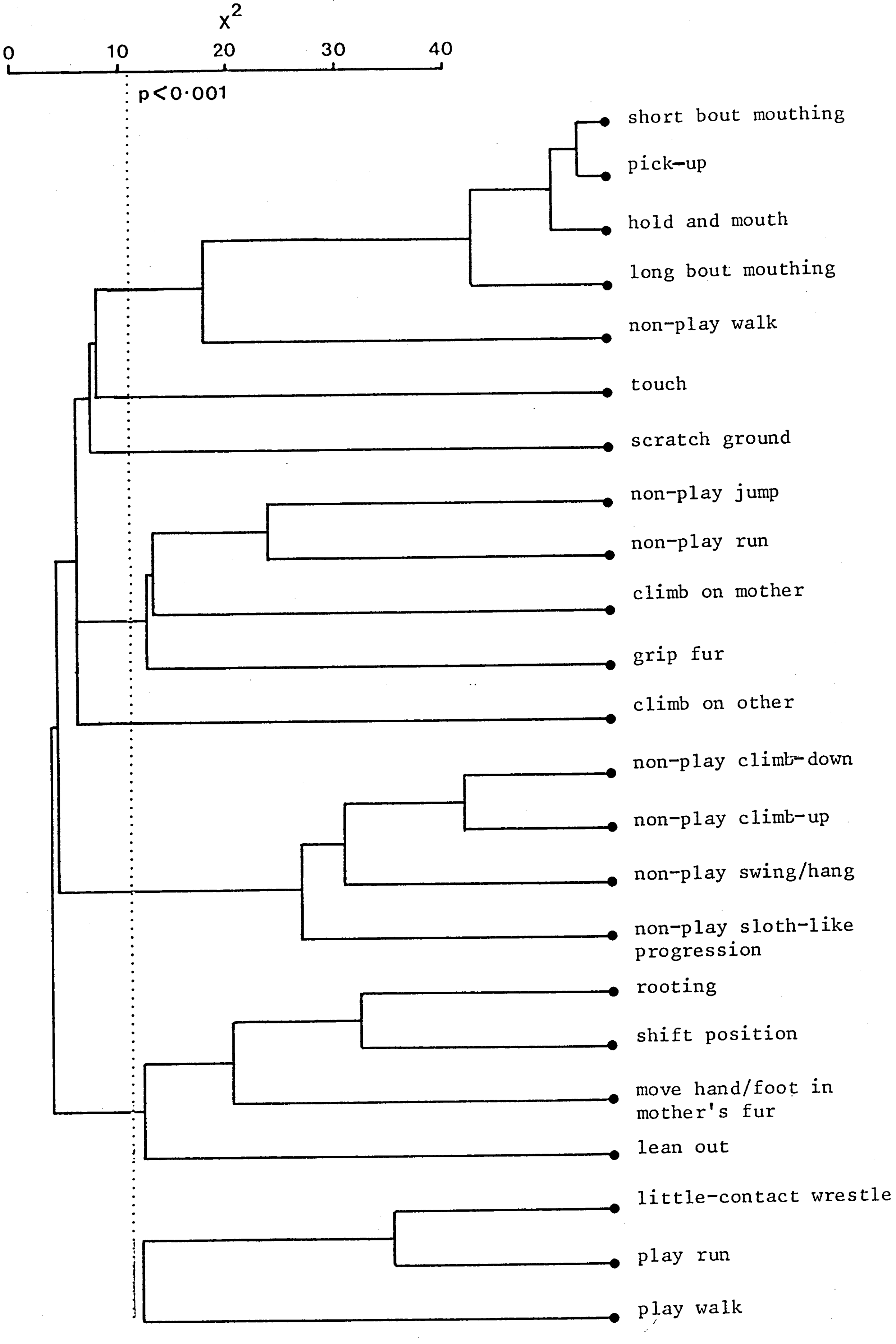


Figure 97. Dendrogram showing the strength of temporal association betwee motor patterns, based on chi-square with Yates' correction. The results are only for those pairings of motor patterns with an observed frequency of at least 5.

Deag, 12-24 weeks

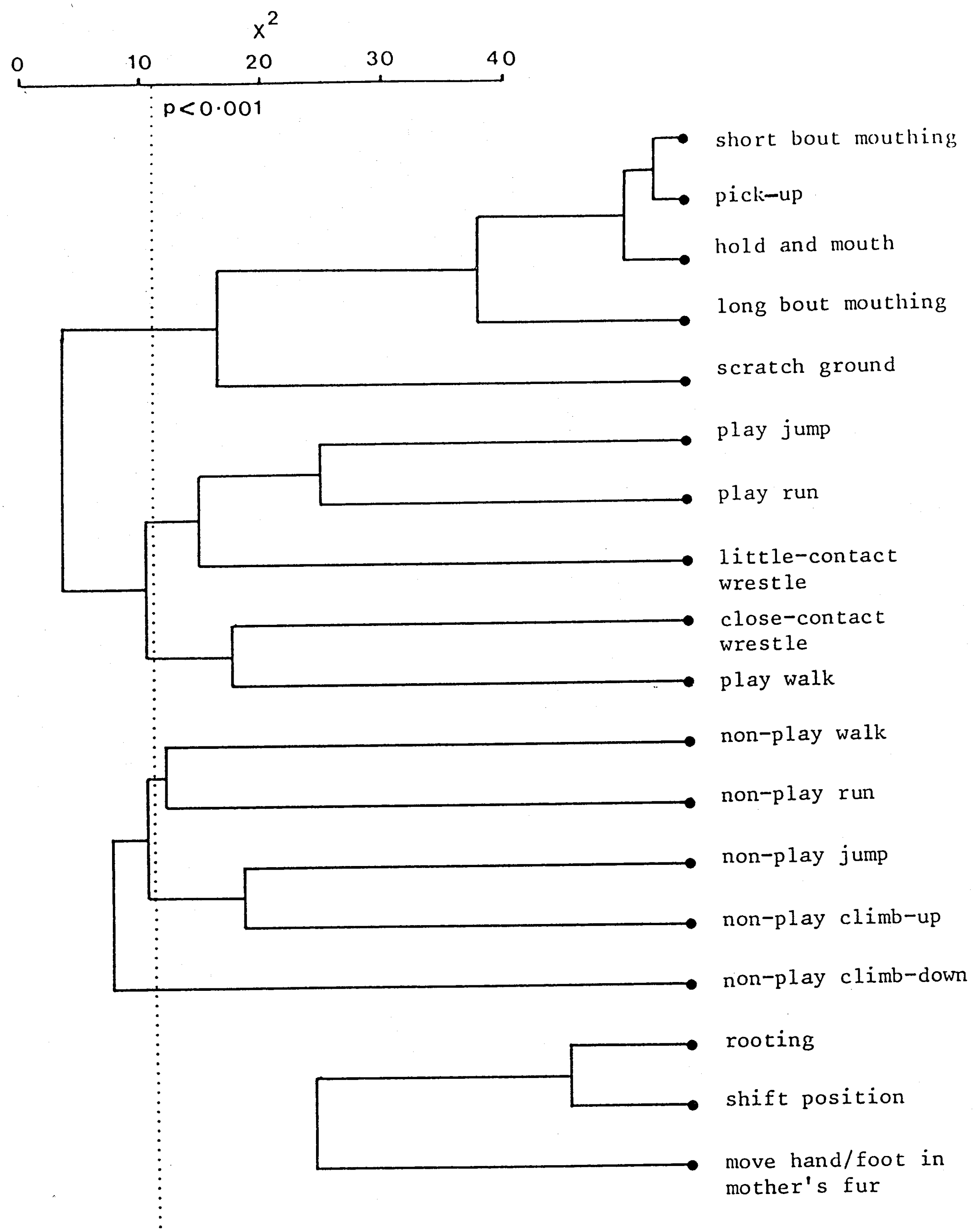


Figure 98. Dendrogram showing the strength of temporal association between motor patterns, based on chi-square with Yates' correction. The results are only for those pairings of motor patterns with an observed frequency of at least 5.

Safron, 25-52 weeks

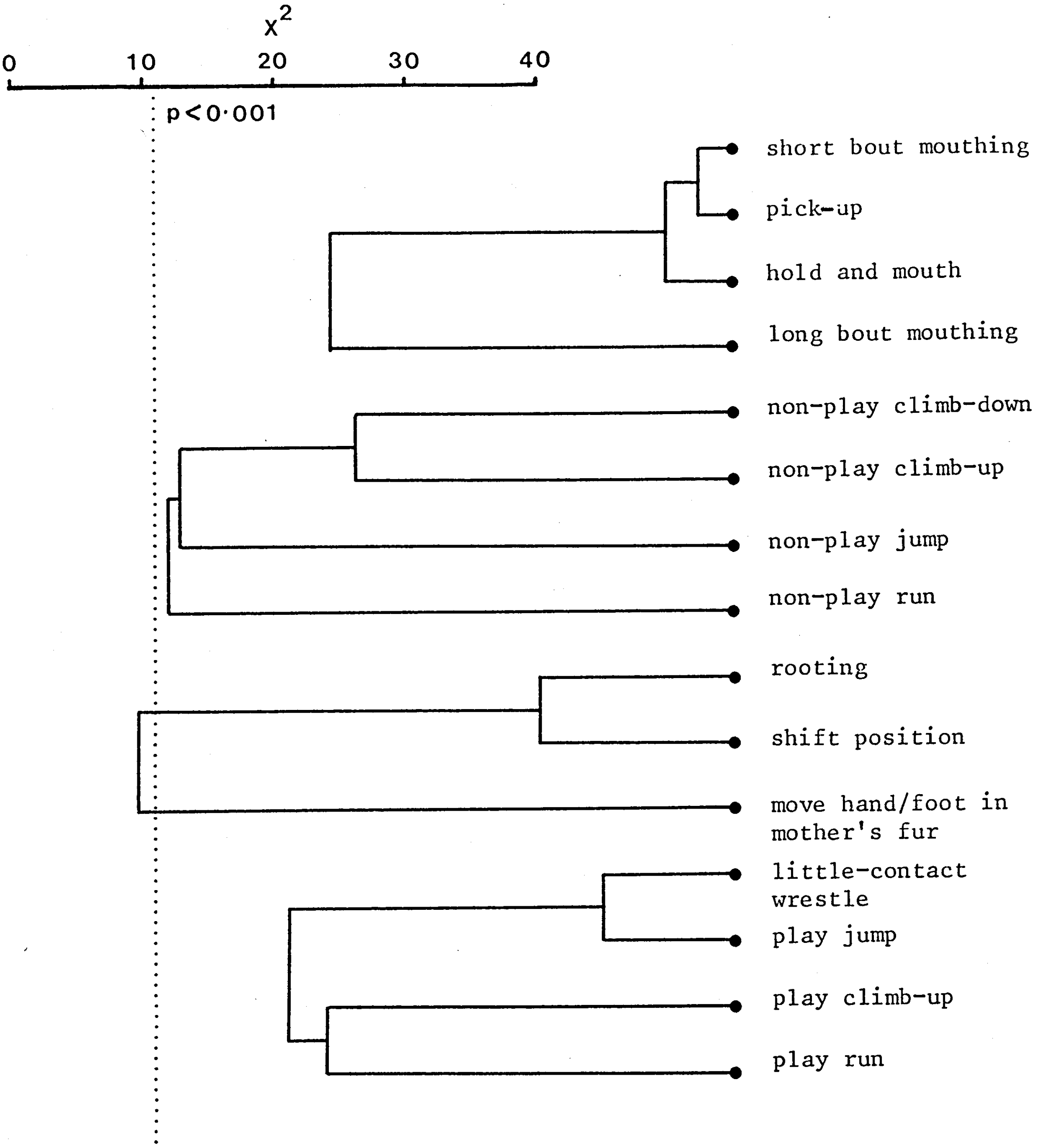


Figure 99. Dendrogram showing the strength of temporal association between motor patterns, based on chi-square with Yates' correction. The results are only for those pairings of motor patterns with an observed frequency of at least 5.

Deag 29-53 weeks

Table 33. Temporally associated motor pattern clusters derived from Figures 95 to 99.

The criterion for a cluster is chi-square > = 10.83, p < 0.001.

Kenya 6-12 weeks	Safron 10-21 weeks	Deag 12-24 weeks	Common to Safron and Deag 10-24 weeks
rooting shift position lean out grip fur	rooting shift position h.t.m.f. lean out clamber on mother grip fur	rooting shift position h.t.m.f. lean out	rooting shifting position h.t.m.f. lean out
pick-up hold and mouth short bout mouthing long bout mouthing	pick-up hold and mouth short bout mouthing long bout mouthing non-play walk scratch ground	pick-up hold and mouth short bout mouthing long bout mouthing non-play walk	clamber on mother grip fur
non-play climb-down non-play climb-up non-play walk	non-play run non-play jump	non-play run non-play jump clamber on mother grip fur	pick-up hold and mouth short bout mouthing long bout mouthing non-play walk
play run little-contact wrestle close-contact wrestle	play run play jump little-contact wrestle close-contact wrestle	non-play climb-down non-play climb-up non-play swing/hang non-play sloth-like progression	non-play run non-play jump
		play walk play run little-contact wrestle	play run little-contact wrestle

h.t.m.f. = hand to mother's fur

Table 33 continued

Safron 25-52 weeks
rooting shift position h.t.m.f.
pick-up hold and mouthing short bout mouthing long bout mouthing scratch ground
non-play climb-up non-play jump non-play walk non-play run
play walk close-contact wrestle
play run play jump little-contact wrestle

Deag 29-53 weeks
rooting shift position
pick-up hold and mouth short bout mouthing long bout mouthing
non-play climb-up non-play climb-down non-play run non-play jump
play run play jump play climb-up little-contact wrestle

Common to Safron and Deag 25-53 weeks
rooting shift position
pick-up hold and mouth short bout mouthing long bout mouthing
non-play climb-up non-play jump
play run play jump little-contact wrestle

h.t.m.f. = hand to mother's fur

patterns while on-nipple.

Object manipulation

The clustering of pick-up and hold and mouth by all subjects at all ages strongly supports the casual observation reported in Chapter 5 that when objects were picked up they were usually held and mouthed immediately afterwards.

Short-bout mouthing and long-bout mouthing which were mutually exclusive appear, by this analysis, to have occurred together. This is simply an artifact of single link clusters. By their definitions short-bout mouthing was associated with both pick-up and hold and mouth and long-bout mouthing was associated only with hold and mouth.

It is interesting that non-play walk was associated with object manipulation by Safron and Deag between 10 and 24 weeks but the association was not there when they were older. I suggest that this reflects the greater dependence of older infants on solid food and the greater proportion of time that they would have spent foraging compared with younger infants. The older infants would have fed in longer, stationary bouts, that is, less interrupted by walking.

Non-play locomotion

Each subject at each age has at least one non-play locomotion cluster but they vary in composition between subjects. The only associations which appear more than once are non-play run with non-play jump (Safron and Deag 10-24 weeks) and non-play climb-up and non-play climb-down (Kenya 6-12 weeks, Deag 12-24 and 29-53 weeks). This reflects the broad scope of the non-play category. Infants could engage in non-play in any part of their environment and under the control of various internal and external factors.

One pattern which should be noted is that climbing and jumping in non-play were not associated before 24 weeks but appear together in Safron's and Deag's clusters after 25 weeks. The emergence of a climbing and jumping cluster between 25 and 52 weeks of age cannot be attributed simply to increasing frequency of non-play climbing and non-play jumping, because although jumping reached a peak at 24-29 weeks, it had been fairly frequent since 6-11 weeks and climbing had been at the top of a plateau for several weeks (see Figures 67 and 69). It is more likely that at around 25 weeks jumping and climbing were becoming organized into functional sequences used for progression over complex raised structures and so tended to be performed together.

Play

Each subject at each age has a play cluster with play run and little-contact wrestle consistently present. There is less variation than within non-play clusters. Running and little-contact wrestling probably formed a central element of approach-withdrawal and rough and tumble.

At 25-52 weeks play jump became clustered with play run and little-contact wrestle in Safron and Deag. This could mean that play became more complex with age. Deag also added play climb-up; a further complexity. On the other hand, close-contact wrestling which was part of Kenya's play cluster at 6-12 weeks and of Safron's at 10-21 weeks, became separated in later weeks. Safron has it associated with play walk at 25-52 weeks. This age change is based on only one subject and so any interpretation is highly speculative, but it is possible that close-contact wrestling became less associated with play locomotion as infants became older.

Discussion

Motor patterns which consistently occur close together in time will show similar frequency changes over time. Such was the case with pick-up and hold and mouth, and also with play run and little-contact wrestle.

Picking up an object and holding and mouthing it could rightly be considered a single functional unit. That is not to say that they could not be performed separately; they clearly were as in long-bout mouthing, but they formed the central element in most cases of object manipulation. Touch developed independently of pick-up and hold and mouth and there was no significant tendency for it to be performed close to them in time.

Therefore object manipulation as a whole was heterogeneous in development, temporal associations and, it follows, in causation. But within that diversity was the composite pattern "pick-up then hold and mouth" which was homogeneous in development and temporal associations and therefore probably homogeneous in its causal factors.

Similarly, play had a central element consisting of running and little-contact wrestling which was homogeneous in development and temporal association. But play was heterogeneous with respect to other motor patterns. While running and little-contact wrestling might have shared causal factors, some of which might also have controlled other play motor patterns, it is likely that those other motor patterns were also controlled by different factors. For instance, climbing and acrobatics were constrained by the physical environment. Infants could not climb if there was nothing available to climb. This would explain the lack of temporal association between play run/little-contact wrestle and play climbing (except in Deag 29-53 weeks). Since there was always something available to climb somewhere in the enclosures, infants could always climb eventually. If, then, play climbing and acrobatics shared causal factors with play run/little-contact wrestle such that they would be performed together provided the environment allowed, then they would be expected to show similar development trends. This is supported by the results (Figure 94).

Play jumping was temporally associated with play running and little-contact wrestling in Safron (in both age ranges) and Deag (when she was older). They may have shared causal factors, particularly in older infants. Play jumping was not necessarily constrained by the environment. Provided an infant had the ability, it could play jump anywhere because the category "jump" included jumping up from the ground and jumping down from a raised position. It is, however, reasonable to suggest that there was a greater tendency to jump when infants were on raised structures. It was argued earlier that during the 25-52 week age range non-play jump and non-play climb-up became organized into functional sequences. This suggests that older infants were spending more of their time locomoting on raised structures such as trees and fences. When they then entered into play bouts it follows that there would have been a high probability of those bouts including climbing and jumping.

A motor pattern which might be expected to have shared causal factors with other play patterns is close-contact wrestle, but the results do not support this expectation. Its course of development correlated more highly with those of non-play locomotor patterns and except in the two younger subjects it tended not to occur in temporal association with other play patterns.

There is no obvious reason for thinking that the physical environment controlled its occurrence, but there are other possible reasons for its weak developmental and temporal associations with other play patterns.

1. it might have served different functions from little-contact wrestling and play running. The benefit to be gained from it might not have required that it was performed with running. The possibility of it providing a different kind of exercise from little-contact wrestle was discussed in Chapter 8;
2. it might have been controlled by different motivational factors from little-contact wrestle. Owens (1975a) was more specific when he suggested that different types of play wrestling were brought about by different levels of fear.
3. the sequencing of motor patterns in play may have been such that close-contact wrestle tended to occur in isolation or, if it did occur in bouts with running, separated from running by other motor patterns. This is consistent with the findings of Leresche (1976) concerning the sequence of motor patterns in the play of zoo-living hamadryas baboons. Her behaviour categories were not identical to those in the present study but there is a rough equivalence between "chase", "face-off" and "wrestle" in her study and "play run", "little-contact wrestle" and "close-contact wrestle" respectively in the present study. Face-off and chase occurred

in sequence more frequently than would be expected by chance, as did wrestle and face-off; but wrestle and chase occurred in sequence with less than chance frequency. She described wrestling as being more likely to occur on its own than integrated into a sequence with other play activities; but if it was followed by chasing the two patterns would be separated by face-off. The findings of the present study are not entirely consistent with those of Leresche in respect of the relationship between close-contact and little-contact wrestle. If it is assumed that the behaviour categories in the two studies were reasonably equivalent then Leresche's study predicts that close-contact and little-contact wrestle in the present study should be temporally associated. That prediction was borne out only by Kenya at 6-12 weeks and Safron at 10-21 weeks;

4. Close-contact wrestle depended more on the type of partner than did other play patterns. It was shown in Chapter 8 that close-contact wrestle was typically performed by young infants and against older partners, and that in those partnerships the younger partner was less likely to perform little-contact wrestle.

The results suggest that play as a whole is heterogeneous in respect of development and temporal associations, and hence, it can be argued, heterogeneous in its causal factors. Those factors might include aspects of the physical environment, which put constraints on the performance of such patterns as climbing and acrobatics; the type of play partner, which determines the type of wrestling and (from Chapter 8) the proportions of contact and non-contact; the stage of neuro-muscular development, which limits the degree to which an infant can climb and engage in acrobatics; and motivational factors which might control the type of wrestling. On the other hand the two motor patterns play run and little-contact wrestle, are homogeneous in development and temporal association. They probably represent a composite behaviour pattern present in most, but not all, bouts of play.

In both the developmental and temporal analyses it was shown that play patterns and non-play patterns tended to form separate clusters; a finding which supports the notion that play is a behavioural phenomenon distinct from other activities. But it could be argued that no other finding was possible in this study, or any other, where play was defined by operational criteria at the start. That is, play was bound to be shown to exist because it was decided at the start that it should exist! This criticism can be challenged. If play were merely an imaginary category which a researcher imposed on a subject's repertoire of mobile activity then those samples of activity designated as playful would show age changes in the frequencies of component motor patterns similar to those in the overall population of behaviour from which the sample was taken. Thus one would expect the play and non-play versions of a given motor pattern to be correlated in their development trends. The present results show that, except for jumping, the development of play and non-play versions of any locomotor patterns correlate less highly with each other than with other locomotor patterns within the same context. Play is therefore unlikely to have been an artificial construct containing a sample of the current behaviour repertoire.

The only other baboon study to have described the development of locomotor patterns in different contexts is that of Chalmers (1980a and b). The two contexts were not play and non-play but social encounters and non-encounters. Unpublished results show that once certain motor patterns develop they are used irrespective of whether the context is an encounter or non-encounter, but that other motor patterns are performed with frequencies which depend on the context. Crawling and hanging had similar age changes of frequency in both contexts. Walking developed differently in the two contexts, increasing in frequency in non-encounters and remaining constant in encounters. Run, jump and climb showed development trends in the two contexts (from birth to over 6 years) which gave high rank correlation coefficients. But their frequencies declined, after 20 weeks, more rapidly in non-encounters than in encounters, enabling Chalmers to conclude that age changes were different in the two contexts.

Not all encounters were necessarily playful just as in the present study not all non-play was non-social. Results from these two studies may be mutually consistent but they do not represent replications of the same findings.

Summary

Developmental groups were identified among the motor patterns which could be performed away from the mother. The most highly intercorrelated groups were the object manipulatory patterns related to feeding, and the play patterns of running and little-contact wrestling. The motor patterns which formed the most consistent temporal clusters were those which were performed solely on the mother, object manipulatory patterns related to feeding and play patterns, particularly running and little-contact wrestling. These findings suggest that play running and little-contact wrestling formed a composite pattern which was a genuine phenomenon.

Around that central element play consisted of other motor patterns with different development trends and different degrees of temporal association. Play could therefore be considered heterogeneous in those respects, comprising elements which were under the control of different causal factors and possibly with different functions.

Chapter 10. Results: an investigation of associations between object manipulation and play

A suggestion was made in Chapter 5 that when an infant held and mouthed an object it had the opportunity to discover some of that object's properties, and that this opportunity was greatest on occasions when it held and mouthed for a long time. Put in another way, when an infant investigated an object it would probably have held and mouthed it for longer than otherwise. Intervals in which hold and mouth was scored, but not pick-up, were offered as a measure of long-bout mouthing and hence of investigation.

Investigation and play have frequently been linked in the literature, both functionally and causally. They might serve similar functions, such as in acquiring information or calibrating an animal's developing abilities; or they might share causal factors, such as a certain degree of novelty or some aspect of motivation.

In this chapter evidence is sought for such an association by examining correlations between long-bout mouthing and measures of play and other activity. Three types of correlation are examined: between development trends, temporal association and between frequencies in individual subjects.

1. Development trends: correlation of age changes in weighted mean frequencies

Figure 94 showed that age changes in the frequency of long bout mouthing correlated highly with mobile activity.

This could reflect an inverse relationship with time spent feeding. A greater dependence on solid food may have meant that the frequency of pick-up and hold and mouth increased, and possibly that the time spent mouthing each food item did not increase, or even decreased, causing the long bout mouthing scores to vary accordingly. This would have been especially so if the chosen food items were small, such as shoots, buds and livestock pellets. With more time spent on feeding there would have been less time for mobile activity. So, long bout mouthing and mobile activity may have been forced to vary together through shared opportunity.

Table 31 shows that age changes in the frequency of long bout mouthing correlated most highly with non-play locomotion, particularly walking and jumping; but of the various measures of play it correlated most highly with close-contact wrestle.

2. Temporal association (Figures 95 to 99)

The temporal association reported in Chapter 9 between long bout mouthing and hold and mouth resulted from the way long bout mouthing was defined. There were no other significant associations with long bout mouthing with an observed frequency of 5 or more and chi-square giving $p<0.001$. However, when matrices from which Figures 95 to 99 were drawn were examined applying reduced criteria (observed frequency greater than 1 and $p<0.05$) other associations became apparent (see Table 34).

The positive associations were with non-play locomotor patterns, especially climbing and acrobatics. There were no significant temporal associations between long bout mouthing and any form of play, including close-contact wrestle. Any temporal association with play was at the level of chance.

3. Correlation between frequencies shown by individual subjects

The data from each of 9 subjects between the ages 6 and 89 weeks were lumped (Safron, Aubrey, Gush, Sigmund, Capone, Rover, Deag, Kenya, Viola). These subjects were selected because they were off-nipple in more than 50 intervals and so their data came from a reasonably sized sample of intervals. One subject, Davey, was not included because in that age range he had been off-nipple in less than 20 intervals. Gilian was also not included because there were no data for her on some of the motor patterns; she had died before touch and wrestling types were added to the behaviour catalogue.

Spearman rank correlation coefficients were calculated between frequencies (percentage of off-nipple intervals) of 5 object manipulation patterns (long bout mouthing, short bout mouthing, pick-up, hold and mouth and touch) and behaviours contributing to mobile activity (non-play mobile

Table 34. Temporally associated motor patterns (derived from the matrices for Figures 95 to 99) with cluster criteria less rigorous than for Table 33 (observed frequency > 1, chi-square $> =3.84$, $p < 0.05$)

	long bout mouthing associated with:	subject	age, weeks	observed frequency	expected frequency	$p <$
positive associations	non-play swing/hang	Deag	12-14	4	0.7	0.01
	non-play climb-up	Deag	12-24	6	2.5	0.02
	non-play swing/hang	Safron	10-21	4	1	0.02
	non-play run	Safron	10-21	12	6.7	0.05
negative associations	rooting	Safron	10-21	1	5.9	0.05
	scratch ground	Kenya	6-12	5	1.4	0.01

activity, play walk, play run, play jump, play climb-up, play swing/hang, close-contact wrestle, little-contact wrestle, poke/touch). They are shown in Table 35. The only significant positive correlations are between long bout mouthing and non-play, and long bout mouthing and close-contact wrestle. In other words, long bout mouthing was performed most by those individuals who were most active outside of play and who also performed close-contact wrestling most frequently. Long bout mouthing had a stronger relationship with non-play than with close-contact play.

The nature of this three-part intercorrelation was investigated further by examining the correlations between long-bout mouthing, close-contact wrestle and the component locomotor patterns of non-play (Table 36). The significant correlations are with climbing and acrobatic motor patterns, the strongest being between long bout mouthing and non-play climb-up. Infants who climbed and locomoted most on raised structures also tended to be the ones who did most close-contact wrestling and who did most long bout mouthing.

Discussion

None of these results support a strong relationship between long bout mouthing and any form of mobile activity. However, the frequency of long bout mouthing changed with age following a trend more similar to those of non-play locomotor patterns than to those of play patterns; and close-contact wrestle followed age changes more similar to those of long bout mouthing than did any other form of play. Temporal association was not responsible for this latter similarity in development since long bout mouthing and close-contact wrestle occurred together no more frequently than predicted by chance. There was some evidence (based on few observed instances and at lower significance levels) that long bout mouthing did tend to occur close in time to non-play climbing and acrobatics. Those developmental and temporal relationships were strengthened by correlations which suggested that those infants who did more long bout mouthing also

Table 35. Correlation of motor patterns contributing to mobile activity with object manipulation patterns. Spearman rank correlation coefficients are between the frequencies shown by 9 subjects; for each subject data are lumped between ages 6-89 weeks.

	non-play mobile activity	play walk	play run	play jump	play climb-up	play swing/ hang	close-contact wrestle	little-contact wrestle	poke/ touch
long bout mouthing	+0.87 **	+0.18	+0.37	+0.33	+0.45	+0.45	+0.77 *	+0.48	+0.54
short bout mouthing	+0.02	-0.52	0.00	+0.37	-0.04	-0.17	-0.40	-0.22	-0.57
pick-up	-0.33	-0.42	+0.03	+0.33	+0.13	-0.03	-0.40	-0.22	-0*78
hold and mouth	+0.07	-0.58	+0.13	+0.35	+0.14	-0.03	-0.28	-0.18	-0.67
touch	-0.35	-0.20	-0.67	-0.38	-0.23	-0.27	-0.58	-0.28	-0.01

** ..... two-tailed $p < 0.01$

* ..... two-tailed $p < 0.05$

Table 36. Correlation of non-play locomotor patterns with long bout mouthing and with close-contact wrestle. Spearman rank correlation coefficients are between the frequencies shown by 9 subjects; for each subject data are lumped between ages 6-89 weeks

	non-play mobile activity	non-play walk	non-play run	non-play jump	non-play climb-up	non-play climb-down	non-play swing/hang
long bout mouthing		+0.20	+0.22	+0.28	+0.82 **	+0.75 *	+0.75 *
close contact wrestle	+0.55	-0.07	+0.07	+0.42	+0.63 *	+0.77 *	+0.68 *

** ..... One tailed $p < 0.01$

* ..... One tailed $p < 0.05$

climbed and swung more and did more close-contact wrestling.

Although solitary, self-motion play (Means and Harlow, 1975) was not among the behaviour categories defined in this study, it is reasonable to assume that had it been included, energetic climbing and acrobatics would have been component patterns. The present results can be interpreted as showing a relationship between a form of object investigation and behaviour which in other studies might have been called solitary play. No claim can be made for a relationship with social play as a whole but there may be an association with at least one type, close-contact wrestle.

Chalmers (1980b) showed a developmental link between the use of hands and mouth in manipulating objects and their use in manipulating and wrestling with conspecifics. He described an ontogenetic sequence in which, soon after birth, infants touched and grasped objects and other baboons indiscriminately, later simultaneously mouthing the things they grasped, and eventually differentiating between them so that, increasingly, edible objects were eaten, inedible objects were mouthed, group members at a distance were mouthed *at* (given the open mouth play-face) and group members close-to were mouthed and wrestled *with*. Chalmers was at pains to point out that while these behaviours might be considered "the same type" of behaviour because they shared ontogenetic precursors, that did not indicate that they necessarily shared causal mechanisms.

Results from the present study hint at a relationship between a category of object manipulation and a type of wrestling. It would be worthwhile, in the light of Chalmers' findings, to investigate this relationship further, as well as the possible relationship between energetic locomotor activity and object manipulation. Such a study could be similar in general design to that of the present one and that of Chalmers. The frequency of motor patterns could be measured in several contexts, such as during object manipulation, social interaction and non-social activity. For instance, object manipulatory patterns could be observed in social and non-social activity, or in socially playful and non-playful contexts, and particular locomotor patterns could be described in social, non-social and object manipulatory contexts. It would require that motor patterns were sub-divided to a finer degree than in either Chalmers' or the present study to allow for the possibility that motor patterns which are only subtly different in form might have significantly different associations. Chalmers' and the present study were restricted by the limits of the observers' perceptual abilities. In a future study cine photography or video would be useful techniques for obtaining high resolution descriptions for an ethogram of subtle motor patterns and for comparing the manner with which motor patterns are performed in the different contexts.

Summary

Some associations were found between long bout mouthing of objects and close-contact wrestling, but there was no evidence to link object manipulation with play as a whole. Long bout mouthing was more closely related to non-play climbing and acrobatics in development, temporal associations and correlation between subjects. It is possible that non-play in the present study contained behaviour which in other studies would have been considered as solitary locomotor play, and that object manipulation was in some way related to that.

Chapter 11. General discussion

This study was an attempt to describe age changes in the frequency of motor patterns, and to understand the changes which took place in play by comparing them with changes in other, non-play, contexts. Hypotheses were sought rather than tested; but one result of comparing motor pattern development in play and non-play contexts was to find evidence contrary to predictions from the practice hypothesis of play's function. If social play were the context in which locomotor patterns emerged and developed then those patterns would have been likely to have appeared first in social play and then shown increasing frequency in that context before becoming more frequent in other contexts. In fact, all locomotor patterns appeared first outside of social play and were only used in play once they were being performed quite frequently in the general repertoire. Infants of a given age appeared to use the locomotor skills they already had to generate bouts of play. In doing so they may have been creating situations which were beneficial to their development in other ways.

It is possible that motor pattern frequency is not the most useful variable to measure when trying to detect a practice phenomenon. The context in which a motor pattern appears most frequently may not be the one which provides most valuable practice. If a particular behavioural context does provide the optimum conditions for practice it may be structured in such a way as to promote maximum improvement with a minimum of repetitions. In other words, an infant might improve its performance of a motor pattern as much through performing it a few times in social play as by performing it many times in non-play. Future investigations of practice in play could quantify limb and body movements using cine photography or video and obtain measures of the relative efficiency of practice in play and non-play contexts.

In all four behavioural contexts (behaviour associated with the mother, object manipulation, play, non-play) some noteable changes happened between 18-23 weeks and 24-29 weeks which marked the 4 to 6 months period as an interesting phase in development. Infants of that age had a full locomotor repertoire which they used in both play and non-play, but at 24-29 weeks there was a peak in the proportion of that activity which was play. Future research into baboon play should perhaps focus on the 4 to 6 months age range in the expectation of it being particularly rich in clues to play's roles in development. Soon after that age infants lead a fairly independent life, feeding themselves and entering into frequent interactions with other group members. Inefficiencies in early independent life might be especially costly for survival. Altmann (1980) reported that the highest mortality rate in wild baboons is in first year infants. If play functions to increase an individual's efficiency at coping with independent life, then it should be most effective just before the level of independence becomes critical.

Fagen's (1975, 1981) computer models predict that there will be most play at an age when there is least other demand on an infant's complement of energy and time; that is, while it still uses its mother for nutrition and protection and is not yet required to spend a great deal of time foraging.

From the description which has come out of the present study of development in object manipulation, mother related behaviour and general mobile activity, the age blocks 12-17 weeks and 18-23 weeks might have been expected, from Fagen's model, to be the ones in which play activity was greatest. Contact with mother was still high, general mobile activity was at a maximum and objects were still very frequently manipulated when infants were in contact with the mother. The latter observation might indicate that infants of that age were feeding on pieces of solid food which the mother had foraged. Non-play locomotion was at its peak then but not play.

This highlights the problem of definition which is met in all studies of play. Should all vigorous infant activity be considered playful or only that accompanied by special signals? If the former, then the results from the study are consistent with Fagen's models. If, however, play is defined as a behavioural and communicatory transaction the predictive models should weigh heavily for the energy and risk costs and benefits deriving from social consequences.

In this study I have opted for the second, social definition. In doing so I have been able to offer an explanation for age changes in play's frequency and the playful performance of particular locomotor patterns, which is an alternative to those based on energy and time budgeting. There was a conspicuous increase in the playful performance of vigorous locomotor patterns during the same age block, 24-29 weeks, as infants achieved their full, mature colouration. I have suggested that social play is a strategy which extends some of the immunity that the black natal coat may originally have given. This is not the only possible interpretation of the data. In fact the evidence is not strong, with only two subjects in the crucial age block. I wish only to draw attention to the possible effects of infant colour on play; a point which has received only slight consideration in the literature.

An interesting thought provoked by this topic is that play signals might achieve their effect by mimicking infantile movements. Fagen (1976) has argued that since the speed of contraction of muscle fibres is the same in infants as it is in adults, in relation to body size infant muscles seem to contract more slowly. He has suggested that this produces the apparently relaxed, loose body tone of infant play. He has not taken this argument further but by the same logic all infant movements would have a quality different from those of mature animals. Young infants might move in a "cute" and "playful" way because of the properties of their muscles. Older, larger infants who are capable of a more mature style of movement might sometimes perform exaggerated but relaxed movements which mimic the appearance of young infant behaviour and thereby transmit a signal as if from a young infant.

A problem which arises from viewing play as social behaviour in which older animals mimic much younger animals is that it disqualifies very young infants from playing. This obstacle would be overcome if it were shown that very young infants can assume a mode of movement which is even more exaggerated and relaxed than their usual immature form and which humans can recognize as play. Loizos (1966) has given this to be the case. The question can only be answered by analysing movements with cine photography or video.

Some authors have questioned the validity of play as a single distinct category of behaviour (e.g. Berlyne, 1969; and Lazar and Beckhorn, 1974). Their criticisms are aimed at the use of one term to cover a diversity of social and solitary behaviours. In the present study the problem was simplified by restricting the term play to social behaviour where clear signals were transmitted or where there was a quality which most people would agree was "playful". The behaviour within that definition was analysed to see if it could best be described as a single category or whether there were clear sub-categories with separate patterns of development and temporal association. Development trends and temporal associations were also compared between play and non-play to find whether the play category was distinct on grounds other than the operational definition. The development and temporal groupings which emerged supported the view that playfully performed motor patterns in social encounters are a distinct category compared with basically similar motor patterns in other contexts, but that the category is heterogeneous in its internal development and temporal associations.

The design of the study can be criticised as not allowing the results to distinguish the effects of a play/non-play dichotomy from social/non-social, because the composition of non-play - how much was social and how much was non-social - was not recorded. If the bulk of social behaviour was playful then the results may simply show that the frequency of a locomotor pattern in social encounters changed with age differently from the way it changed in solitary activity, thus validating social and non-social behaviours as distinct categories.

I believe, however, that the results say something more useful than that. I know from my unrecorded observations that infant non-play included much behaviour which was directed at other group members and that socially directed behaviour was by no means all playful.

Another criticism concerns the finding that play and non-play motor patterns formed separate temporal clusters. That would have been the inevitable result had the record of continuous activity been divided up into periods of play and non-play. If that were the case then there would be no justification for using those clusters as independent support of the play/non-play distinction. I would answer this by pointing out that the behaviour was not partitioned into play and non-play bouts. When a subject switched from performing one motor pattern to performing another a fresh decision was made as to whether it was in play or non-play. That is, I made an effort to score each new motor pattern independently. Because of this I believe that the reported temporal associations are more than simply artifacts of the recording technique.

No form of object manipulation recorded in this study can be regarded as a category of play by virtue of developmental or temporal association with social play. During observation sessions I was aware of young baboons handling objects, particularly sticks, in rather bizarre ways. Occasionally a floppy or whip-like object was waved energetically from side to side or an infant might hold one end of a stick in its mouth and pull on the other end with its hands or feet. Apart from my finding these events very entertaining there were no objective criteria by which I could class them as play. It was reasonable to expect that if there were developmental or causal links between, at least, those involving extended use of the mouth and social play, they would show up as correlated development trends or temporal clusters. No strong relationships of that nature were discovered.

Smith (1981) reviewed accounts of manipulative play in primates and cited reports of chacma baboons (Hamilton, Buskirk and Buskirk, 1977) and macaques (Chevalier-Skolnikoff, 1977; Parker, 1977) engaging in repetitive, non-nutritive manipulation of objects. He gave the main example as bouncing on branches, a behaviour not recorded in the present study and which certainly would not have counted as object manipulation. He went on to discuss the possible origin of object play motor patterns: from functional object manipulation or from social behaviour? He argued in favour of a relationship between object play and social manipulative play because both involve "trial and error" manipulation. He surmised that social play would be a likely context for young baboons and macaques to engage in repetitive, playful object manipulation. My results do not support his proposition.

The study of play development falls between the structuralist and functionalist approaches to play research (Fagen, 1974). The present study was primarily concerned with describing development, questioning the validity of the play concept and examining its possible heterogeneity, rather than vigorously testing hypotheses of cause and function. It was therefore based more in the structuralist camp; but since its findings are relevant to discussions of cause and function it does make a contribution to the functionalist view.

It was begun at a time when the most clearly defined questions about play were structural, concerning definitions and the constituent motor patterns; and answers were interpreted with reference to the three main functional themes of motor training, information gathering and socialization. Fagen (1981) has claimed that the plea for quantification led during the early 1970's to an over-abundance of structural data which was not purposive, in that it was collected without the aid of a strong theoretical framework. He has gone a long way towards providing a suitable framework based on resource allocation and sociobiological principles. If that framework had been available earlier more attention might have been given in this study to the questions of feeding, identification of play partners and partner preferences.

Fagen would criticise this study, with its particular emphases, as providing quantitative data without theoretical guidance. Nonetheless I believe that it can contribute to the current debate on play. Future investigations into play's functions and cause will be carried out with the advantage of clear hypotheses; but decisions will always have to be made on how to define play: whether to regard it as one or several phenomena, and what weight to give to play signals as defining criteria? What is more, since functional and causal theories have implications for development, age changes in motor pattern frequency may be useful dependent variables with which to test functional and causal hypotheses.

This study complements those of Owens (1975, a and b) and Chalmers (1980, a and b) which remain the only long term, high resolution, quantitative studies of baboon play motor pattern development, by providing some supportive and some contradictory data. The result is that for at least one primate group (the baboons) there is a body of quantified information on several aspects of play development in wild and semi-wild conditions. This background will help future investigators of play to ask useful research questions and to formulate testable hypotheses.

References

Altmann, J. 1974. Observational study of behaviour sampling methods. Behaviour, 49, 227-267.

Altmann, J. 1980. Baboon mothers and infants. Cambridge, Mass.: Harvard University Press.

Altmann, S.A. 1962. Social behaviour of anthropoid primates: Analysis of recent concepts. In E.L. Bliss (ed.), Roots of behaviour. New York: Hoeber.

Altmann, S.A. and Altmann, J. 1970. Baboon ecology. Chicago: University of Chicago Press.

Angus, S. 1971. Water contact behaviour of chimpanzees. Folia Primat., 14, 51-58.

Bajpai, R.K. 1980. The effects of early social deprivation on rhesus monkeys: Social responsiveness. Primates, 21, 4, 510-514.

Baldwin, J.D. 1969. The ontogeny of social behaviour of squirrel monkeys (Saimiri sciureus) in a semi-natural environment. Folia Primat., 11, 35-79.

Baldwin, J.D. and Baldwin, J.I. 1971. Squirrel monkeys (Saimiri) in natural habitats in Panama, Columbia, Brazil and Peru. Primates, 12, 45-61.

Baldwin, J.D. and Baldwin, J.I. 1973. The role of play in social organization: Comparative observations of squirrel monkeys (Saimiri). Primates, 14, 369-381.

Baldwin, J.D. and Baldwin, J.I. 1974. Exploration and social play in squirrel monkeys (Saimiri). Am. Zool., 14, 303-315.

Baldwin, J.D. and Baldwin, J.I. 1977. The role of learning phenomena in the ontogeny of exploration and play. In S. Chevalier-Skolnikoff and F.E. Poirier (eds.), Primate bisocial development, pp.343-406. New York: Garland.

Barnett, S.A. 1958. Exploratory behaviour. Brit. J. of Psychol., 49, 289-310.

Barnett, S.A. 1963. The rat, a study in behaviour. Chicago: University of Chicago Press.

Barrett, P. and Bateson, P.P.G. 1978. The development of play in cats. Behaviour, 66, 106-120.

Bateson, G. 1955. A theory of play and fantasy. Psychiat. Res. Rep., 2, 39-51.

Bateson, P., Martin, P. and Young, M. 1981. Effects of interrupting cat mothers' lactation with bromocriptine on the subsequent play of their kittens. Physiology and Behaviour, 27, 841-845.

Bateson, P. and Young, M. 1981. Separation from the mother and the development of play in cats. Anim. Behav., 29, 173-180.

Beach, F.A. 1942. Comparison of copulatory behaviour of male rats raised in isolation, cohabitation and segregation. J. Genet. Psychol., 60, 121-134.

Beach, F.A. 1945. Current concepts of play in animals. Am. Nat., 79, 523-541.

Beach, F.A. 1968. Coital behaviour in dogs. III, effects of early isolation on mating in males. Behav., 30, 218-238.

Bekoff, M. 1972. The development of interaction, play and metacommunication in mammals: An ethological perspective. Q. Rev. Biol., 47, 412-434.

Bekoff, M. 1974. Social play and play soliciting by infant canids. Am. Zool., 14, 323-340.

Bekoff, M. 1976. Animal play: Problems and perspectives. In P.P.G. Bateson and P.H. Klopfer (eds.), Perspectives in ethology, Vol.2, pp.165-188. New York and London: Plenum Press.

Bekoff, M. and Fox, M.W. 1972. Postnatal neural ontogeny, environmental-dependent and/or environmental-expectant. Dev. Psychobiol., 5, 323-341.

Berlyne, D.E. 1960. Conflict, arousal and curiosity. New York: McGraw-Hill.

Berlyne, D.E. 1969. Laughter, humour and play. In G. Lindzey and E. Aronson (eds.), The handbook of social psychology, Vol.3, pp.795-949. Mass.: Addison-Wesley.

Berman, C.M. 1978. The analysis of mother-infant interaction in groups: Possible influence of yearling siblings. In D.J. Chivers and J. Herbert (eds.), Recent advances in primatology, Vol.1, pp.111-113. London: Academic Press.

Berman, C.M. 1980. Mother-infant relationships among free-ranging rhesus monkeys on Cayo Santiago: A comparison with captive pairs. Anim. Behav., 28, 860-873.

Bertrand, M. 1969. The behaviour repertoire of the stumptail macaque. New York: S. Kargen.

Biben, M. 1979. Predation and predatory play behaviour of domestic cats. Anim. Behav., 27, 81-94.

Bierens de Haan, J.A. 1952. The play of a young solitary chimpanzee. Behaviour, 4, 144-156.

Blurton Jones, N. 1967. An ethological study of some aspects of social behaviour of children in nursery school. In D. Morris (ed.), Primate ethology. London: Weidenfeld and Nicholson.

Blurton Jones, N. 1972. Categories of child-child interaction. In N. Blurton Jones (ed.), Ethological studies of child behaviour, pp.97-127. Cambridge: Cambridge University Press.

Bolwig, N. 1959. A study of the behaviour of the Chacma baboon (Papio ursinus). Behaviour, 12, 136-163.

Brownlee, A. 1954. Play in domestic cattle, an analysis of its nature. Brit. Vet. J., 110, 48-68.

Bruner, J.S., Jolly, A. and Sylva, K. 1976. Play, its role in development and evolution. Harmondsworth, Middlesex: Penguin Books.

Byers, J. 1980. Play partners in Siberian Ibex (Capra ibex sibirica). Z. Tierpsychol., 53, 23-40.

Carpenter, C.R. 1934. A field study of the behaviour and social relationships of howling monkeys. Comp. Psychol. Monogr., 10, 1-168.

Chalmers, N.R. 1980a. The ontogeny of play in feral olive baboons (Papio anubis). Anim. Behav., 28, 570-585.

Chalmers, N.R. 1980b. Developmental relationships among social, manipulatory, postural and locomotor behaviours in olive baboons (Papio anubis). Behaviour, 74, 22-37.

Chalmers, N.R. and Locke-Haydon, J. 1981. Temporal patterns of play bouts in captive common marmosets (Callithrix jacchus). Anim. Behav., 29, 1229-1238.

Cheney, D.C. 1978. The play partners of immature baboons. Anim. Behav., 26, 1038-1050.

Chepko, B.D. 1971. A preliminary study of the effects of play deprivation on young goats. Z. Tierpsychol., 28, 517-526.

Chevalier-Skolnikoff, S. 1977. A Piagetian model for describing and comparing socialization in monkey, ape and human infants. In S. Chevalier-Skolnikoff and F.E. Poirier (eds.), Primate bisocial development. New York: Garland.

Cochran, W.G. 1954. Some methods for strengthening the common chi-square tests. Biometrics, 10, 417-451.

Colgan, P.W. 1978. Hierarchical cluster analysis. In P.W. Colgan (ed.), Quantitative ethology. London: Wiley.

Dawkins, R. 1976. Hierarchical organization: A candidate principle of ethology. In P.P.G. Bateson and R.A. Hinde (eds.), Growing points in ethology. Cambridge: Cambridge University Press.

De Vore, I. 1963. Mother-infant relationships in free-ranging baboons. In H.L. Rheingold (ed.), Maternal behaviour in mammals. New York: Wiley.

Dunbar, R.I.M. 1974. The social organization of the gelada baboon (Theropithecus gelada). Ph.D. Thesis, University of Bristol.

Egan, J. 1976. Object play in cats. In J.S. Bruner, A. Jolly and K. Sylva (eds.), Play, its role in development and evolution. Harmondsworth, Middlesex: Penguin Books.

Eibl-Eibesfeldt, I. 1963. Angebornes and erworbenes im Verhalten einiger Säuger. Z. Tierpsychol., 20, 705-754.

Eibl-Eibesfeldt, I. 1975. Ethology - the biology of behaviour. New York: Holt, Rinehart and Winston.

Eifermann, R.K. 1972. It's child's play. In E. Bower, L.M. Shears and C.C. Thomas (eds.), Games in education and development. Springfield, Illinois.

Einon, D.F., Morgan, M.J. and Kibbler, C.C. 1978. Brief periods of socialization and later behaviour in the rat. Devel. Psychobiol., 2, 3, 213-225.

Espmark, Y. 1971. Mother-young relationships and ontogeny of behaviour in reindeer (Rangifera tarandus L). Z. Tierpsychol., 29, 42-81.

Etkin, W. 1964. Theories of socialization and communication. In W. Etkin (ed.), Social behaviour and organization among vertebrates, pp.167-205. Chicago: University of Chicago Press.

Ewer, R.F. 1966. Juvenile behaviour in the African ground squirrel, Xerrus erythropus. Z. Tierpsychol., 23, 190-126.

Ewer, R.F. 1968. Ethology of mammals. Logos Press.

Fady, J.C. 1969. Les jeux sociaux: le compagnon de jeux chez les jeunes. Observation chez Macaca irus. Folia Primat., 11, 134-143.

Fagen, R.M. 1974. Selective and evolutionary aspects of animal play. Amer. Nat., 108, 850-858.

Fagen, R.M. 1975. Modelling how and why play works. In J.S. Bruner, A. Jolly and K. Sylva (eds.), Play, its role in development and evolution, pp.96-115. Harmondsworth, Middlesex: Penguin Books.

Fagen, R.M. 1976. Exercise, play and physical training in animals. In P.P.G. Bateson and P.H. Klopfer (eds.), Perspectives in ethology, Vol.2, pp.189-219. New York: Plenum Press.

Fagen, R.M. 1980. Ontogeny of animal play behaviour: Bimodal age schedules. Anim. Behav., 28, 1291-1292.

Fagen, R.M. 1981. Animal play behaviour. Oxford: Oxford University Press.

Fagen, R.M. and George, T.K. 1977. Play behaviour and exercise in young ponies (Equus caballus L). Behav. Ecol. and Sociobiol., 2, 267-269.

Farentinos, R.C. 1971. Some observations on the play behaviour of the stellar sea lion (Eumetopius jabata). Z. Tierpsychol., 28, 428-438.

Fedigan, L. 1972. Social and solitary play in a colony of vervet monkeys (Cercopithecus aethiops). Primates, 13, 347-364.

Ferchmin, P.A., Bennett, E.C. and Rosenzweig, M.R. 1975. Direct contact with enriched environment is required to alter cerebral weight in rats. J. Comp. Phys. Psychol., 88, 360-367.

Ferchmin, P.A. and Eterovic, V.A. 1977. Brain plasticity and environmental complexity: role of motor skills. Physiol. and Behav., 18, 455-461.

Fox, M.W. 1970. Facial expression in canids. Behaviour, 36, 49-73.

Fox, M.W. and Clark, A.L. 1971. The development and temporal sequencing of agonistic behaviour in the coyote (Canis latrans). Z. Tierpsychol., 28, 262-278.

Fuller, J.L., Easler, C.A. and Banks, E.M. 1950. Formation of conditioned avoidance responses in young puppies. Amer. J. Physiol., 3, 462. Cited in A.L. Steiner (1971).

Garvey, C. 1976. Some properties of social play. In J.S. Bruner, A. Jolly and K. Sylva (eds.), Play, its role in development and evolution, pp.570-583. Harmondsworth, Middlesex: Penguin Books.

Gentry, R.L. 1974. The development of social behaviour through play in the stellar sea lion. Am. Zool., 14, 391-403.

Globius, A., Rosenzweig, M.R., Bennett, E.C. and Diamond, M.C. 1973. Effects of differential experience on dendritic spine counts. J. Comp. Physiol. Psychol., 82, 175-181.

Greif, E.B. 1976. Sex role playing in pre-school children. In J.S. Bruner, A. Jolly and K. Sylva (eds.), Play, its role in development and evolution. Harmondsworth, Middlesex: Penguin Books.

Groos, K. 1898. Play in animals. New York: Appleton Co.

Hall, K.R.L. 1962. The sexual agonistic and derived social behaviour patterns of the wild chacma baboon, Papio ursinus. Proc. Zool. Soc. Lond., 139, 283-327.

Hall, K.R.L. and De Vore, I. 1965. Baboon social behaviour. In I. De Vore (ed.), Primate behaviour, field studies of monkeys and apes. New York: Holt, Rinehart and Winston.

Hamilton, W.J. III, Buskirk, R.E. and Buskirk, W.H. 1977. Environmental determinants of object manipulation by chacma baboons (Papio ursinus) in two southern African environments. J. of Hum. Evol., 7, 205-216. Cited in P.K. Smith (1981).

Hansen, E.W. 1966. The development of maternal and infant behaviour in the rhesus monkey. Behav., 27, 107-149.

Harlow, H.F. 1961. The maternal affectional system. In B. Foss (ed.), Determinants of infant behaviour. London: Methuen.

Harlow, H.F. 1969. Age mate and peer affectional system. Adv. Study Behav., 2, 333-383.

Harlow, H.F. and Harlow, M.K. 1963. The maternal affectional system of rhesus monkeys. In H.L. Rheingold (ed.), Maternal behaviour in mammals.

Harlow, H.F. and Harlow, M.K. 1965. The affectional systems. In Behaviour of non-human primates, modern research trends, Vol.2, 287-334. A.M. Schrier, H.F. Harlow and F. Stollnitz (eds.), New York and London: Academic Press.

Harlow, H.F. and Harlow, M.K. 1966. Learning to love. Am. Scientist, 54, 244-271.

Harlow, H.F. and Zimmermann, R.R. 1959. Affectional responses in the infant monkey. Science, 130, 421-432.

Harper, L.V. 1968. The effects of isolation from birth on the social behaviour of guineapigs in adulthood. Anim. Behav., 16, 58-64.

Henry, J.D. and Herrero, S.M. 1974. Social play in the American black bear: Its similarity to canid social play and an examination of its identifying characteristics. Am. Zool., 14, 371-389.

Hinde, R.A. 1959. Unitary drives. Anim. Behav., 7, 130-141.

Hinde, R.A. 1970. Animal behaviour, a synthesis of ethology and comparative psychology, 2nd Edn. New York: McGraw Hill.

Hinde, R.A. 1971. Development of social behaviour. In A.M. Schreier and F. Stollnitz (eds.), Behaviour of non-human primates, Vol.3. New York and London: Academic Press.

Hinde, R.A. 1974. Biological bases of human social behaviour. New York: McGraw-Hill.

Hinde, R.A., Rowell, T.E. and Spencer-Booth, Y. 1964. Behaviour of socially living rhesus monkeys in their first 6 months. Proc. Zool. Soc. Lond., 138, 1-21.

Hinde, R.A. and Spencer-Booth, Y. 1967. The behaviour of socially living rhesus monkeys in their first 2½ years. Anim. Behav., 15, 169-196.

Hinde, R.A. and Spencer-Booth, Y. Review lecture. The study of mother-infant interaction in captive group-living rhesus monkeys. Proc. Roy. Soc., B., 169, 177-201.

Hinde, R.A. and White, L.E. 1974. The dynamics of a relationship: Rhesus mother-infant ventro-ventral contact. J. Comp. Physiol. Psychol., 86, 8-23.

Hines, M. 1942. The development and regression of reflexes, postures and progression in the young macaque. Contrib. Embryol. Carneg. Inst., 196, 155-209.

Holloway, R.L. Jnr. 1966. Dendritic branching: Some preliminary results of training and complexity in rat visual cortex. Brain Res., 2, 393-396.

Hooff, J.A.R.A.M. van 1962. Facial expressions in higher primates. Symp. Zool. Soc. Cond., 8, 97-125.

Hooff, J.A.R.A.M. van 1967. The facial displays of the catarrhine monkeys and apes. In D. Morris (ed.), Primate ethology. London: Weidenfeld and Nicholson.

Horwich, R.H. 1972. The ontogeny of social behaviour in the grey squirrel (Sciurius carolinensis). Z. Tierpsychol. Suppl., 8.

Hutt, C. 1966. Exploration and play in children. Symp. Zool. Soc. Lond., 18, 61-81.

Jay, P.C. 1963. Mother-infant relationships in langurs. In H. Rheingold (ed.), Maternal behaviour in mammals. New York: Wiley.

Jay, P.C. 1965. The common langur of N. India. In I. De Vore (ed.), Primate behaviour, pp.197-249. New York: Holt, Rinehart and Winston.

Jay Dolhinow, P.C. and Bishop, N. 1970. The development of motor skills and social relationships among primates through play. Minn. Symp. on Child Psychol., 3. University of Minnesota Press.

Jolly, A. 1972. The evolution of primate behaviour. New York: Macmillan.

Kagen, J. and Beach, F.H. 1953. Effects of early experience on mating behaviour in male rats. J. Comp. Physiol. Psychol., 46, 204-208.

Kaufman, J.H. 1966. Behaviour of infant rhesus monkeys and their mothers in a free-ranging band. Zoologica N.Y., 51, 17-28.

Kaufman, I.C. and Rosenblum, L.A. 1969. The waning of the mother-infant bond in two species of macaque. In B. Foss (ed.), Determinants of infant behaviour, Vol. 4. London: Methuen.

Lancaster, J.B. 1971. Play-mothering: The relation between juvenile females and young infants among free-ranging vervet monkeys (Cercopithecus aethiops). Folia Primat., 15, 161-182.

Latta, J., Hopf, S. and Ploog, D. 1967. Observations on mating behaviour and sexual play in squirrel monkeys (Saimiri scuirens). Primates, 8, 229-246.

Lawick-Goodall, J. van 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr., 1.

Lazar, J.W. and Beckhorn, G.D. 1974. Social play or the development of social behaviour in ferrets (Mustela putorius). Amer. Zool., 14, 405-414.

Leresche, L.A. 1976. Dyadic play in Hamadryas baboons. Behaviour, 57, 190-205.

Leyhausen, P. 1965. Über die Funktion der relativen Stimmungshierarchie dargestellt am Beispiel der phylogenetischen und ontogenetischen Entwicklung des Beutesfangs von Raubtieren. Z. Tierpsychol., 22, 414-494.

Loizos, C. 1966. Play in mammals. Symp. Zool. Soc. Lond., 18, 1-9.

Loizos, C. 1967. Play behaviour in higher primates. In D. Morris (ed.), Primate ethology, pp.226-282. Chicago: Aldine.

Loizos, C. 1969. An ethological study of chimpanzee play. Proc. 2nd. Int. Congr. Primat., 1, 87-93.

Lorenz, K. 1956. Plays and vacuum activities in animals. In: Symposium. L'instinct dans le comportement des animaux et de l'homme. Paris: Masson.

Lumia, A.R. 1972. The relationship between dominance and play behaviour in the American buffalo (Bison bison). Z. Tierpsychol., 30, 416-419.

Marler, P. and Hamilton, W.J. 1966. Mechanisms of animal behaviour. New York: Wiley.

Mason, W.A. 1960. The effect of social restriction on the behaviour of rhesus monkeys. J. Comp. Physiol. Psychol., 53, 582-589.

Mason, W.A. 1961. Effects of age and stimulus characteristics on manipulatory responsiveness of monkeys raised in a restricted environment. J. Genet. Psychol., 99, 301-308.

Mason, W.A. 1965. The social development of monkeys and apes. In I. De Vore (ed.), Primate behaviour: Field studies of monkeys and apes, pp.514-543. New York: Holt, Rinehart and Winston.

Mason, W.A. 1967. Motivational aspects of social responsiveness in young chimpanzees. In H.W. Stevenson (ed.), Early behaviour: Comparative and developmental approaches. New York: Wiley.

Mason, W.A., Harlow, H.F. and Rueping, R.R. 1959. The development of manipulatory responsiveness in the infant rhesus monkey. J. Comp. Physiol. Psychol., 52, 555-558.

Mears, C.E. and Harlow, H.F. 1975. Play: Early and eternal. Proc. Nat. Acad. Sci. U.S.A., 72, 5, 1878-1882.

Meier, G.W. and Devanney, V.D. 1974. The ontogeny of play within a society: Preliminary analysis. Am. Zool., 14, 289-294.

Menzel, E.W. Jr. 1965. Responsiveness to objects in free-ranging Japanese monkeys. Behaviour, 26, 130-150.

Merrick, N.J. 1977. Social grooming and play behaviour of a captive group of chimpanzees. Primates, 18, 1, 215-224.

Meyer-Holzapfel, M. 1956. Über die Bereitschaft zu Spiel - und Instinkthandlungen. Z. Tierpsychol., 13, 442-462.

Miller, N.E. 1957. Experiments on motivation. Science, 126, 1271-1278.

Miller, R.E., Caul, W.F. and Mirsky, I.A. 1967. Communication of affects between feral and socially isolated monkeys. J. Pers. Soc. Psychol., 7, 231-239.

Miller, S. 1973. Ends, means and galumphing: Some leitmotifs of play. Am. Anthrop., 75, 87-98.

Mitchell, G.D. 1968. Intercorrelations of maternal and infant behaviours in Macaca mulatta. Primates, 9, 85-92.

Mitchell, G.D. 1972. Looking behaviour in the rhesus monkey. J. Phenomenol. Psychol., 3, 53-67.

Morgan, M.J., Einon, D.F. and Nicholas, D. 1975. The effects of isolation rearing on behaviour inhibition in the rat. Q. J. Exp. Psychol., 27, 615-634.

Mowbray, J.B. and Cadell, T.E. 1962. Early behaviour patterns in rhesus monkeys. J. Comp. Physiol. Psychol., 55, 3, 350-357.

Muller-Schwarze, D. 1968. Play deprivation in deer. Behaviour, 31, 144-162.

Muller-Schwarze, D. 1971. Ludic behaviour in young mammals. In M.B. Sterman, D.J. McGinty and A.M. Adinolfi (eds.), Brain development and behaviour. New York: Academic Press.

Nash, L.T. 1978. The development of the mother-infant relationship in wild baboons (Papio anubis). Anim. Behav., 26, 746-759.

Oakley, F.B. and Reynolds, P.C. 1976. Differing responses to social play deprivation in two species of macaque. In D.F. Lancy and B.A. Tindall (eds.), Anthropological study of play: Problems and prospects, pp.179-188. New York: Cornwall.

Oates, J.F. 1982. Coat colour aberrations in Presbytis johnii: a founder effect? Primates, 23, 307-371.

Opie, I. and Opie, P. 1969. Children's games in street and playground. London: Clarendon Press.

Owens, N.W. 1975a. Social play behaviour in free-living baboons, Papio anubis. Anim. Behav., 23, 387-408.

Owens, N.W. 1975b. A comparison of aggressive play and aggression in free-living baboons, Papio anubis. Anim. Behav., 23, 757-765.

Parker, S.T. 1977. Piaget's sensorimotor series in an infant macaque: A model for comparing unstereotyped behaviour and intelligence in human and non-human primates. In S. Chevalier-Skolnikoff and F.E. Poirier (eds.), Primate biosocial development. New York: Garland.

Piaget, J. 1951. Play, dreams and imitation in childhood. London: Routledge and Kegan Paul.

Piaget, J. 1965. The moral judgement of the child. New York: Free Press.

Poirier, F.E. 1969. The Nilgiri langur (Presbytis johnii) troop: Its composition, structure, formation and change. Folia Primat., 10, 20-47.

Poirier, F.E. and Smith, E.O. 1974. Socializing functions of primate play. Amer. Zool., 14, 275-287.

Poole, T.B. 1966. Aggressive play in polecats. Symp. Zool. Soc. Lond., 18, 23-44.

Poole, T.B. 1978. An analysis of social play in polecats (Mustelidae) with comments on the form and evolutionary history of the open mouth play face. Anim. Behav. 26, 36-49.

Poole, T.B. and Fish, J. 1975. An investigation of playful behaviour in Rattus norvegicus and Mus musculus. Proc. Zool., Soc. Lond., 175, 61-71.

Rasa, O.A.E. 1971. Social interaction and object manipulation in weaned pups of the northern elephant seal, Mirounga angustirostris, Z. Tierpsychol., 29, 82-102.

Rasa, O.A.E. 1973. Prey capture in the African dwarf mongoose, Helogale undulata refula. Z. Tierpsychol., 32, 449-488.

Redican, K.W. and Mitchell, G. 1974. Play between adult male and infant rhesus monkeys. Am. Zool., 14, 295-302.

Rhine, R.J. 1973. Variation and consistency in the social behaviour of two groups of stumptail macaques (Macaca arctoides). Primates, 14, 21-36.

Rhine, R.J. and Linville, A.K. 1980. Properties of one-zero scores in observational studies of primate social behaviour: The effect of assumption on empirical analysis. Primates, 21, 111-122.

Richard, A. 1970. A comparative study of the activity patterns and behaviour of Alouatta villosa and Ateles geoffroyi. Folia Primat., 12, 241-263.

Rose, M.D. 1977a. Positional behaviour of olive baboons (Papio anubis) and its relationship to maintenance and social acitivities. Primates, 18, 59-116.

Rose, M.D. 1977b. Interspecific play between free-ranging querezas (Colobus quereza) and vervet monkeys (Cercopithecus aethiops). Primates, 18, 4, 957-964.

Rowell, T.E., Din, M.A. and Omar, A. 1968. The social development of baboons in their first 3 months. J. Zool., 155, 461-483.

Sachs, B.D. and Harris, V.S. 1978. Sex differences and developmental changes in selected juvenile activities (play) of domestic lambs. Anim. Behav., 26, 678-684.

Sade, D.S. 1973. An ethogram of rhesus monkeys: Antithetical contrasts in posture and movement. Am. J. of Phys. Anthrop., 38, 537-542.

Schaller, G.B. 1972. The Serengeti lion. Chicago: University of Chicago Press.

Schapiro, S. and Vukovich, D.R. 1970. Early experience effects upon cortical dendrites. Science, 167, 292-294.

Schenkel, R. 1966. Play, exploration and territory in the wild lion. Symp. Zool. Soc. Lond., 18, 11-22.

Schiller, P.H. 1952. Innate constituents of complex responses in primates Psychol. Rev., 59, 177-191.

Scott, J.P. 1968. Early experience and the organization of behaviour. California: Brooks/Cole.

Siegel, S. 1956. Non-parametric statistics for behavioural sciences. New York: McGraw-Hill.

Simonds, P. 1965. The bonnet macaque in South India. In I. De Vore (ed.), Primate behaviour, field studies of monkeys and apes, pp.175-197. New York: Holt, Rinehart and Winston.

Simonds, P. 1974. The social primates. New York: Harper and Row.

Simpson, M.J.A. 1976. The study of animal play. In P.P.G. Bateson and R.A. Hinde (eds.), Growing points in ethology. Cambridge: Cambridge University Press.

Simpson, M.J.A. and Simpson, A.E. 1977. One-zero and scan methods for sampling behaviour. Anim. Behav., 25, 726-731.

Slater, P.J.B. 1978.
In P.W. Colgan (ed.), Quantitative ethology. London: Wiley.

Smith, P.K. 1981. Does play matter? Functional and evolutionary aspects of animal and human play. In
The behavioural and brain sciences. In press.

Smith, P.K. and Hagan, T. 1980. Effects of deprivation on exercise play in nursery school children. Anim. Behav., 28, 922-928.

Steiner, A.L. 1971. Play activity of Columbian ground squirrels. Z. Tierpsychol. 28, 247-261.

Stevenson, M.F. and Poole, T.B. 1982. Playful interactions in family groups of the common marmoset (Callithrix jacchus jacchus). Anim. Behav., 30, 886-900.

Suomi, S.J. 1973. Surrogate rehabilitation of monkeys reared in total isolation. J. Child Psychol. Psychiat., 14, 71-77.

Symons, D. 1974. Aggressive play and communication in rhesus monkeys (Macaca mulatta). Am. Zool., 14, 317-322.

Thorpe, W.H. 1963. Learning and instinct in animals. 2nd Edn. London: Methuen.

Toates, F.M. 1980. Animal behaviour - a systems approach. London: Wiley.

Voland, E. 1977. Social play of the common marmoset (Callithrix jacchus) in captivity. Primates, 18, 4, 883-901.

Washburn, S. and Hamburg, B. 1965. The implications of primate research. In I. De Vore (ed.), Primate behaviour, field studies of monkeys and apes, pp.607-623. New York: Holt, Rinehart and Winston.

Weisler, A. and McCall, R.B. 1976. Exploration and play. Am. Psychol., 31, 492-508.

Weiss-Bürger, M. 1981. An investigation on the influence of exploration and playing on learning by polecats (Mustela putorius and Mustela furo). Z. Tierpsychol., 55, 33-62.

Welker, W.I. 1956a. Some determinants of play and exploration in chimpanzees. J. Comp. Physiol. Psychol., 49, 84-89.

Welker, W.I. 1956b. Effects of age and exercise on play and exploration of young chimpanzees. J. Comp. Physiol. Psychol., 49, 223-276.

Welker, W.I. 1961. An analysis of exploration and play behaviour in animals. In D.W. Fiske and S.R. Maddi (eds.), Functions of varied experience. Illinois: Dorsey Homewood.

Wemmer, C. and Fleming, M.J.. 1974. Ontogeny of playful contact in a social mongoose, the meerkat, suricata suricata. Amer. Zool., 14, 415-426.

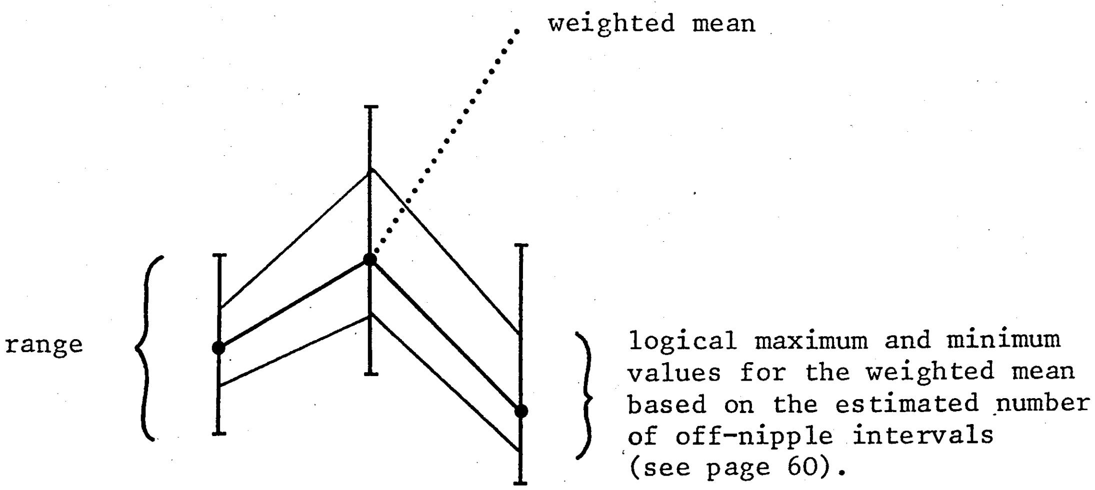
West, M. 1974. Social play in the domestic cat. Am. Zool., 14, 427-436.

Wilson, S. 1974. Juvenile play of the common seal, Phoca vitulina vitulina, with comparative notes on the grey seal, Halichoerus grypus. Behaviour, 48, 37-60.

Wilson, S. and Kleiman, D.G. 1974. Eliciting play: A comparative study (Octodon, Octodontomys, Pediolagus, Phoca, Choeropsis, Ailuropoda). Am. Zool., 14, 341-370.

Appendix I

Key to symbols used in the figures



J	juvenile
SA	sub-adult
AF	adult female
AM	adult male
M	mother

Other symbols are explained in the relevant figures.

Appendix II

Subject sample sizes

The number of subjects in each age block or age class are as shown below unless otherwise stated.

Age block (weeks) or age class	0-2	3-5	6-11	12-17	18-23	24-29	30-41	42-53	54-65	66-77	78-89	juv.	sub adult	adult fem.	adult male
No. of subjects	7	7	6	3	4	2	4	5	1	1	2	7	5	6	5

Where the sample sizes were different from these they are indicated by numbers above the relevant figures.

Appendix III

Calculating the weighted mean

Suppose the one-zero score for behaviour A is expressed as a percentage of the one-zero score for behaviour B.

Let A_1 and B_1 = scores for subject 1

A_2 and B_2 = scores for subject 2

$$\text{Thus } P_1 = \frac{A_1}{B_1} \times 100\% = \text{percentage for subject 1}$$

$$\text{and } P_2 = \frac{A_2}{B_2} \times 100\% = \text{percentage for subject 2}$$

$$\text{Weighted mean percentage Pw} = \frac{P_1B_1 + P_2B_2}{B_1 + B_2}\%$$

$$= \frac{100A_1B_1/B_1 + 100A_2B_2/B_2}{B_1 + B_2}\%$$

$$= \frac{A_1 + A_2}{B_1 + B_2} \times 100\%$$

$$\text{Thus Pw} = \frac{\Sigma A}{\Sigma B} \times 100\%$$

Tables A and B give the denominator (ΣB) for each weighted mean frequency in each figure.

TABLE A

figure number	Age blocks (weeks) or age/sex classes														
	0-2	3-5	6-11	12-17	18-23	24-29	30-41	42-53	54-65	66-77	78-89	J	SA	AF	AM
8, 9	2071	1096	3230	2834	2318	904	1732	2411	822	387	348	-	-	-	-
10	57	63	807	1460	1236	522	1316	2102	822	387	348	-	-	-	-
11	2071	1096	3230	2834	2318	904	1732	2411	822	387	348	-	-	-	-
12, 13	2071	1096	3230	2834	2318	904	1732	2411	822	387	348	-	-	-	-
14,15, 16	2071	1096	3230	2834	2318	904	1732	2411	822	387	348	483	528	477	653
17	1751	929	2897	2630	2156	889	1681	2577	-	-	-	-	-	-	-
18, 19	2071	1096	3230	2834	2318	904	1732	2411	822	387	348	-	-	-	-
21	2071	1096	3230	2834	2318	904	1732	2411	822	387	348	-	-	-	-
22, 23, 24, 25,	2071	1096	3230	2834	2318	904	1732	2411	822	387	348	-	-	-	-
26, 27	1933	946	3012	2834	2318	904	1509	2411	822	387	348	-	-	-	-
28	1719	896	2297	1410	1157	401	415	245	-	-	-	-	-	-	-
29	2006	1035	2634	1640	1208	390	429	302	-	-	-	-	-	-	-
30	1033	579	1528	936	718	343	314	191	-	-	-	-	-	-	-
31, 32, 33	2006	1035	2634	1640	1208	390	429	302	-	-	-	-	-	-	-
34	1872	891	2446	1640	1208	390	429	302	-	-	-	-	-	-	-
35	1933	946	3012	2834	2318	904	1509	2411	822	387	348	-	-	-	-
36	1919	921	2610	1790	1508	447	552	360	-	-	-	-	-	-	-
37	2006	1035	2634	1640	1208	390	429	302	-	-	-	-	-	-	-

TABLE A continued

figure number		Age blocks (weeks) or age/sex classes														
		0-2	3-5	6-11	12-17	18-23	24-29	30-41	42-53	54-65	66-77	78-89	J	SA	AF	AM
38		1492	602	518	1317	1133	390	361	302	-	-	-	-	-	-	-
39		632.5	235.5	464.0	1688.3	1440.6	581.3	974.8	1147.7	822.0	387.0	348.0	483.0	528.0	477.0	653.0
40,41,42		831.5	395.6	1695.1	1953.6	1704.2	581.3	1427.8	2331.0	822.0	387.0	348.0	483.0	528.0	477.0	653.0
43	on mother	572	197	321	653	536	73	103	36	-	-	-	-	-	-	-
	in cont. with mother	108	68	137	291	441	78	127	68	-	-	-	-	-	-	-
	off mother	42	42	195	1275	1044	522	872	1104	822	387	348	-	-	-	-
44 45	on mother	2006	1035	2634	1640	1208	390	429	302	-	-	-	-	-	-	-
	in cont. with mother	119	74	348	323	510	83	176	69	-	-	-	-	-	-	-
	off mother	57	63	807	1460	1236	522	1316	2102	822	387	348	-	-	-	-
46,47		831.5	395.6	1695.1	1953.6	1704.2	581.3	1427.8	2331.0	822.0	387.0	348.0	483.0	528.0	477.0	653.0
48		852.6	381.9	1549.9	1821.5	1556.1	556.0	1408.2	2215.1	822.0	387.0	348.0	483.0	528.0	477.0	653.0
49,51,52,53,54,55,56,57,58,59		831.5	395.6	1695.1	1953.6	1704.2	581.3	1427.8	2331.0	822.0	387.0	348.0	483.0	528.0	477.0	653.0
61a		52	78	1221	1680	1445	482	1095	1749	520	261	169	194	147	0	140

TABLE A continued

	Age blocks (weeks) or age/sex classes														
	0-2	3-5	6-11	12-17	18-23	24-29	30-41	42-53	54-65	66-77	78-89	J	SA	FA	AM
62,63,64,65,67,68,69 70,71,72,73,74,75	831.5	395.6	1695.1	1953.6	1704.2	581.3	1427.8	2331.0	822.0	387.0	348.0	483.0	528.0	477.0	653.0
76	49	64	692	930	881	332	625	1226	408	224	132	185	119	0	0
77	6	6	349	671	508	243	543	760	216	93	64	24	29	0	0
78	1	14	200	298	210	161	327	445	93	45	16	14	20	0	0
79	0	13	61	281	290	104	266	275	61	46	19	0	0	0	0
80	0	1	14	100	114	52	137	110	22	16	11	0	4	0	0
81	0	3	4	75	96	20	108	107	19	10	2	0	0	0	0
82	0	0	0	19	47	8	40	13	2	6	0	0	0	0	0
83,84	2071	1096	3230	2834	2318	904	1732	2411	822	387	348	483	528	477	653
85	831.5	395.6	1695.1	1953.6	1704.2	581.3	1427.8	2331.0	822.0	387.0	348.0	483.0	528.0	477.0	653.0
86	2	16	223	469	333	215	471	618	229	76	36	8	19	0	1
87,88,89	632.5	235.5	648.2	1787.5	1440.6	581.3	974.8	1187.7	822.0	387.0	348.0	483.0	528.0	477.0	653.0
90	0	16	73	356	250	164	205	259	176	53	23	6	12	0	1

TABLE B

			age blocks (weeks) or age classes						
			6-23	24-49	50-89	J	SA	A	M
figure number	91	a	155	22	119	114	104	177	35
		b	-	242	53	122	66	104	6
		c	87	55	70	322	93	86	0
	93	a	87	17	98	87	98	158	35
		b	-	165	40	93	47	73	6
		c	76	37	46	226	62	54	0