The behavioural significance of animal play

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THE BEHAVIOURAL SIGNIFICANCE OF ANIMAL PLAY.

by

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I declare that the work described in this thesis is all my own, and has not been submitted for any other degree. The work described in Chapter 5 has been published in _Anim. Behav._ 29, 259-270.

TABLE OF CONTENTS

List of Figures v
List of Tables. vi
Abstract. vii

CHAPTER 1 INTRODUCTION. 1

1.1 Play. 1
1.2 Definition of play. 3
1.3 Costs of play 13
1.4 Functions of play 17
    1.4.1 Classical theories 17
    1.4.2 Current theories 18
1.5 Approaches to the study of play 28
1.6 The present study 38

CHAPTER 2 RECOGNITION OF PLAY BY NAIVE OBSERVERS. . . . 41

2.1 Introduction. 41
2.2 Method. 42
2.3 Treatment of results. 45
2.4 Results 48
2.5 Discussion. 51

CHAPTER 3 LONGITUDINAL STUDY OF ACTIVITY PATTERNS AND SOCIAL BEHAVIOUR IN LITTERMATE GROUPS OF JUVENILE RATS. 57

3a General introduction 57
3b General method 57
3.1 Organisation of play and other behaviours. 60
    3.1.1 Introduction 60
    3.1.2 Method 62
    3.1.3 Results. 64
    3.1.4 Discussion 76
3.2 Activity patterns 80
    3.2.1 Introduction 80
    3.2.2 Method 81
    3.2.3 Results. 82
    3.2.4 Discussion 90
3.3 Behaviour patterns: frequency and order 92
    3.3.1 Introduction 92
    3.3.2 Method 94
    3.3.3 Results. 98
    3.3.4 Discussion 107
3d Summary. 111

CHAPTER 4 EFFECTS OF RECENT SOCIAL EXPERIENCE ON AMOUNTS OF PLAY 114

4.1 Introduction. 114
4.2 Method. 115
4.3 Results 118

4.4 Discussion. 122

CHAPTER 5 THE REINFORCING VALUE OF PLAY 125

5a General Introduction 125
5b General method 127
  5.1 Experiment: food/no food. 130
    5.1.1 Method 130
    5.1.2 Results. 131
5c Social choice experiments: general method 135
  5.2 Experiment: caged/free companion. 137
    5.2.1 Method 137
    5.2.2 Results. 138
    5.2.3 Discussion 141
  5.3 Experiment: amphetamine-treated/ normal companion. 142
    5.3.1 Method 142
    5.3.2 Results. 143
    5.3.3 Discussion 147
  5.4 Experiment: chlorpromazine-treated/ normal companion. 148
    5.4.1 Method 148
    5.4.2 Results. 149
    5.4.3 Discussion 156
5d General discussion 158

CHAPTER 6 DISCUSSION. 162

  6.1 Properties of rat play. 162
    6.1.1 Recognition by naive observers . .162
    6.1.2 Characteristics of the activities recognised as play 163
  6.2 Costs of play for rats. 172
  6.3 Regulation of play in rats. 173
    6.3.1 Short-term 173
    6.3.2 Long-term. 173
  6.4 Benefits of play for rats 173
  6.5 Implications for play as a whole: summary and speculations. 183
    6.5.1 Identification 183
    6.5.2 Functions. 185
  6.6 Conclusion. 188
  6.7 Suggestions for further work. 189

  Appendix A: photographs of play 195
  Appendix B: description of behaviour categories used 200
  Appendix C: behaviour sequence pairs. 202

  References. 205

FIGURES

2.1 Category use by observers 46
2.2a Concordance on play 49
2.2b Agreement on all categories 50
3.1a Time spent in play per 24hr by litters A and B. . 65
3.1b Time spent in play per 24hr by litters C and D. . 66
3.2a Play bouts per 24hr for litters A and B 68
3.2b Play bouts per 24hr for litters C and D 69
3.3 Mean play bout lengths. 71
3.4a Log survivorship plot of play bout lengths. . . . 72
3.4b Log survivorship plot of interbout intervals. . . 73
3.5 Play group size 75
3.6 Proportions of light and dark periods spent sleeping. 83
3.7 Mean sleep bout length in light and dark periods 85
3.8 Time spent playing per 12hr in light and dark periods. 86
3.9 Play bouts per 12hr in light and dark periods . . 87
3.10 Mean play bout lengths in light and dark periods 88
3.11 Proportion of waking time spent in play during light and dark periods 89
3.12a Frequencies of playful behaviours 99
3.12b Frequencies of non-playful behaviours 100
3.13a Common response sequence pairs, younger 102
3.13b Common response sequence pairs, older 103
3.13c Common response sequence pairs, all ages. 104
4.1 Experimental design 117
4.2 Relative amounts of different behaviours during each recording interval. 120
5.1 Learning in experiment 5.1 (food/no food) 133
5.2 Learning in experiment 5.2 (caged/free partner). 139
5.3 Learning in experiment 5.3 (amphetamine-treated/normal partner) 144
5.4 Behaviour profiles for experiment 5.3 145
5.5 Learning in experiment 5.4 (chlorpromazine-treated/normal partner) 150
5.6 Behaviour profiles for experiment 5.4(i). 152
5.7 Behaviour profiles for experiment 5.4(ii) 153
5.8 Behaviour profiles for experiment 5.4(iii). 154
5.9 Scale of Relative Attractiveness of partners. . .160

LIST OF TABLES

1.1 Characteristics of play 6

2.1 Differences between intraobserver agreement and observer-experiment .r agreement. 52

2.2 Frequency of classification of each behaviour category as playful. 53

3.1 Behaviour categories used for analysis and statistical treatment 95

3.2a Percent of play occurring as a response to each behaviour. 106

3.2b Percent of Paws-on receiving each behaviour as a response. 106

4.1 Differences between behaviour scores in different recording intervals 121

5.1 Analysis of variance of side choice scores in all experiments 134

5.2 Mean trial times in experiment 5.2. 140

5.3 Analysis of variance of behaviour scores in experiments 5.3 and 5.4 146

5.4 Correlations between Relative Attractiveness and behaviour scores. 155

6.1 Characteristics of play and their validity for rats. .164

THE BEHAVIOURAL SIGNIFICANCE OF ANIMAL PLAY

ABSTRACT

Play is frequently reported to be difficult to define but nevertheless easy to recognise. Other workers' attempts at definition are reviewed. These commonly involve initial subjective recognition of play followed by description in terms of characteristics which are frequently shared with the play of other species. Play appears to have certain associated costs and is therefore assumed to benefit the animal in some way in order to justify its existence in evolutionary terms, but the nature of this benefit is unknown. Theories regarding the functions of play are discussed in the light of its properties and potential costs.

Chapter 2 describes an experiment to test the common assumption that observers agree on what constitutes play. Comparison of the judgements of ten naive observers on the behaviour of young rats indicated that the majority agreed, and the activities which they called play formed the basis of the working definition of rat play which is used in the studies described below.

A longitudinal study of aspects of the play and other behaviour of littermate groups of rats is described in Chapter 3. The quantitative findings are used to test the validity of certain characteristics for rat play. The experiments described in Chapters 4 and 5 examined aspects of the rat's motivation to play. The nature of recent social experience was found to influence the rat's tendency to play, and a series of choice experiments showed that play was highly reinforcing by comparison with other forms of social experience.

The extent to which existing definitions of play can be applied to that of rats is examined in the light of the observational and experimental evidence described in Chapters 2 - 5 concerning its characteristics. The cost of play for rats is estimated using indirect evidence and tentative suggestions are made as to its functions.

CHAPTER 1

INTRODUCTION

1.1

Play

Play is a somewhat unusual class of behaviour in that its definition and, to some extent, its very existence, are subjects of academic debate. The term, borrowed like so many others from everyday usage, covers a wide range of behaviours in a large number of species (mainly mammals but also some birds) from the wrestling of lion cubs to the fantasy games of human children. It is this diversity which makes play notoriously hard to define (Darling 1937, Owens 1975, Smith and Fraser 1978, Chalmers 1978, Smith 1978). The lack of any objective definition or criterion presents a problem to those wishing to theorise or generalise about play, and several of them, e.g. Berlyne (1969), Weisler and McCall (1976), Lazar and Beckhorn (1974), see this as a reason to abandon the term as a behaviour category, replacing it with narrower, more easily defined classes. However, there seems to be general agreement among those actually observing the behaviour that there is something about play which is instantly recognisable (Ewer 1968, Miller 1973, Poole and Fish 1975, Bekoff 1976a), and therefore criteria for identifying it are not immediately necessary as each observer carries a working definition in his own head. Objective descriptions are then given of the behaviours which were recognised as play in the species in question. Behaviours commonly included under the heading of play are rough and tumble wrestling and chasing in which neither participant dominates, solitary leaping and twisting movements and fragments of predatory behaviour in which inappropriate objects are preyed upon. More sedate manipulatory behaviour may also be included, but the most distinctive play behaviours are those involving vigorous activity and what is probably best described as youthful exuberance. Play is often discussed in the three subclasses of social, object and solitary locomotor play, according to who or what is being played with.

Because each observer operates using his own working definition, there is no guarantee that two separate accounts of play in a species actually refer to the same behaviour. However, there is evidence that independent observers' descriptions are comparable; for example, Caine and Mitchell (1979) were able to come to general conclusions about play in the genus Macaca because the independent studies which they reviewed, although not using standardized criteria, had similar ideas of play. This suggested that, as appears to be implicit in many accounts, the corporate human non-verbal definition of play is a valid one. This matter is discussed further in Chapter 2 where naive observers' views of what constitutes play in a strange species are compared.

Despite the continuing debates about its identity and existence, play has recently become the subject of increasing numbers of observational and (with varying degrees of success) experimental studies over a wide range of free-living and captive species. Fagen (1981), in the first single-author work this century to tackle the subject area of animal play as a whole, has provided an excellent review of both theoretical issues and practical studies. Other useful overviews have been written by Symons (1978b) who draws his empirical evidence from his own extensive studies of rhesus monkeys (*Macaca mulatta*), Aldis (1975) who confined his attention to play-fighting, and others. Various multi-author collections and symposia (e.g. American Zoologist 14, 1974, and works edited by Smith (1978), Bruner, Jolly and Sylva (1976) and Muller-Schwarze (1978)) give descriptive accounts of play in different species as well as discussions of definition and function, which are widely disagreed upon. I shall attempt to summarise the current viewpoints on these issues, and how they have been reached, with reference to descriptive studies of the play of different species. However, for a fuller review of descriptive play studies, organised taxonomically, see Tables 3.1 - 3.30 in Fagen (1981).

1.2

Definition

As has been indicated, there is no single accepted definition of play. Although many studies and discussions of play offer concise definitions of the behaviour in question, e.g. Bekoff (1972) defined canid play as behaviour involving

> "...a decrease in social distance between the interactants and no evidence of social investigation or of agonistic... or passive-submissive behaviours... although these actions may occur as derived acts during play."

and Symons (1978b) defined rhesus monkey play as behaviour patterns which

> "... lack immediate function or, at the least, lack the function of the patterns they resemble..."

these tend to be merely summaries of more informative lists of characteristics which are also given. The list-of-characteristics approach was first taken by Beach (1945) in his review of the current work on play, in which he attempted to persuade the unruly literature of his day into a more homogeneous framework. Choosing to "overlook this source of difficulty" (lack of definition) he extracted "outstanding characteristics" of behaviour referred to as playful, stressing that, while play might possess these features, they were not exclusive to it.

Many others (e.g.Meyer-Holzapfel 1956, Loizos 1966, Marler and Hamilton 1966, Ewer 1968, Eibl-Eibesfeldt 1970, Bekoff 1976a) have since described play in this way, listing characteristics which, though neither necessary nor sufficient conditions for play, are nevertheless applicable. (Fagen (1981, Appendix 2) has collected a number of these lists together.) This treatment gives a form of definition on the basis of shared characteristics. Wittgenstein (1953) referred to a class defined in this way as a "family", held together by "family resemblances" such that each member of the group bears some similarity to at least one other, but no single feature need be common to the whole group. It is interesting, and not entirely coincidental, that Wittgenstein chose "games" as his example of a linguistic family with no agreed definition which is nevertheless an entity maintained by shared characteristics.

> "...if you look at them [games] you will not see something that is common to all, but similarities, relationships, and a whole series of them at that... don't think but look!"

He considered this type of class definition to be both valid in its own right and flexible, since it is capable of including any novel example which shares features with an existing member. Meyer-Holzapfel (1956) suggested that play should be defined in this way, with a central core of generally-agreed play behaviours being established which share many characteristics, while the more peripheral types of activity are allowed to merge into other classes defined in similar ways.

A survey of play studies for which characteristics were quoted produced the list summarised in Table 1.1 and discussed below. It can be seen that while none of these features is exclusive to play, the more a behaviour possesses, the more likely it is to be playful (e.g. not all enjoyable behaviours, nor all juvenile behaviours, are playful, but a behaviour enjoyed by juveniles is more likely to be playful than either alone.)

The characteristics themselves fall into three groups on the basis of the aspects of play to which they refer:

(a)Motor patterns and their organisation in individuals.

(b)Motivation, outcomes and environmental effects.

(c)Behaviour towards play partners in social play.

(a)Motor patterns
- Patterns seen in other contexts
- Play versions differ from non-play:
  - exaggerated
  - loose muscle tone
- Sequences fragmented and re-ordered
- Elements repeated
- Play-specific patterns may be included
- Innovative

(b)Motivation, outcomes and environmental effects
- Reinforcing
- Self-motivated
- No immediate results
- No goals/ intrinsic goals
- Predominantly in juveniles
- Optimum conditions:
  - relaxed, familiar environment
  - No immediate physical needs
- Easily interrupted
- Influenced by weather

(c)Social factors
- Involves signals
- Partners rarely inflict serious injuries
- Roles exchanged
- Dominance relations not expressed
- Larger individuals may self-handicap
- Play bouts last longer than equivalent non-play
- Play may turn serious, especially near puberty

<u>Table 1.1</u>

Characteristics of play.

(a) Motor Patterns

It is generally agreed that many of the motor patterns involved in play are also seen in other, serious, motivational contexts (Lorenz 1956, Loizos 1967,1969, Ewer 1968, Eibl-Eibesfeldt 1970, Bekoff 1974,1975a, Symons 1978b). For example, certain species-specific aggressive motor patterns are frequently seen in play: polekittens (*Mustela putorius*, Poole 1966) wrestle in close contact and bite each other, while ibex (*Capra ibex*, Byers 1977) and lambs (*Ovis aries*, Sachs and Harris 1978) butt and push each other in aggressive play. The playful manifestations of motor patterns tend to differ in form from their non-play counterparts (Loizos 1969, West 1974, Hill and Bekoff 1977), being described as exaggerated or uneconomical (Loizos 1966, Poirier and Smith 1974), or as relaxed and having loose muscle tone (Aldis 1975, Hill and Bekoff 1977, Poole 1978). Poole (1978) has objected to the use of the word 'exaggerated' to describe play on the grounds that this implies the existence of an exactly equivalent non-play behaviour which is not exaggerated. He has recommended the view put forward by West (1974) that play actions occur at a typical intensity which helps enhance their signal value. Hill and Bekoff (1977) found that coyote (*Canis latrans*) aggressive play was not exaggerated in duration or frequency of behaviour patterns by comparison with their serious equivalents, and Henry and Herrero (1974) found the same for black bear (*Ursus americanus*) play. Both concluded that the difference lay in the form of the behaviour, which has been described as involving bouncing, jerky movements (Poole 1978: polecats) or a "gallumphing" gait (Miller 1973: primates).

The sequences in which motor patterns occur in serious contexts are fragmented and reordered in play (Loizos 1966, Muller-Schwarze 1971, Henry and Herrero 1974), with individual elements often being repeated (Ewer 1968, Geist 1971, Bekoff 1974, Egan 1975). Play-specific patterns may also be incorporated into these fragmented sequences. Because of this fragmentation, reordering and repetition play sequences are often described as being highly variable or labile (Meyer-Holzapfel 1956, Loizos 1966, Poirier and Smith 1974, Fagen 1974,1977, Baldwin and Baldwin 1977). Bekoff's (1974) preliminary analysis suggested that canid play sequences were effectively random, with each act occurring independent of its predecessor, but Hill and Bekoff (1977) have shown that the play-fighting of coyotes is actually less variable in structure than their aggressive fighting. Play in a number of other species has also been described as an activity organised into definite sequences (black-tailed deer (<u>Odocoileus hemionus</u>): Muller-Schwarze 1971, cats (<u>Felis</u> <u>catus</u>): West 1974, Hamadryas baboons (<u>Papio</u> <u>hamadryas</u>): Leresche 1976). Bekoff (1975a) has described a method by which the variability of different forms of behaviour can be measured and thus compared. From these conflicting reports, it seems that the play of some species is more predictable than that of others. Play is also described as innovative, involving the frequent invention of novel behaviours (Eibl-Eibesfeldt 1950, van Lawick Goodall 1968, Fagen 1974), a property which will be discussed further in relation to the functions of play.

(b) Motivation, Outcomes and Environmental Effects.

Play has been shown to act as a reinforcer for other tasks (Mason, Saxon and Sharpe 1963, Mason 1967, and Chapter 5), although Schiller (1957) found it impossible to reinforce play with food rewards. It is assumed to be self-motivated (Beach 1945, Piaget 1962, Bekoff 1974,1978), an assumption which is born out by the absence of tangible results (Beach 1945, Fagen 1976,1977, Poole 1978, Symons 1978b). Some authors have also described play as having no goals (Meyer-Holzapfel 1956, Poole 1966, Poole and Fish 1975) but these appear to be observer-defined rather than player-defined goals. Symons (1978b) interprets the play-fighting of rhesus monkeys as an activity with the intrinsic goal for both participants of biting without being bitten, and Smith (1981) has suggested that play may function by providing intrinsic goals to ensure the frequent repetition of certain beneficial behaviours. Since play is a predominantly juvenile activity (Fady 1969, Muller-Schwarze 1971, Aldis 1975) occurring most in species with delayed maturation (Poirier and Smith 1974), these motivational considerations apply mainly to the young.

Conditions conducive to play include a relaxed and familiar environment (Bally 1945, Hutt 1966) and the absence of immediate physical needs (Welker 1971, Steiner 1971, Poole and Fish 1975, Fagen and George 1977). It is easily interrupted if anything requiring urgent attention should happen (Loizos 1966, McDonald 1977) and may therefore be referred to as low priority behaviour (Weisler and McCall 1976). Environmental conditions such as weather

(Schaller 1963, Muller-Schwarze 1971, Geist 1971) can also affect the occurrence of play.

(c) Social Factors

Since play so often involves behaviour also used in other contexts, animals playing together need to be able to communicate to each other that the behaviour is being used playfully if the encounter is to be maintained (Hinde 1970, Fagen 1974, Bekoff 1974,1975b, Aldis 1975). A number of gestures have been identified which function as play signals, some serving only to solicit play and therefore occurring before rather than during bouts, e.g."bow" in canids (Bekoff 1974), while others may occur at any time in a play bout, e.g. open-mouth play face in many species (primates: van Hooff 1962, polecats: Poole 1978, black bear: Henry and Herrero 1974), and seem to serve more to maintain the play bout. It has also been suggested that some of the structural peculiarities of play discussed above such as loose muscle tone and rotational movements (Sade 1973) may also serve a communicatory function. Bateson (1955) saw the communication inherent in play as an example of abstraction by animals because it changed the meaning of certain other acts, and he consequently referred to it as metacommunication. This term is not universally accepted and Bekoff (1978) criticised it as being an excessively complex term for a relatively straightforward concept, but it has been shown that play signals are sufficiently powerful to override other conflicting signals when both occur within the same encounter (e.g. play signals override threat signals between juvenile coyotes, Bekoff 1974).

Playful interactions themselves also possess a number of features which distinguish them from serious interactions. Although much social play closely resembles fighting, playing animals very rarely inflict serious injuries on each other (West 1974, Fagen 1975, Symons 1978a), as potentially dangerous behaviours such as biting are inhibited (Ewer 1968, Aldis 1975, Poole 1978). Bekoff (1972) has suggested that young canids may learn appropriate bite intensity in play, but Eibl-Eibesfeldt (1950) was convinced that badger (Meles meles) play involved a built-in bite intensity which was suitable for badger skin and that no amount of teaching would alter this intensity to suit human skin or clothes:

> "One always had to protect one's face from the frequent, very sudden snapping." and later "... the caretaker usually had to terminate the bout prematurely out of fear for his trousers."

Several mechanisms appear to exist which ensure that playing animals remain equal. Roles are exchanged frequently (Loizos 1966, Marler and Hamilton 1966, Steiner 1971, Aldis 1975) and dominance relations do not appear to be expressed in play (Bertrand 1969, Symons 1978a) even though they may already govern other areas of social behaviour, as they do in coyotes and other solitary-living canids (Bekoff 1972) when play begins. Larger individuals may handicap themselves when playing with smaller individuals (Poole 1966, van Lawick Goodall 1968, Leresche 1976, Bekoff 1978), appearing to make an effort to play less boistrously than they would with an animal of their own size in order to maintain the equality of the encounter. The stronger individual may take the "subordinate" role more often than its weaker partner as if to compensate for the imbalance, e.g. dominant chimpanzees (Pan troglodytes) initiated play with subordinates by fleeing from them (Loizos 1969).

Play bouts have been shown to last longer than comparable non-play encounters (Owens 1975, Braggio 1978, Chalmers 1980), and involve more changes of behaviour (Chalmers 1980), indicating that these properties serve to keep play encounters going. Occasionally the system can break down and play may abruptly turn into its serious counterpart (Rensch and Ducker 1959, Blurton-Jones 1967, Muller-Schwarze 1971). There is some evidence suggesting that such breakdowns of play may be more frequent among adolescent individuals for whom the serious versions of the behaviours are becoming increasingly important: Meaney and Stewart (1981) have reported that, in male rats (Rattus norvegicus), play begins to reflect dominance relations around puberty and Panksepp (1981) has reported a similar finding for isolated rats placed with the same partner for short periods at regular intervals. Steiner (1971) noted that Columbian ground squirrel (Spermophilus columbianus) play became more violent and involved less role swapping with age and Eibl-Eibesfeldt's badger (1950) only began to "grumble angrily" when older.

In summary, therefore, play includes a wide variety of behaviours, many vigorous and some more calmly experimental, which may be social or solitary and are carried out with no apparent purpose but considerable apparent enjoyment. Some of the vigorous activities are illustrated in the photographs included in Appendix A.

1.3

Costs of play

Such activity has obvious costs to the organism. Appearance alone suggests that all types of active play must involve considerable energy expenditure per unit time (unit energy cost) by comparison with most other activities. Direct measurements of energy expenditure have recently been carried out for the first time on a playing animal. Martin (personal communication) found that the unit energy cost of play for kittens may not be as high as others have suggested, as playing metabolic rate was only 1.45 times resting metabolic rate. However, indirect calculations on other species have suggested that the energy costs of their play may be large. Moen (1973) has calculated that a white-tailed deer (*Odocoileus virginianus*) should expend energy at approximately three times its basal metabolic rate in play, a value exceeding that for walking uphill but less than that for running, and the figures of Coelho, Bramblett, Quick and Bramblett (1976) suggest that the unit energy cost of play for howler monkeys (*Alouatta villosa pigra*) is comparable to that of fighting. Studies of time budgets have indicated that an animal may devote an appreciable proportion of its time to play (Fagen 1981: various primates spend 1 - 10% of their time in play; Bernstein 1980: stumptail macaques (*Macaca arctoides*) play for a mean of 10% of their time). Spending over an hour of a 12hr day in an activity with such a high unit energy cost would therefore represent a considerable total energy expenditure for the animal, and could carry an additional energy cost in terms of time taken up and therefore made unavailable for feeding to build up energy reserves.

Play also carries a potential cost in terms of risk. Although the inhibition of harmful aggressive behaviour ensures that partner-inflicted injuries are rare, play nevertheless carries a significant risk of injury by virtue of its vigorous and often experimental nature. Byers (1977) noted that the ibex kids which he observed tended to play with apparent abandon on the edges of steep drops. At least a third of the kids suffered injuries in play which were bad enough to cause temporary limps, and two individuals fell considerable distances while playing. Similarly, chimpanzees were seen to fall from trees during vigorous play (van Lawick Goodall 1968), an experience which it was suggested might contribute to their learning to distinguish safe branches from unsafe ones. Fagen (1981) has reviewed the observational evidence that injuries are relatively common in play.

It has also been suggested that playing animals present an easy target for predators, their vigorous activity making them conspicuous and their preoccupation, together with their separation from adults, allowing predators to approach unnoticed. Hausfater (1976) observed adult male yellow baboons (Papio cynocephalus) taking juvenile vervet monkeys (Cercopithecus aethiops) while they played in groups some distance from adults, suggesting that, at least for this species, these assumptions are justified. Also, the minor injuries which occur in play may slow individuals down temporarily, making them more susceptible to predation.

The costs of play in terms of energy and danger to life and limb are thus appreciable, and the continued existence of play in the face of such costs suggests that it also has benefits which prevent natural selection from eliminating it. It is a widely acepted characteristic of play that it appears to be done purely for its own sake as there are no immediate benefits (see 1.2). Therefore, any benefits there may be can be assumed to be long term, affecting fitness some time after the relevant act has been committed. Fagen (1977) examined the life-historical consequences of play as an activity with immediate costs and delayed benefits by basing a mathematical model on these premises. From this he predicted that play should be more frequent in k-selected species (i.e. long-lived species which invest their reproductive effort in small numbers of offspring and have concave survivorship curves (Pianka 1970)) than in r-selected species (relatively short-lived species producing large numbers of offspring but investing little in each one, and having convex log survivorship curves); incidence of play should vary between populations of a single species according to environmental conditions; young animals should play more than older ones, and behaviour patterns should be incorporated into play as soon as they develop. Evidence exists in support of all except the last of these predictions. Reports of play have come almost entirely from mammals and birds which occupy the k end of the r-k continuum; Baldwin and Baldwin (1974) noted that some populations of squirrel monkeys (Saimiri) played a lot while others did not play at all, and play is generally accepted as being commonest in the young. The close correspondence between these predictions and observed properties of play suggests that the original premise was correct and play can be thought of as an activity with immediate costs and delayed benefits.

The nature of these delayed benefits is the subject of much theorising. It is extremely unlikely that the diverse forms of play in different species, or within a species, share a single function and consequently many functional hypotheses have been proposed corresponding to the known characteristics of the lifestyles and play of different species. Symons (1978b) has drawn a distinction between the biological function of a behaviour, being that consequence which it evolved to produce, and any other consequences it may have, emphasising that all beneficial effects are not necessarily functions and that the design of the behaviour itself is a likely source of clues as to its function, since it has been shaped by natural selection. (Symons's term "design" is a useful concept describing the moulding of behaviour by evolution to perform a function as efficiently as possible.)

The current major groups of hypotheses concerning the functions of play are discussed below in relation to the species for which they have been proposed and the evidence for and against. Some of these hypotheses refer mainly to social play, some to object play, some to solitary locomotor play and some to combinations of types.

1.4

Functions of play

1.4.1 Classical theories

The history of theories concerning the functions of play has been reviewed by Gilmore (1966), Millar (1968) and others. Three theories were proposed at around the turn of this century in attempts to explain this apparently useless behaviour.

Spencer (1878) proposed the "Surplus energy hypothesis", which had previously been suggested by the poet Schiller and still lingers today in references to play as "letting off steam". Spencer noted that play was most common in "animals of high types", which he assumed were better nourished than "inferior kinds", and ascribed play to a need to get rid of the excess of energy which this gave them, combined with the tendency of faculties to exercise themselves spontaneously during periods of disuse. Beach (1945) pointed out that this hypothesis employs circular reasoning, since the energy is only considered to be surplus because it is used in play, an activity with no apparent function.

The similarity between the form of some playful behaviours and adult behaviours caused Groos (1898) to suggest that young animals "of the higher orders" used play to practise skills which they would need in adult life. He assumed that their behaviour was less rigidly governed by instincts than that of other species, and therefore that each individual needed to perfect the more complex skills required of it by practising them in play during a period of protected youth which evolved for the purpose. This view is still widely supported today, and current thought on the subject is discussed below.

Hall (1908) disagreed with Groos, being of the opinion that play was the result of the species' past, and therefore needed no explanation in functional terms:

> "The view of Groos that play is practice for future adult activities is very partial, superficial and perverse. It ignores the past where lie the keys to all play activities."

Hall proposed that, in play, each individual carried out the behaviours which had been of adaptive significance to its evolutionary ancestors but had become redundant, progressing through successive historical stages with age. However, the packing of outmoded adult behaviours into the youth of the next evolutionary stage, which Hall implied, could not be accomplished by natural selection, and this theory is therefore no longer supported.

1.4.2 Current theories

1. Practice hypotheses.

These are based on the obvious similarities of form between some types of play and some adult activities, such as fighting and prey-catching, which have a direct influence on survival and reproductive success. It has been suggested that the performance of these behaviours in play conditions, where success and failure do not exist, allows the perfection of certain necessary skills without environmental pressure (Symons 1978b, Byers 1980, Bildstein 1980). Symons (1978b) noted that the playfighting of juvenile rhesus monkeys was very similar in many ways to serious fighting, and suggested, on grounds of the design of the behaviour and the observed sex differences (males playfight and fight more than females), that this play functioned to increase fighting skills. Similarly, Berger (1980) showed that sex differences in the contact play of bighorn lambs (Ovis canadensis) corresponded to sex differences in mating strategies. Young males of this polygynous species indulged in more contact play (e.g. butt, push) than their female contemporaries, and adult males were considerably more aggressive than females.

However, the practice hypotheses are contested, also on grounds of design. It has been argued that, although play is similar in form to some adult activities, it also differs from them in certain important respects (Poole 1966). As was discussed above, it is characteristic of play that its behaviour sequences differ from serious ones and consummatory behaviours are absent, so that playful predatory behaviours do not lead to killing and play fights do not lead to victory or defeat. Play would therefore provide very misleading practice for these behaviours as whole sequences, but could nevertheless contribute towards the improvement of specific aspects such as the orientation and timing of pounces (West 1974).

2. Physical training hypotheses

Brownlee (1954) proposed that the active play of calves (Bos taurus) served to strengthen the "muscles, tendons, ligaments, bones and joints" involved so that structurally similar adult activities could be performed more effectively. Fagen (1976) provided evidence, gathered from more recent advances in exercise physiology, in support of this hypothesis. While exercise at any age increases cardiopulmonary capacity, stimulates muscle and blood vessel development and improves muscle biochemical efficiency, such training responses are often most striking in young animals and some may occur only in immature individuals. Consideration of optimal training principles led Fagen to make some predictions about active play. It should involve short bouts of strenuous exercise, interspersed with periods of lighter activity and repeated frequently, and should provide exercise of the overload, high intensity and endurance types to produce the three corresponding training responses. Play fulfills these predictions, being characteristically repititious and consisting of many patterns in varied sequences. Overload and high intensity exercise are provided by activities such as static pushing (e.g. ibex: Byers 1977, bighorn lambs: Berger 1980) and rough-and-tumble wrestling (e.g.rhesus monkeys: Symons 1978b), while endurance exercise is provided by locomotor play. Playful exercise should be appropriate to adult requirements and should therefore make use of muscle groups which are important in certain adult activities. Byers (1977) has shown that ibex indulge in locomotor play preferentially on steep slopes, an activity appropriate for training the muscles which they use as adults to flee to safety up steep hillsides. However, when McDonald (1977) set out to test the prediction that play bouts should have an optimum length for the best training results, he found that California ground squirrel (Otospermophilus beecheyi) play bout lengths were randomly distributed. This may be because he included all forms of play and did not separate the bouts providing different types of exercise, which could each have different optimal lengths.

Playful exercise may also be important for strong bone growth, as Brownlee (1954) suggested. Geist (1971) noted that fractured limbs were much more common in a non-playing flock of bighorn sheep than in comparable groups in which play was common. While the lack of play and weak bones may both have been the results of a single nutritional deficit, it is also possible that the former led to the latter.

The physical training hypotheses have widespread support (e.g. ibex: Byers 1977; ponies (Equus caballus): Fagen and George 1977) as explanations of the function of active play, and recently Fagen (1982) has proposed that exploratory and manipulative play may stimulate cerebral changes (enrichment responses) through a comparable process.

3. Learning hypotheses

A car-sticker advertising pre-school playgroups best embodies these theories in its succinct message "Playing is learning for living". It has been suggested that play facilitates learning about the environment and how it is likely to act and react (Ewer 1968, Geist 1971, Bekoff 1972, Fagen 1974) on the basis of design, as much play is sufficiently variable to expose the animal to novel situations, and sufficiently active to elicit responses from the environment. Some species, especially primates (e.g. chimpanzee: van Lawick Goodall 1968) also exhibit manipulative or solitary play which appears to be experimental in nature, involving the repetition of an act with slight variations, and is therefore well-suited to information gathering. Fagen (1975) has drawn parallels between play and the behaviour of artificial "learning" systems which function most effectively by exhibiting play-like behaviour. Evidence has also been provided by Sylva, Bruner and Genova (1975) and Smith and Dutton (1979) that playful experience helped young children to solve manipulative problems, particularly those requiring an imaginative approach.

Individuals may also learn about their own abilities in play (Ewer 1968, Bekoff 1974). The activity allows them to try out behaviours they might not otherwise experience, and may lead them into novel physical postures, facilitating learning about their own limitations. Similarly, social play may provide an opportunity for animals to learn about each other's abilities (Rhine 1973, Fagen 1974). In this activity, they perform rapid and vigorous interactions during which they may be able to assess each other's strength and speed, although the equality preserved between players (see 1.2) seems to minimise any differences in strength between them, and may make it difficult for animals to assess their partners' true capabilities.

4. Innovation hypotheses

Related to the above hypothesis concerning self-directed learning are those which suggest that play functions to produce novel behaviours and behaviour combinations. There is ample evidence that such behaviours do occur in play (e.g. badger somersaulting: Eibl-Eibesfeld 1950; chimpanzee pirouetting: van Lawick Goodall 1968;) but there is some disagreement as to whether this is a true function of play or merely a by-product. Fagen (1974) saw play as analogous to the process of meiosis in which genetic material is shuffled in the production of gametes so that the next generation receives new and untried genetic combinations. In the case of the highly variable play which occurs in some species, different behaviours are being brought together in new combinations and may result in an advantageous discovery for the playing individual. However, Symons (1978b) and Smith (1981) have argued that such discoveries appear to be so rare in the play of all species, except perhaps man, that they could not confer an appreciable selective advantage on playing animals, and therefore could not be responsible for the evolution or the continued existence of play. Fagen (1975) has modelled the evolution of innovative play, and concluded that it could evolve, even if other individuals were able to benefit from the discoveries through observational learning, but only in extremely benign conditions: when the costs of play are negligible, even very small benefits can outweigh them.

5. Social hypotheses

This group is concerned with the functions of social play.

(a) Development of complex social behaviour.

It has been proposed that play in a number of primate species promotes the development of complex social behaviour (e.g. baboons (Papio anubis): Owens 1975), its rapid and variable nature increasing individuals' sensitivity to their peers' more subtle actions and signals. Baldwin and Baldwin (1974) have reported that social interactions were less complex in a non-playing troop of squirrel monkeys than in comparable troops where play was common. However, such an explanation cannot be extended to cover the social play of solitary species such as polecats which indulge in rapid and vigorous social play (Poole 1966,1978) with apparent enthusiasm but have little need of complex social behaviour in adulthood when opportunities for interaction are rare. (It should be remembered that there is no reason to assume that squirrel monkey and polecat social play share the same function: in fact, the evidence of their very different lifestyles suggests that this is extremely unlikely.)

(b) Development of communicatory skills.

Since social play involves a considerable amount of communication (see 1.2), it has been suggested that it develops individuals' skills in this field (West 1974, Poirier and Smith 1974, Bekoff 1974). Individuals of many species reared in isolation show marked deficits in communication (e.g. rhesus monkeys: Harlow 1969; humans: Einon 1980) as might be expected, but there is no evidence that lack of play specifically is responsible for this effect, although Einon (1980) has pointed out that the critical period for these effects coincides with the peak play period.

The arguments against this hypothesis are similar to those against the practice hypotheses. It has been pointed out that the main quality of playful communication is its power to override other signals inherent in the behaviours employed (Symons 1974, Smith 1981). It is thus unlikely that animals learn the meaning of serious signals in play, since these signals no longer convey their serious meanings. However, it is possible that play helps develop communicatory skills in a more general way by focussing the individual´s attention on the relevant signalling areas of conspecifics, e.g. the face, and, as was mentioned above, by increasing sensitivity to small and subtle signals (Bekoff 1974).

(c) Social integration

It has been suggested, largely in relation to primate species, that, since a young animal´s first social interactions with individuals other than its mother are largely playful, this activity must be important in its integration into the group (Bekoff 1974, Poirier and Smith 1974, Poirier, Bellisari and Haines 1978). Nowicki and Armitage (1979) have made a similar suggestion for a non-primate species, the marmot. However, Smith (1981) has pointed out that juvenile males in many primate species emigrate from the natal troop, and thus have no particular need to be integrated into it, while females remain. Thus if play functioned to integrate young individuals into the group, females would be predicted to play considerably more than males, which is not usually the case.

Poirier and Smith (1974) have also suggested that animals may find their places in the dominance hierarchy through play, using the activity to test each other's speed and strength, and Panksepp (1981) has made a similar suggestion for rats. Symons (1978a) has argued convincingly against such a function for play, pointing out that, while fear is the basis of hierarchies it inhibits play, and that playfights involve inhibition of aggression and are therefore not good indicators of the likely winner of a serious fight. He saw play as incompatible with rank ordering since play is only possible in the absence of competition, upon which hierarchies are based. He also noted that, in rhesus monkeys, the rank of a young individual could be predicted from that of its mother. For females, such predictions were quite precise, and the ranks they aquired in this way were retained throughout adulthood. Males were more unpredictable, and reassorted themselves by fighting at puberty. However, while rank appears to be related to maternal rank for certain primates, evidence suggests that play may contribute to the learning of individuals' relative strength in other species, e.g. rats (Meaney and Stewart 1981, Panksepp 1981). The distinction between play and aggression also becomes less clear in older animals (e.g. humans: Neill 1976).

(d) Litter cohesion

This explanation applies mainly to social play in solitary species which defy attempts at explanation by other social hypotheses. It has been suggested that social play provides an incentive for the young of such solitary animals as mustelids to stay together by overriding their tendencies to intraspecific hostility (Ewer 1968, West 1974). Play in captive litters of kittens appears to decline at the time when the young would disperse in the wild (West 1974). While play may help to keep litters together, this function can be, and is, served in other ways which are less energy-expensive, such as the nose-to-tail "caravanning" behaviour shown by young shrew litters (*Sorex cinereus*: Goodwin 1978). Litter cohesion is therefore unlikely to be a major function for play in any species, although it may be a secondary function or useful side-effect.

6. Flexibility/adatability hypotheses

It has been suggested that the varied nature of play helps individuals to cope with a wide variety of situations by making them accustomed to surprises (Miller 1973, Bekoff 1974, Symons 1978b). Lorenz (1956) noted that play tended to be common in "generalist species" such as the rat and the raven (*Corvus corax*) which survive by exploiting a wide range of niches through individual adaptation. and suggested that this adaptability was achieved in play. Evidence from play deprivation experiments (Einon, Morgan and Kibbler 1978) indicated that rats reared without the chance to play behaved less flexibly than peers with play experience in the novel test situations presented to them, and therefore suggested that they might be less well equipped to deal with novelty in a natural environment.

1.5

Approaches to the study of play

Unlike some activities, such as foraging, play has no effects on the external environment that can be easily measured or counted in the way that food intake or predatory success can be, and consequently most studies, with the exception of experiments in which play is manipulated and effects on the animal noted, have focussed on the behaviour itself. Play studies have thus progressed in quality and detail of observation as observational methods have become more sophisticated. The earlier accounts of play (e.g. chimpanzees: Kohler 1931; lion cubs (*Panthera leo*): Cooper 1942 (cited by Beach 1945); black bear: Leyhausen 1949; badger: Eibl-Eibesfeld 1950; mongoose: Rensch and Dücker 1959) were anecdotal descriptions of the behaviour, often accutely observed but usually only referring to one or a few animals, often domestic pets, and therefore tending to emphasize individual idiosyncrasies rather than species generalities.

The methods of quantitative ethology encouraged a more objective and unbiased approach. Quantitative studies such as that of Loizos (1969) on the relations between dominance and the way in which play was initiated in chimpanzees have provided useful information on aspects of play. (In the case cited, it was found that dominant individuals tended to initiate play with subordinates by performing the otherwise subordinate act of fleeing and so inviting pursuit while maintaining equality.)

Growth in awareness of the potential pitfalls in observational method (Slater 1973, Altmann 1974) made later studies more reliable in terms of lack of sampling bias, objectiveness of behaviour categorisation, observer agreement and accuracy of recording method (e.g. Owens 1975a, Barrett and Bateson 1978, Nowicki and Armitage 1979, Meaney and Stewart 1981). Many of these have made use of technological developments to extend observers' abilities. Cassette tape recorders (Byers 1977) have enabled observers to make continuous records of ongoing behaviour without taking their eyes off the subject of study. Ciné film (Poole and Fish 1975, Aldis 1975, Barrett and Bateson 1978) and video (Lazar and Beckhorn 1974, Einon, Humphreys, Chivers, Field and Naylor 1981) have contributed to play studies by providing a means of slowing the rapid interaction sequences down and so making it possible to discern actions, which, in real time, occur too fast for detailed recording. (Altmann (1965), using pencil and paper, omitted play from his study of behaviour sequences in rhesus monkeys because it happened too fast to record.) Such methods also provide a "hard copy" on which observer consistency and agreement can be checked. Wide availability of computing facilities has allowed data analyses to be carried out on a scale that would not have been possible without electronic help, such as examinations of behaviour sequences (Altmann 1965), which involve the computation of the probability of very large numbers of possible permutations.

Using these observational methods, records have been made of the frequency and duration of different behaviour patterns in play, the number and length of bouts, the identities of partners and of individuals initiating and terminating bouts and the sequences in which behaviour patterns tend to occur both within and between animals, as well as more general properties such as when and where play tends to occur.

Studies have been made using these tools of observation and analysis to answer different questions concerning play. Longitudinal examinations have followed the developmental time-course of play and its component behaviours (West 1974, Barrett and Bateson 1978, Meaney and Stewart 1981), showing how the activity fits in with the development of other behaviours and how its own structure changes with age. In a longitudinal study of kitten play, Barrett and Bateson (1978) noted that object play and social play had distinct developmental patterns, with object play peaking as social play declined. Where the longitudinal approach has proved impossible or impracticable, as in primate species that take several years to mature, development has been studied by comparing individuals of different ages (Owens 1975, Bramblett 1978, Cheney 1978, Chalmers 1980). By this method, Chalmers (1978) found that different aspects of the play of olive baboons (Papio anubis) developed with separate time-courses, like the object and social play of kittens. Such findings indicate, as Chalmers has pointed out, that play is not a single discrete class of behaviour but includes a number of separate activities which develop independently and may well serve separate functions.

A number of observational play studies have attempted to test the applicability of accepted definitions or characteristics to the play of a particular species, or to test the validity of predictions based on certain function theories, by concentrating on specific aspects of the behaviour such as behaviour sequences or choice of partners or locations. In some studies, differences in the chosen aspect of play between different populations, or different sections of a single population (e.g.sexes), have been examined. Theses studies can be thought of as "natural experiments", with the different natural groups corresponding to treatment groups in a manipulative experiment.

In a study of this type carried out by Hill and Bekoff (1977) comparisons were made between the playful and aggressive manifestations of three motor patterns performed by young coyotes to examine the validity for this species of the claim that play is a highly variable activity. Comparison of the coefficients of variation for these acts in playful and aggressive contexts showed that this play was in fact no more variable than its serious counterpart. Other observational studies (e.g.Henry and Herrero 1974) have tested the validity of other assumed play characteristics in similar ways and have thus helped to base the description of play on a more solid factual footing.

Attempts have also been made to find reliable play indices whose frequency of occurrence correlates with amounts of play occurring, so that estimates of play can be obtained with minimum observational effort. Panksepp and Beatty (1980) found that the behaviour "pinning" was a reliable index of play in rats, and used it as such in their experimental studies of the effects of social deprivation. Chalmers (1978) noted that, while the so-called "play markers" occurred only in play, play did not necessarily include these behaviours and they could not therefore be used as indices.

The applicability of the physical training hypothesis to the play of ungulate species has been tested by Byers (1977, 1980) and Fagen and George (1977) in observational studies of the "natural experiment" type. Byers found that this theory could account for several properties of the play of Siberian ibex kids. The tendency of kids to carry out locomotor play on steep slopes, mentioned above, could serve to train the muscles used in escape, while social play provided exercise for the muscles of the neck and body which are involved in aggressive butting and pushing. The natural experimental groups for the test of the first proposal were the proportions of locomotor play occurring on the different types of surface, the comparison showing that more locomotor play occurred on steep ground. For the second proposal, the sexes were compared, since aggression is considerably more important for males, who should therefore indulge in more of the appropriate exercise than females. The young males took part in more social play, as predicted, and also chose play partners of their own size, each thus providing the other with exercise of an appropriate intensity. Similar findings were made for the play of another polygynous ungulate, the bighorn sheep (Berger 1980).

However, here the author has pointed out that such play properties could equally well be explained by a practice function, allowing animals to perfect the skills needed for predator avoidance and aggression. Fagen and George (1977) examined the applicability of the physical training hypothesis to the play of pony foals in the light of their energy budgets, starting from the premise that, if play is to provide significant muscular exercise, a high proportion of the most strenuous behaviours should be playful. They focussed attention on two of the most energetic motor patterns occurring, gallop steps and gallop turns, and found that the majority of these (68% and 98% respectively) occurred in play, providing strong indirect evidence that pony foals obtain most of their physical exercise through play.

Studies of this type show how observational methods can be used to address specific questions concerning play by exploiting natural groupings and thus avoiding experimental manipulation of the animals or their experience. However, experimental studies have also provided information on these and other aspects of play.

Because play has few measurable or independently variable correlates, a large proportion of the experiments involving this activity consist of preventing its occurrence and observing the effects. Methods of play deprivation have included total social isolation (Panksepp and Beatty 1980), restraint by physical means (Chepko 1971) or by confinement (Chepko 1971, Smith and Hagan 1980), distraction by offering food (Muller-Schwarze 1968), providing only a social partner who has been treated with drugs which inhibit play (Einon et al. 1978) and taking up the animals´ time with some other activity such as feeding (Baldwin and Baldwin 1976). Short term (i.e.a few hours´) play deprivation has been shown to be followed by a rebound of play to higher than previous levels in goats (Capra hircus; Chepko 1971), rats (Panksepp and Beatty 1980, and see also Chapter 4) and humans (Smith and Hagan 1980). Baldwin and Baldwin (1976) demonstrated a similar rebound effect in squirrel monkeys after more than 10 days´ play deprivation. These animals were forced to spend a large proportion of their time in foraging by the use of a specially designed food dispenser, and consequently had little time for play. Panksepp and Beatty (1980) also noted a fall-off in play following the initial rebound (see also Chapter 4), which they took as an indication that the amount of play is under homeostatic control, and therefore that mechanisms exist which aim to regulate play about some specific level.

The rebound effect has also been used as a tool for manipulating experience over longer periods of time. In an experiment examining the results of long-term play deprivation, rats were reared in social isolation for all but one hour per day during which they played intensely (Einon et al. 1978). Their performance on certain tests as adults was later compared with that of peers who had either been reared in total isolation or with constant company, so that the effects of play experience could be separated from those of non-play social experience. In the same series of experiments, drugged partners were also used to manipulate play experience. The drugs used (amphetamine and chlorpromazine, whose effects are discussed in more detail in Chapter 5) both inhibited play but had opposite effects on non-play social behaviour, so that any effect seen in animals with both types of partner as well as in individuals reared in isolation could be assumed to result from a lack of play.

Experiments of the type carried out by Einon et al. (1978) and Baldwin and Baldwin (1976)show that it is possible to deprive an animal of social play while having minimal effects on other forms of social behaviour. Other methods, particularly total social isolation, may prevent play while at the same time preventing all other forms of social interaction (Bekoff 1976b), so that the results of such treatments cannot be ascribed to lack of play alone.

Knowledge aquired from observational studies has provided some information on the ways in which certain factors influence play, and made way for experimental examination of these relationships. Bateson and Young (1981) manipulated the weaning age of kittens experimentally to see whether the previously noted discontinuity in play development (Barrett and Bateson 1978) was relatd to weaning age. It was found that this treatment did not appear to lower the age of the discontinuity, but instead accentuated it by increasing the frequency of specific play categories at the stage when they were maximal under normal circumstances.

Sex differences have been reported in both amount and type of play in many species (e.g.Hamadryas baboon: Leresche 1976, ibex: Byers 1980, lamb:Sachs and Harris 1978, rat: Meaney and Stewart 1981, and see Meaney, Stewart and Beatty, in press, for a review). Olioff and Stewart (1978) showed that, in rats, this may be brought about by hormonal differences, since testosterone given soon after birth caused females to play, as juveniles, as much as males.

Kittens show a comparable form of sex effect in object play (Bateson and Young 1979). Males indulge in more of this type of play than do females, but females with brothers also indulge in more than females with no brothers. Manipulation of litter composition combined with observation of females with and without their brothers showed that this effect was a long term one, demonstrated by females whether their brothers were present or not, and did not depend on the more playful males providing extra stimulation for their sisters by setting objects in motion. The effect might have resulted from a difference in intrauterine environment (see effects of androgens at birth, Olioff and Stewart 1978, above), or in maternal treatment of litters, or from some long term behavioural influence of males on females, or from a combination of hormonal and environmental factors.

Voles were found to exert a more immediate influence over the extent of each other´s play (Wilson 1973). Young born in the spring played more than young born in the autumn and this difference persisted in animals reared in laboratory conditions where the seasons were simulated only by manipulating day-length. The fact that play tended to be preceded by nosing of the partner´s neck region suggested that a secretion from this area could affect the likelihood of play. This theory was tested by applying an ether extract from the neck of each type of young to that of the other type. The treatment induced autumn juveniles to play like their spring counterparts, suggesting that a pheromone is produced by spring-born voles which stimulates play in their littermates.

The way in which play may influence other skills in human children and young chimpanzees has been examined in experiments comparing the merits of playful experience with those of other forms of experience. These experiments looked at the short term effects of manipulative play on puzzle solving success. Subjects were given an initial period of experience which consisted either of free play with the components of the puzzle, or of various types of control experience which attempted to provide similar information but without play, such as direct tuition or observation of another child playing. Performance with the puzzle was then observed immediately after the experience period, from which it was found that individuals with playful experience were more successful than others only when the puzzle required an innovative approach (Smith and Dutton 1979), although they appeared to be more highly motivated and better organised than those with other types of experience (Sylva et al. 1975).

Experimental approaches to the study of play have thus helped to define the characteristics of its relationships with other variables, both preceding and following its occurrence.

1.6

Present study

The work described below focussed on various aspects of the play of young rats. Chapter 2 addresses the problem of defining play for this species, and arrives at a working definition which is used throughout. Although play is hard to define, it has been pointed out that observers experience little difficulty in recognising play, and tend to agree on what they recognise (Miller 1973, Bramblett 1978). In this experiment, levels of agreement between naive observers and the experimenter on videotapes of young rats were measured, giving quantitative support to these assertions, and the behaviours classified as play by a majority of naive observers were identified and used as the basis of a working definition for rat play.

Chapter 3 describes longitudinal observational studies on the development of play and other aspects of behaviour, following littermate groups of rats through from weaning to sexual maturity. Timelapse video recording was used to obtain 19 - 22 hr long records of activity from which daily time-budgets for play and general activity could be extrapolated, and play characteristics such as bout and interbout interval lengths and play group size ascertained. Aspects of the fine structure of behaviour were also studied by examining these records at real time playback speeds, and recording behaviours, and the identities of individuals by whom and at whom they were directed, on a computer keyboard. This gave information on behaviour frequencies, and on which behaviours occurred as common responses to which others. This response sequence information was used to construct ethograms representing common interaction patterns in animals below and above 40 days of age.

In Chapters 4 and 5, experimental manipulations are used to test the validity for rats of certain characteristics that play is assumed to possess. Chapter 4 describes an experiment examining the effects of recent social experience on play and other types of social behaviour. Panksepp and Beatty (1980) found that social isolation was followed by an increase in play, but that play subsequently decreased as animals became "socially satiated". The experiment described demonstrated these effects and then examined the behaviour of a socially satiated animal with a partner fresh from isolation whose social tendencies therefore differed, to see what behavioural compromise would be reached. As might be predicted, the resulting behaviour was intermediate between the isolate and satiated conditions, with the isolate making repeated efforts to persuade its partner to play, as indicated by the abnormally high levels of a gesture previously identified as a play invitation.

Since play is often described, with little evidence, as being reinforcing, Chapter 5 describes a series of experiments which test the validity of this assumption for rats. In all cases, the young rats had to run to one side of a T-maze for an opportunity to play, which was provided by a normal young play partner who was restrained there. Various types of non-play social experience awaited them on the other side in the different experiments, provided by social partners who were confined and therefore physically inaccessible or treated with amphetamine or chlorpromazine and therefore not likely to play (Einon et al. 1978). The levels of preference shown for each experience, together with quantitative analyses of the behaviour carried out on either side, showed which activities were most strongly reinforcing.

The main aim of this study was therefore to provide quantitative data on play, its characteristics and the conditions necessary for its occurrence. Further experiments are suggested in Chapter 6, based on the information obtained concerning norms for play and manipulations affecting it, which would explore some of the correlates of this behaviour and so help to reveal its functions.

CHAPTER 2

RECOGNITION OF PLAY BY NAIVE OBSERVERS

2.1

Introduction

Although play has proved hard to define (see 1.1) the term nevertheless continues to be used to describe behaviour. Those studying the behaviour have tended to report that play was easy to recognise, and the lack of a verbal definition did not present a problem.

It is reasonable to assume that, like any other word, the meaning of the word "play" must be generally agreed upon if it is to perform its function as part of a language. Lorenz (1956) advises us to

> "...use the word "play" just as every man in the street would use it..."

because it is a

> "...real natural unit corresponding to a concept for which the natural growth of common language has developed a word."

Because of this, he felt that no further definition was necessary.

Lorenz reached this conclusion by considering the nature of language and, presumably, his own subjective idea of the meaning of a word with which he had been familiar since early childhood. The more objective approach of Miller (1973) led him to make a similar suggestion. He carried out an informal survey among zoo visitors and found that individuals were very definite in their classification of an animal's activity as play, and that they agreed closely on this judgement, although they were unable to say precisely what they were recognising. He concluded that they might be

> "...responding to the summation of numerous subtle cues coming from the animal...",

and suggested that, as recognition was taking place,

> "...there must be a something being recognised.",

i.e. that play is a natural entity. The observer was seen as analogous to an organism used in a bioassay.

A number of workers (e.g. Mason 1965, Loizos 1966, Bramblett 1978) have noted that both experienced and inexperienced observers agreed with a high degree of accuracy in their identification of behaviour as play. The experiment described below attempted to quantify this agreement.

Since it was of interest to know not only whether observers could agree on play but also what they agreed constituted this class of activity, the characteristics of the behaviours which were identified as play were also examined.

2.2

Method

Subjects. The observers were 10 first year university students, five male and five female. They had no prior experience of behaviour recording and were not familiar with the behaviour of rats.

Material. The test material shown to observers was two 10 min sections of videotape taken from 30 min recordings of two pairs of 31 day old rats. An extra seven minute section was used to train observers in the recording method. Each pair of animals consisted of a brown female and a hooded male who had shared a cage since weaning at 21 days. For the recording sessions, novel objects (crumpled paper, a cardboard tube and a wooden block) were placed in the animals' cages, as prior observation had indicated that novelty in the environment stimulates play.

Procedure. Observers were required to classify the behaviour of the female in each pair at 10 sec intervals. They recorded their classifications on check-sheets on which columns corresponded to behaviour categories and rows to successive recording instants. The nine behaviour categories fell into two groups:

1. Actions: Approach, Contact, Move away, Solitary.
2. Social context: Aggressive, Playful, Sexual, Friendly, Neutral.

At every recording instant, observers marked one column in each of these two groups to describe the behaviour of the animal towards its partner.

Recording instants were signalled by a buzzer which sounded at 10 sec intervals. (The sound was recorded onto the audio track of the videotape to ensure that the two were synchronized, and therefore that all observers were judging the same pieces of behaviour.)

Before being shown any videotape, observers were told the animals' basic biographical details, and were told that they were taking part in a study of observer agreement on social behaviour as a whole. The difference between Actions and Social context was explained but the individual categories were not discussed. Observers were therefore identifying play by their own criteria and were not aware that this category was the major one being studied.

Observations were made in two sessions five to seven days apart. Session 1 consisted of an introductory two minutes of watching only, during which observers practised applying categories to behaviour, confining their judgements to the signalled instants and attending to one animal only. They then spent a further five minutes in becoming accustomed to recording these judgements on the check sheets provided. After this, observers were shown, and made judgements on, the test material. Session 2 involved a repetition of this final stage only. All observers were shown the same two 10 min sections of videotape in the same order in both sessions. The experimenter also went through this procedure, and then performed a second analysis categorising the material into the classes defined in Appendix B.

From the four sets of judgements obtained from each observer, it was possible to measure individuals' consistency, and the extent of agreement between individuals and the experimenter, or between different naive observers. Using these judgements and the detailed analysis it was also possible to ascertain which behaviours tended to be identified as playful by the majority of observers.

2.3 Treatment of results

Agreement was measured between classifications of behaviour. Two types of comparison were made between pairs of records:

(a)Within observers, between their first and second scorings of the material, to gauge their consistency.

(b)Between observers and the experimenter (who is used as a standard) to show the extent of interobserver agreement.

A third type of comparison was made between all 10 observers' records:

(c)Behaviours identified as play by the majority of observers.

For each paired comparison, overall agreement was ascertained from the total number of observations which were classified the same, and agreement on play alone was classified separately. To ensure that agreement on play alone did not result from blanket use of this category by an observer, the mean numbers of observations on which naïve observers and the experimenter used each Social context category were plotted on a histogram (Fig. 2.1). This shows that both used the categories to approximately the same extent, and that the class "Playful" was used on only about 29% of observations.

The measure of agreement calculated for play was one of several types of concordance discussed by Caro, Roper, Young and Dank (1979) for describing agreement on a single category. It is calculated from

$$C = A/A+(D/2)$$

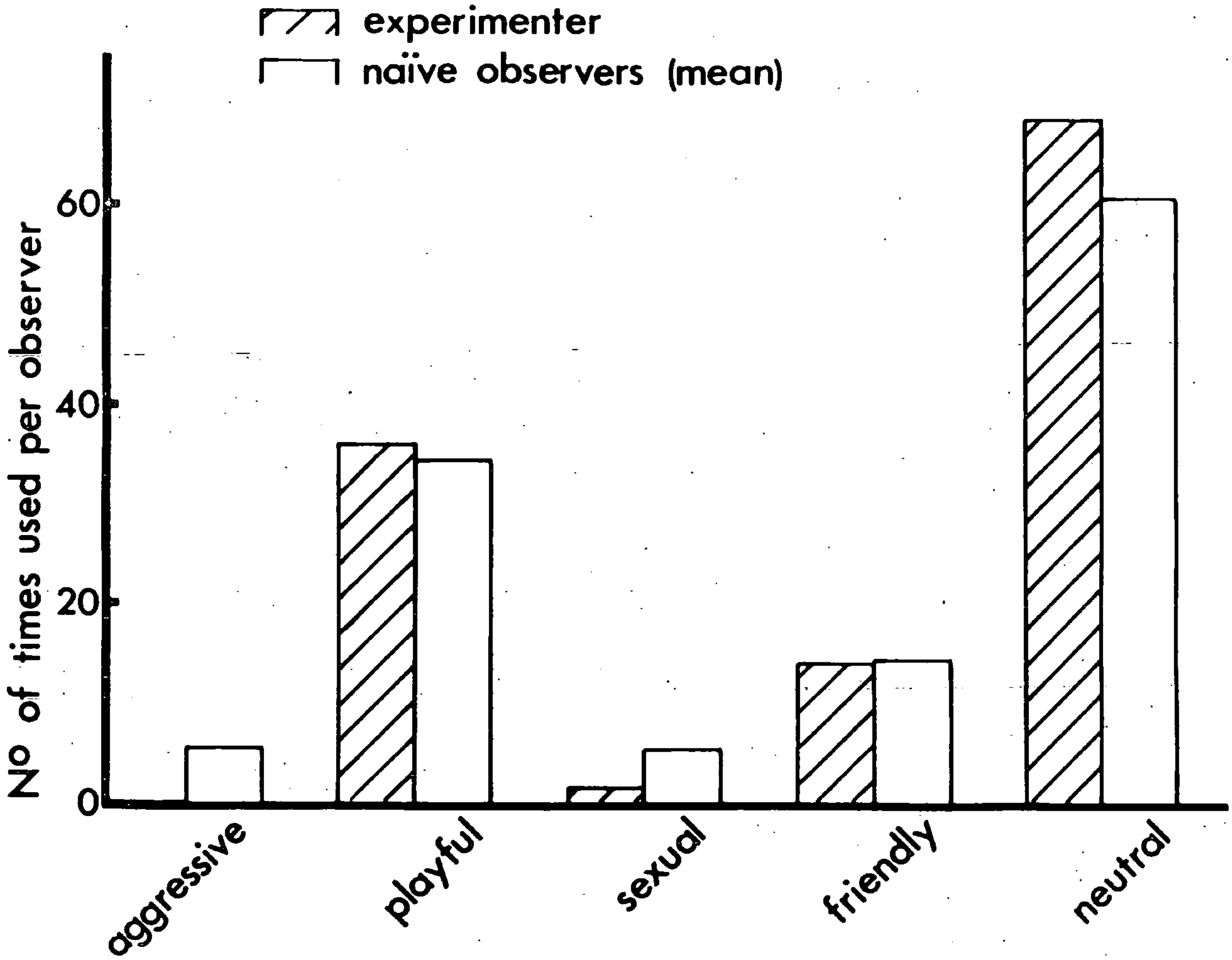


Fig. 2.1

Category use by observers: mean number of uses of each category by the experimenter (hatched columns) and by all naïve observers over all 120 point samples.

where C = concordance, A = agreements and D = total disagreements. C represents the proportion of actual occurrences of the behaviour on which the two observers agreed, if (A+D/2) is the best available measure of the actual number of occurrences. The coefficient of agreement, kappa (Cohen, 1960) was also calculated for overall agreement on Actions and Social context in each comparison.

$$\text{kappa} = \frac{p_o - p_c}{1 - p_c}$$

where p_o = observed proportion of agreement and p_c = chance (expected) proportion of agreement.

To gain an idea of the standard of observers' agreement with the experimenter, these two indices of agreement between naïve observers and the experimenter were compared back to observers' internal consistency indices in Wilcoxon tests. Since an individual's ability to judge behaviour consistently sets the ceiling on his ability to agree with other observers, such a comparison shows how close interobserver agreement is to its optimum. Such a treatment is more informative than standard tests of difference from chance since, as Cohen (1960) and Caro et al. (1979) point out, difference from chance is trivial when agreement on the same material is being studied.

A combination of more detailed examination of the behaviour and pooling of observers' opinions showed which behaviours were most commonly identified as play. After detailed analysis of the videotapes had classified the rat's behaviour at each sampling point into one of the 13 categories listed in Table 3.1, p.95, observer opinion on each of these categories was examined in turn. All the sampling points at which the behaviour occurred were listed and the number of observers classifying each point sample as playful was counted. From this the mean number of "Playful" classifications per occurrence for each behaviour could be calculated.

2.4

Results

(a) Consistency within observers.

1. Agreement on play.

Individuals´ concordance scores are plotted in Fig. 2.2a with those of the experimenter. Naïve observers show concordances of approximately 60%, and the experimenter´s are approximately 80%.

2. Overall agreement.

Individuals´ agreement scores (observations out of 60 which were classified the same on both occasions) are plotted in Fig. 2.2b. Mean kappa for actions was 0.66 and for social contexts 0.48. As Fig. 2.2b suggests, agreement on actions categories is higher than on social context categories ($p<0.01$) indicating that actions are judged with greater reliability than social contexts overall.

(b) Agreement with the experimenter.

1. Agreement on play.

Scores for concordance on play between observers

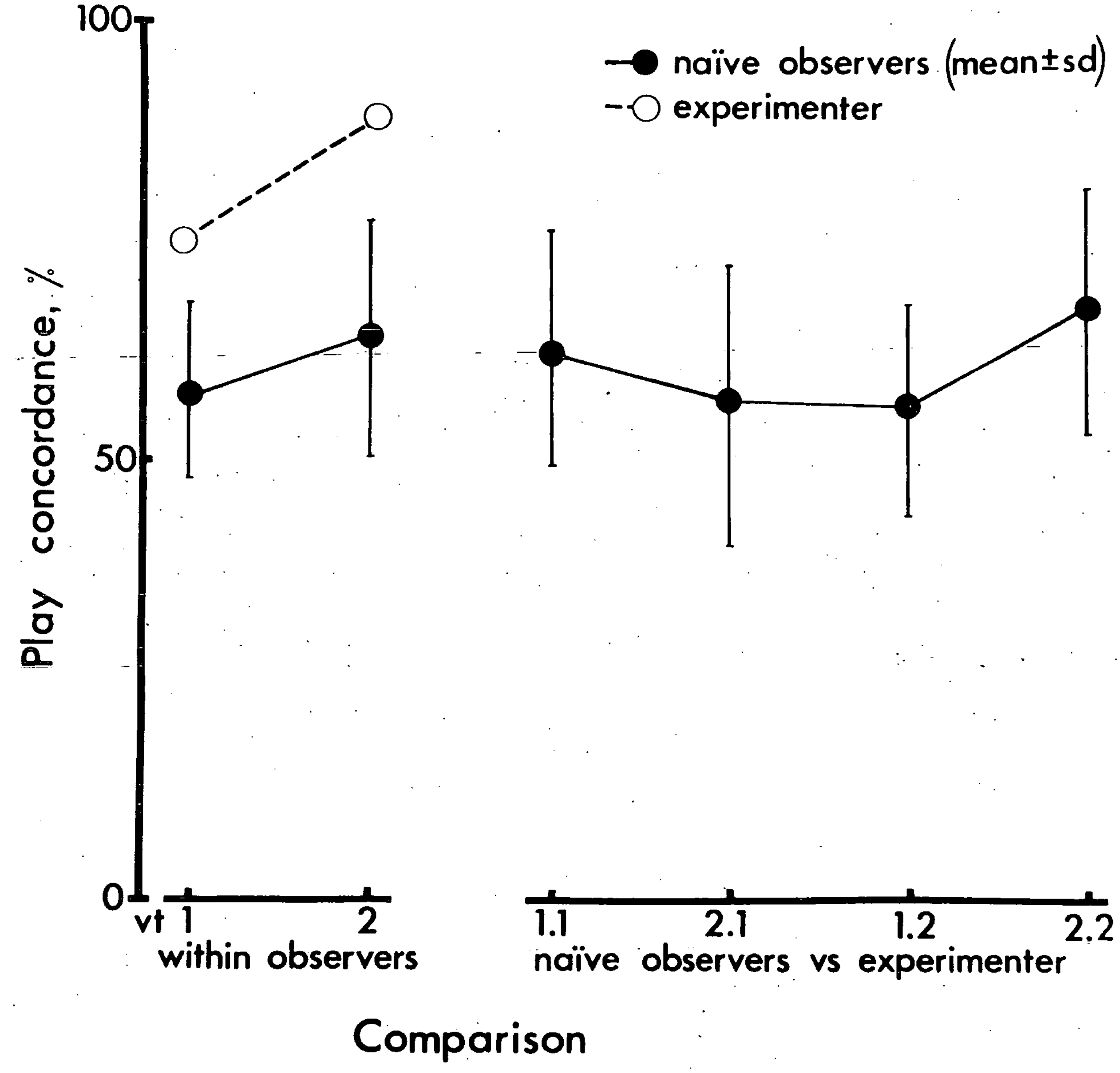
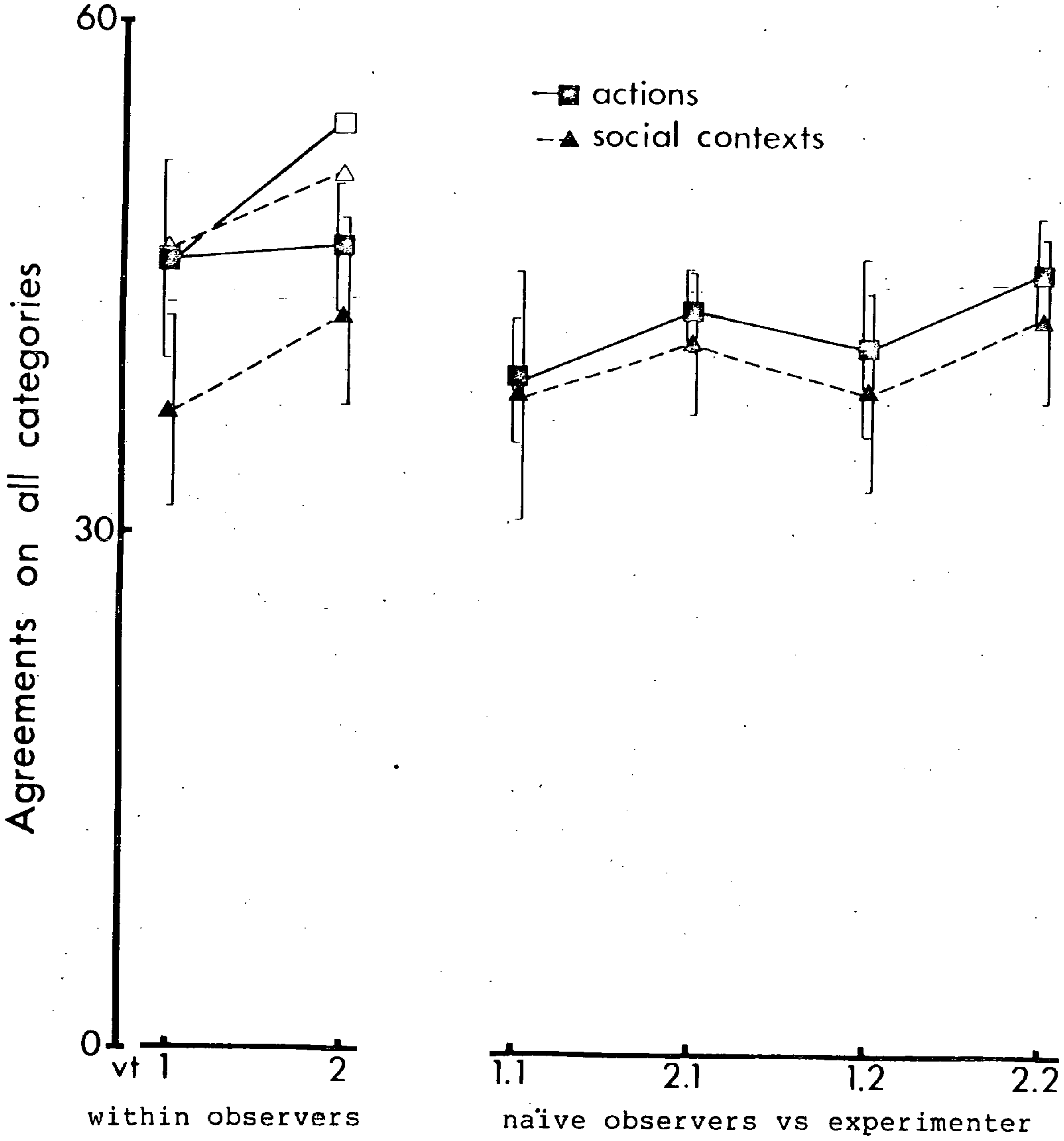


Fig. 2.2a

Concordance on play, within observers (left) and between naïve observers and the experimenter, for each videotape (vt).



Comparison

Fig. 2.2b

Agreement on all categories: agreements out of 60 within observers and between naïve observers and the experimenter. Filled and unfilled symbolsrepresent naïve observers and the experimenter respectively.

and the experimenter are plotted in Fig. 2.2a. These are not significantly different from intraobserver play concordance scores (see Table 2.1).

2. Overall agreement.

Mean agreements between observers and the experimenter are plotted in Fig. 2.2b. Agreement on social context is not significantly different from intraobserver scores, but agreement on actions is significantly lower for 3 out of four records (see Table 2.1). Mean kappa values for first and second records were 0.55 and 0.57 for actions, and 0.46 and 0.48 for social contexts.

(c) Behaviours identified as play.

The extent to which each of the 13 behaviour categories used was identified as playful is shown in Table 2.2. The behaviours with a majority vote of ´playful´ (i.e. with a mean of more than five ´playful´ classifications out of 10 per occurrence of the behaviour) were:

Approach-fast, Flee-fast, Paws-on, Wrestle-top and Wrestle-under.

2.5

Discussion

From the observers´ reliability scores it is apparent that, despite their lack of experience, they attained levels of consistency not far below that of the experimenter. The classification of kappa values devised by Landis and Koch (1977) would describe most individuals´

VT	Concordance on play	Agreement on actions	social context
1.1	NS	0.05	NS
2.1	NS	0.01	NS
1.2	NS	0.01	NS
2.2	NS	NS	NS

Table 2.1

Levels of significance of differences between observer-experimenter agreement and intra-observer agreement from Wilcoxon tests.

Behaviour	Play classifications
Approach-fast	6.3
Flee-fast	7.6
Paws-on	6.6
Wrestle-top	5.6
Wrestle-under	5.5
Sniff	3.3
Passive contact	1.6
Sexual advance	1.0
Approach-slow	0
Flee-slow	4.0
Eat/drink	0.6
Solitary	1.2

Table 2.2

Mean number of naïve observers (out of 10) classifying each occurrence of each behaviour as playful.

overall consistency as ´moderate´ to ´substantial´. The fact that Actions were judged with greater consistency than Social contexts suggests that it is easier to decide what an animal is doing than to interpret the social implications of its actions, but it is apparent that observers were able to make both types of decision, and thus identify play, with reasonable reliability.

This indicated that individuals were classifying behaviour by their own relatively constant criteria. Comparison between observers and the experimenter showed how much different individuals´ criteria had in common, the experimenter serving as an arbitrary standard against which all individuals were compared. Agreement between observers and the experimenter was found to be as good as that within observers on play and Social contexts, but worse on Actions in three out of four records. This suggests that observers´ criteria for identifying play and other Social contexts are very similar, and that the factor limiting agreement is individual consistency in applying these criteria. For Actions, where individual consistency is comparatively high, it may be that similarity of criteria becomes limiting, although since these categories are relatively unambiguous it seems more likely that individual differences in timing of observations limit agreement.

The behaviours which observers´ criteria classed as play correspond well with those defined as playful in other studies. Approach-fast and Flee-fast correspond to the "p-charge" and "p-withdraw" of Poole and Fish (1975). They are also equivalent to the "Chase" of Meaney and

Stewart (1981) which is not specifically described as playful although it occurs at high frequencies at the ages when play occurs. This behaviour and its properties at different ages will be discussed further in section 3.3 in the light of detailed longitudinal behaviour studies. Paws-on corresponds to "p-pounce" (Poole and Fish, 1975) and "Pouncing" (Meaney and Stewart, 1981) and is considered by the latter to be a play initiation act. Wrestle-top and Wrestle-under correspond to "p-aggressive posture" and "p-submissive posture" (Poole and Fish, 1975) and to "On-top Posture" and "On-the-back Posture" (Meaney and Stewart, 1981) and are often referred to collectively as play-fighting because of their structural similarity to adult agonistic behaviour. These behaviours have thus been recognised as playful by independent experienced observers as well as by the 10 naïve observers and one experimenter in this study, and therefore agreement extends beyond the videotape extracts used here.

Coelho and Bramblett's recent (1981) study of agreement between highly trained observers using 200 behaviour categories shows how closely observers can agree. The present study has looked at the other end of the scale, testing agreement between untrained observers with no knowledge of the animal and no prior explanation of the behaviour categories. Even under these circumstances overall agreement was 'moderate' to 'substantial' (Landis and Koch, 1977), and agreement on play was as good between as within observers. This lends support to the assumptions of Lorenz, Miller and others that people are able to recognise certain activities as play, and to reach broad agreement, even though they are uncertain which properties cause them to do so. However, it should be remembered that these findings apply only to rough and tumble in young rats, whose status as play appears to be relatively undisputed. It seems likely that behaviour such as the solitary ´play´ of mice, which is the object of disagreement between experienced observers (see 6.5.1), would elicit a more mixed response from pannels of naïve observers. In species with comparatively large behavioural repertoires such as primates, it is likely that some behaviours would be identified as play with high levels of agreement, while opinions would differ to varying degrees over others. Such a core of agreement with surrounding behaviours of more disputed identity corresponds to the type of definition envisaged by Meyer-Holzapfel (1956) as described in 1.2. Detailed examination of the properties of the behaviours in relation to the extent to which they were called playful could help to reveal what causes behaviour to be interpreted in this way. A comparative approach, in which such studies were carried out on a number of species and the ´playful´ behaviours compared, could also contribute to the development of a more global definition.

For the present study, however, the behaviours described above and listed in 2.4 which were classified as playful by the majority of naïve observers, as well as by independent experienced observers, will be used as a working definition of play in the rat in the hope that they capture as much of this elusive entity as possible. Photographs illustrating some of these behaviours are included in Appendix A.

CHAPTER 3

LONGITUDINAL STUDY OF ACTIVITY PATTERNS AND SOCIAL BEHAVIOUR IN LITTERMATE GROUPS OF JUVENILE RATS

3a

General Introduction

The activities which were identified by observers as play (see Chapter 2) are examined here in the wider context of the young rat's behavioural development. Longitudinal studies of groups of littermates were carried out over the period between weaning and sexual maturity, with observations being made at 2 - 3 day intervals. By means of timelapse video recording, it was possible to build up a picture of the distribution of play and other activities throughout the day. Analysis of these videotapes by three methods gave information on the amount and bout structure of play (3.1), the development of day/night activity differences (3.2) and the frequency and sequence organisation of individual behavioural elements (3.3).

3b

General Method

Time lapse video records were made of littermate groups of juvenile rats at intervals between weaning and puberty. Each video record covered almost a full day (tape lengths varied between 19 and 22 hr) and was analysed to show the distribution and length of active and sleep periods and of play bouts. Selected sections of these records were studied in more detail in an examination of the fine structure of behaviour.

Young rats were weaned at 21 days of age, and litters were culled to four individuals each. These four animal littermate groups will be referred to simply as litters for the rest of this chapter. Records were made of two such groups (litters A and B) at approximately two day intervals between the ages of 21 and 56 days, and of two more groups (litters C and D) at 5 day intervals between 25 and 55 days of age (except at 40 days, when the apparatus failed). Each of these litters consisted of two males and two females. The rats were bred in this laboratory, and were the result of a back-cross between hybrid BN/Lister hooded females and Lister hooded males. Offspring of such crosses typically included black-hooded, brown-hooded, and all-brown individuals of different shades, and litters were culled so that representatives of one sex were hooded and those of the other sex were different shades of plain brown. (Some recordings were also made of a further seven litters of Lister hooded rats, three all-male, three all-female and one mixed, but repeated apparatus failure meant that they were at sparse and irregular intervals. Results from these litters were not subjected to statistical treatments, but are quoted as supporting qualitative evidence.)

Each group of littermates was housed in a white plastic cage (North Kent Plastics RB1, 45 x 28 x 22 cm) with a wire mesh top, and provided with food and water ad lib. Litters were videotaped in their home-cages through clear perspex lids with which the normal wire mesh lids could be replaced.

Recordings were made using a National Panasonic timelapse VTR, set to take 2.5 half-frames per sec, and a low-light sensitive video camera. The animals were kept in a light/dark cycle of 12L:12D (light between midnight and noon) which was maintained during recording, with a red light to allow filming in the dark phase. A digital clock readout was superimposed on the picture at the time of recording. Videotapes were analysed by three different methods which are described separately in the following three sections.

3.1

ORGANISATION OF PLAY AND OTHER BEHAVIOURS

3.1.1

Introduction

Social play is first seen among rat pups at 16 - 17 days of age (Harris 1980) and continues until after they reach sexual maturity. During this juvenile period, many major changes occur in the young rat´s way of life. The first of these is weaning, which may occur at 21 days if the mother gives birth to another litter, or 5 - 10 days later if no such constraint is in force, and marks the beginning of the animal´s independence. Some 5 - 10 days after weaning, wild rats begin to leave their burrows and explore the outside world (Calhoun 1962), which involves a further increase in independence and a considerable broadening of experience. A third milestone of development occurring during the play period is the onset of puberty. Males begin to distinguish behaviourally between the sexes at 36 - 40 days, although they do not begin to mount until 40 - 50 days and only reach full adult sexual competence at 50 - 55 days or older (Meaney and Stewart 1981). Females become sexually mature somewhat earlier and are capable of conception at 40 - 50 days or, in some cases, as young as 35 days. By 50 - 55 days, therefore, rats are becoming young adults.

Throughout this period of discovery and behavioural upheaval, a large proportion of the animal´s social interactions are playful. It therefore seems reasonable to expect these fundamental changes in life-style to influence social behaviour and thus to affect the nature and/or quantity of play. Bateson and Young (1981) have found such a relationship between the play of kittens and a major change in their life-style: weaning appears to be associated with a decrease in social play and a concurrent increase in object play. They base a functional interpretation of their observations on the assumption that play in kittens promotes the acquisition of specific skills. Play should therefore be appropriate to the cat's ultimate needs and, in order to give the maximum advantage for the energy invested, it should be tailored to make the best use of the materials available, which are primarily siblings before weaning and objects and live prey items after, since kittens are moved out of the den after weaning and supplied with food caught by the mother.

The play of rats is almost entirely social, and consists mainly of vigorous wrestling and chasing, which appear to involve the expenditure of large amounts of energy. From the structural characteristics of this play, and from information on other aspects of life at the time when investment in play is highest, it is possible to make tentative suggestions as to potential functions. Such suggestions may then be used to guide further observational or experimental studies addressed at specific hypotheses.

The present study examined the total amounts of time which rats spent in play and thus attempted to compare their investment in play at different ages, and to relate this to major changes in their life-style.

Individuals can control their investment in play either through the amount which they initiate or the length of time for which they choose to continue a single bout. The importance of these factors in the control of investment in play was studied by means of measures of bout number and length, interbout interval length and preferred play group size.

3.1.2

Method

Timelapse videotapes were examined for playful interactions, defined as encounters in which two or more animals engaged in active play (Wrestling or Fast locomotion, as described in Appendix B) for more than 1 sec. (Paws-on was not included unless it received a response within one second since, alone, it did not constitute a playful interaction according to the operational definition of an interaction in 3.3.2.) No solitary behaviours were included. Bouts were taken to have ended when none of these activities had occurred for at least 10 sec. This analysis thus produced two types of bout: individual bouts, which refer to the length of time for which each individual plays continuously, and litter bouts, which refer to the play occurring in the litter as a whole and are by definition as long as, or longer than, the individual bouts of which they are composed.

This analysis was performed with the aid of an Apple II Microcomputer, as was that of the fine structure of behaviour described in 3.3.2. At each change of play group composition (including initiation and termination of bouts) the identities of the new players and the time were recorded. From this, bout lengths and numbers, and therefore total time spent playing, could be calculated for each individual and for the litter as a unit. These measures could also be calculated for specific periods during the day. Information on players' identities allowed examination of partner preferences and play group size.

Observer consistency was tested by comparing the results of two analyses of the same videotape. (These were carried out several weeks apart, and the duplication happened unintentionally.) Concordances were calculated as in Chapter 2 from levels of agreement and disagreement such that

$$C = A/A+(D/2)$$

where A = agreement and D = disagreement, although in this case A & D were measured in total times and frequencies rather than for specific occurrences (see Caro et al., 1979, for methods of checking observer reliability in continuous recording). Consistencies are reported on p.74.

Treatment of results

Data were obtained from the videotape analysis on amounts of play, numbers of play bouts, mean bout and interbout interval lengths and frequency of different play group sizes at all the ages studied. These are plotted graphically against age, and were tested for age-related trends by calculating Pearson product moment correlation coefficients (r, Ferguson 1959) between age and the mean score obtained by litters, or all individuals, at that age. A significant negative correlation between a behaviour score and age indicates a consistent age-related decrease in the frequency of that behaviour. Correlations were also examined between single litters' scores to show the extent of variation between litters, and amounts of play in litters A and B were subjected to a trend analysis.

Where age changes in the relationships between pairs of factors were being examined, data were combined into four age groups: 20 - 29 days, 30 - 39 days, 40 - 49 days and 50 - 56 days. Log survivor functions (Fagen and Young 1978) are plotted for play bout lengths and inter-bout intervals. In these, the number of intervals surviving to each successive length is plotted on a logarithmic scale against length, and the shape of the resulting line reflects the nature of the processes involved in ending the intervals. A straight line indicates that the probability of termination of an interval is constant, and independent of interval length. Intervals are therefore terminated by a random process, the probability of termination being proportional to the slope of the log survivor function.

3.1.3

Results

1. Total play per day.

From Figs. 3.1a and b it can be seen that mean time spent playing by each individual, and by each litter as a whole, rises to a peak at about 30 days of age, and declines

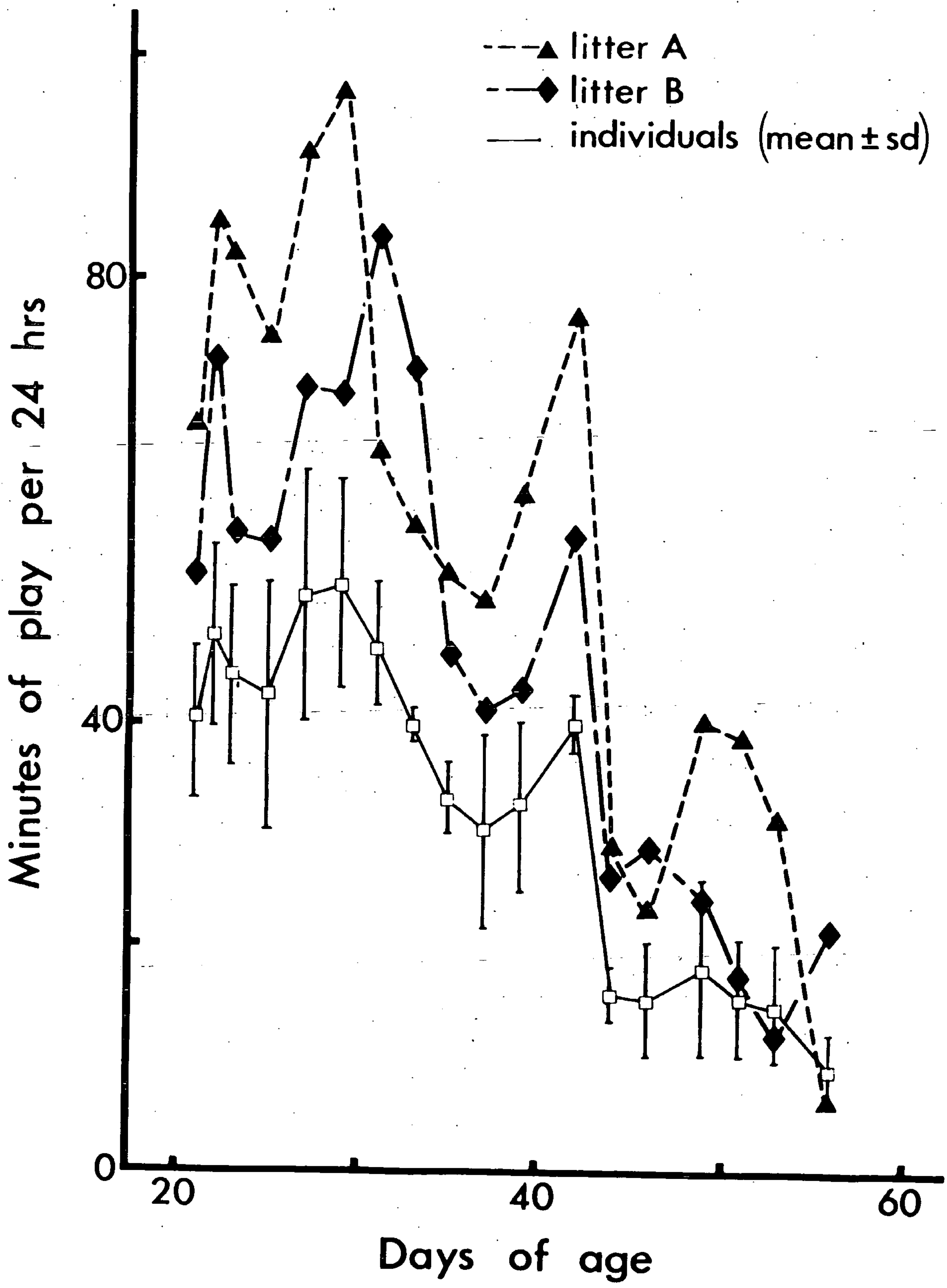


Fig. 3.1a

Time spent playing per 24hrs by litters A and B and individuals (mean ± SD) at different ages.

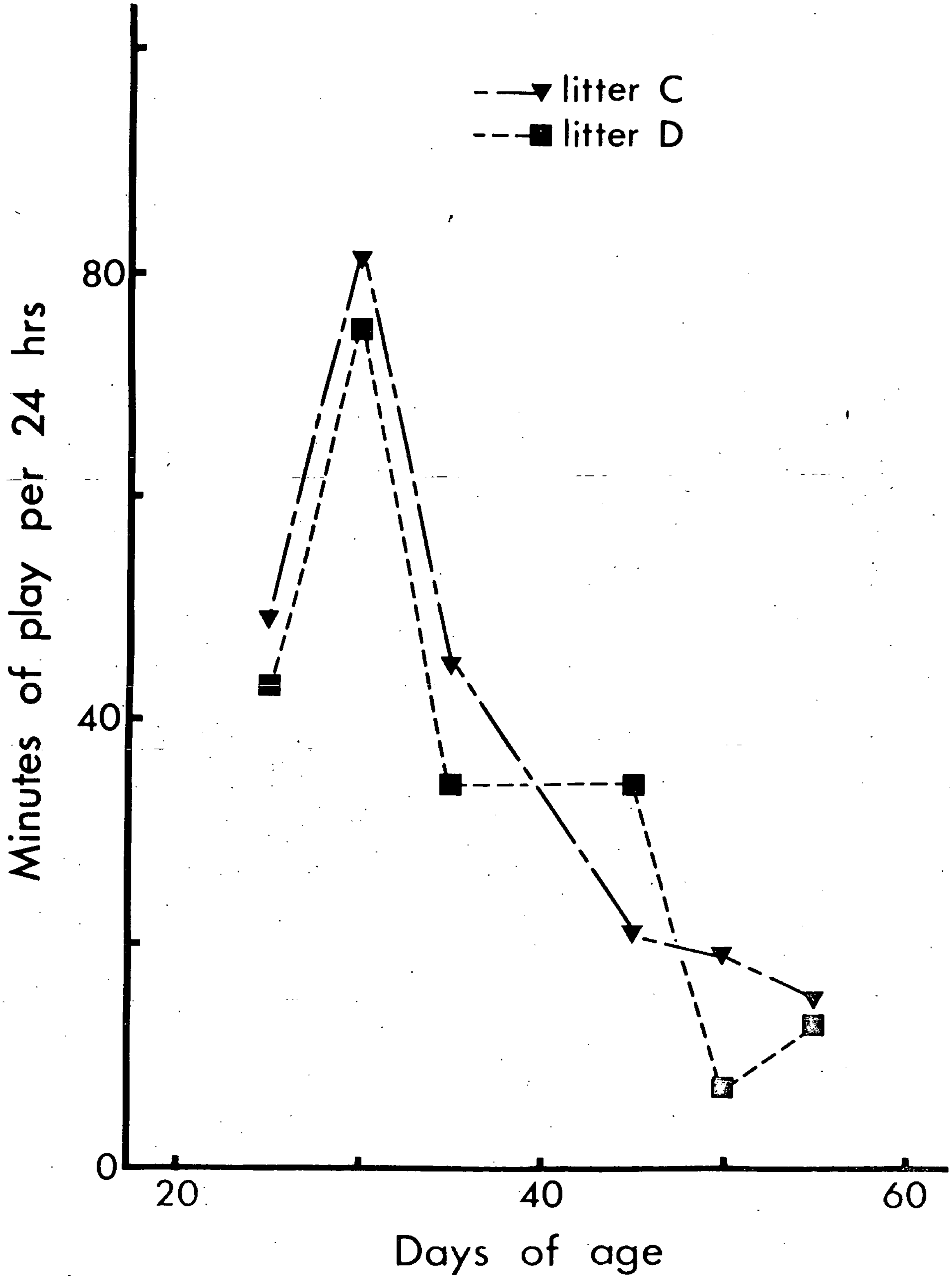


Fig. 3.1b

Time spent playing by litters C and D at different ages.

thereafter. Litters A and B showed a significant negative correlation between time spent playing and age both for individuals ($r = -0.92$, $p<0.001$) and for litters ($r = -0.90$, $p<0.001$) indicating that play decreases with increasing age over the age range studied. Litters C and D showed a similar negative correlation ($r = -0.82$, $p<0.05$). The separate scores for litters A and B correlated closely ($r = 0.80$, $p<0.001$) as did those for litters C and D ($r = 0.93$, $p<0.01$), indicating that simultaneously reared litters devoted similar amounts of time to play at given ages. Mean scores for litters A and B at the appropriate ages also correlated with those for litters C and D ($r= 0.92$, $p<0.01$), although these two pairs of litters were not reared simultaneously, which suggests that this pattern of investment of time in play is a developmental trend rather than the result of environmental fluctuations. Although litters A and B both appear to show a small second peak at about 40 days, the only significant trend revealed by a trend analysis (Keppel 1973) was a linear one ($p<0.01$). Neither the apparent increase from 21 to 30 days, nor the 40 day peak, was sufficient to make quadratic, cubic or quartic components significant. Litters C and D cannot contribute further evidence on this question because of the scarcity of data and the total absence of recordings at 40 days. For these reasons, results of statistical treatments of these litters' scores will not be given in the following treatments of other measures of play.

2. Play bouts per day.

Total bout number per day follows a downward trend similar to that of total play time, see Figs. 3.2a and b. The

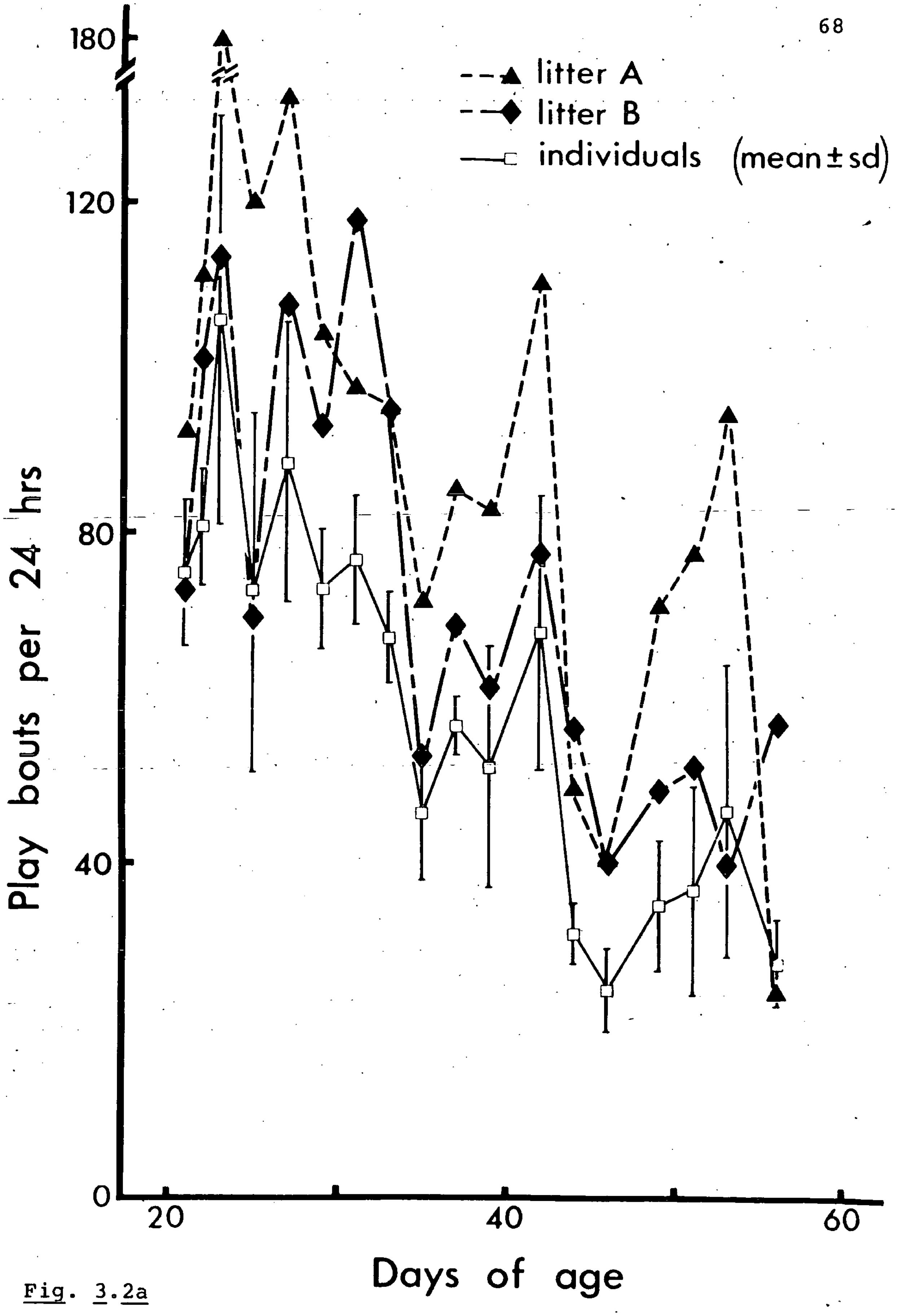


Fig. 3.2a

Play bouts per 24hrs for litters A and B and individuals (mean ± SD) at different ages.

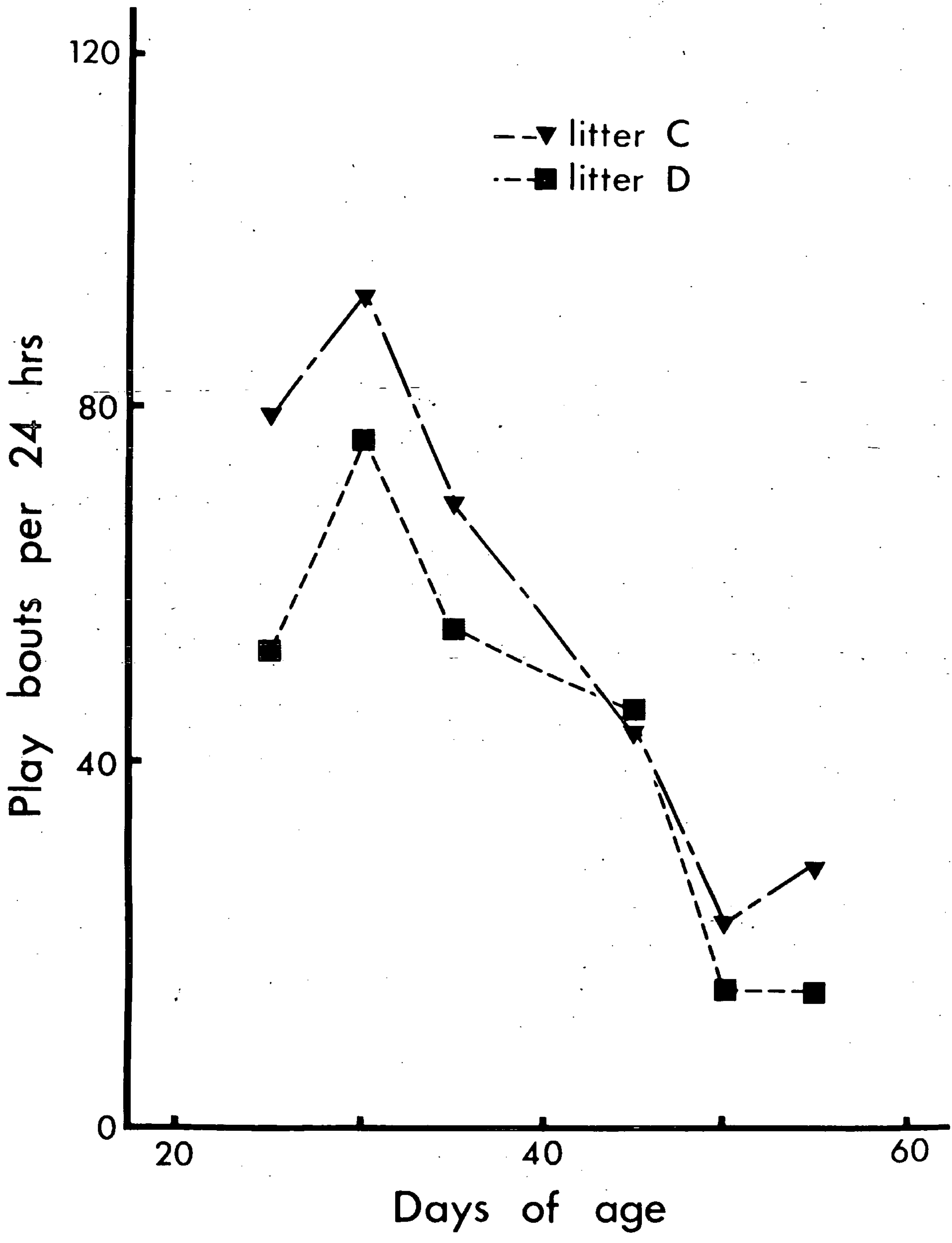


Fig. 3.2b

Play bouts per 24 hrs for litters C and D at different ages.

negative correlation between play bout number and age is significant for litters A and B ($r = -0.83$, $p<0.001$ for litters, and $r = -0.86$, $p<0.001$ for individuals) between 21 and 56 days of age.

3. Play bout lengths.

Both litter and individual mean play bout lengths show small but significant negative correlations with age (litter: $r = -0.66$, $p<0.01$, individual: $r = -0.56$, $p<0.05$) over the whole age range. However, Fig. 3.3 suggests that play bout lengths increase up to 25 days of age, remain around stable maxima between 25 and 45 days, and decrease above this age.

The difference, d, between litter and individual mean bout lengths shows an overall decrease with age ($r = -0.767$, $p<0.001$). From Fig. 3.3 it can be seen that this decrease is the result of litter play bout length decreasing more steeply than individual bout length, and occurs from about 40 days of age. However, litter and individual scores follow the same trend with age, as they do for total play and play bouts (see Figs. 3.1 and 3.2). Where litter data are used in subsequent calculations, therefore, it is assumed that they reflect individual data with reasonable accuracy.

Log survivorship plots of litter bout length for the four age ranges, Fig. 3.4a, give straight lines. The slope of the 30 - 39 day line is the same as that of the 20 - 29 day line, but those for the two older groups are progressively steeper.

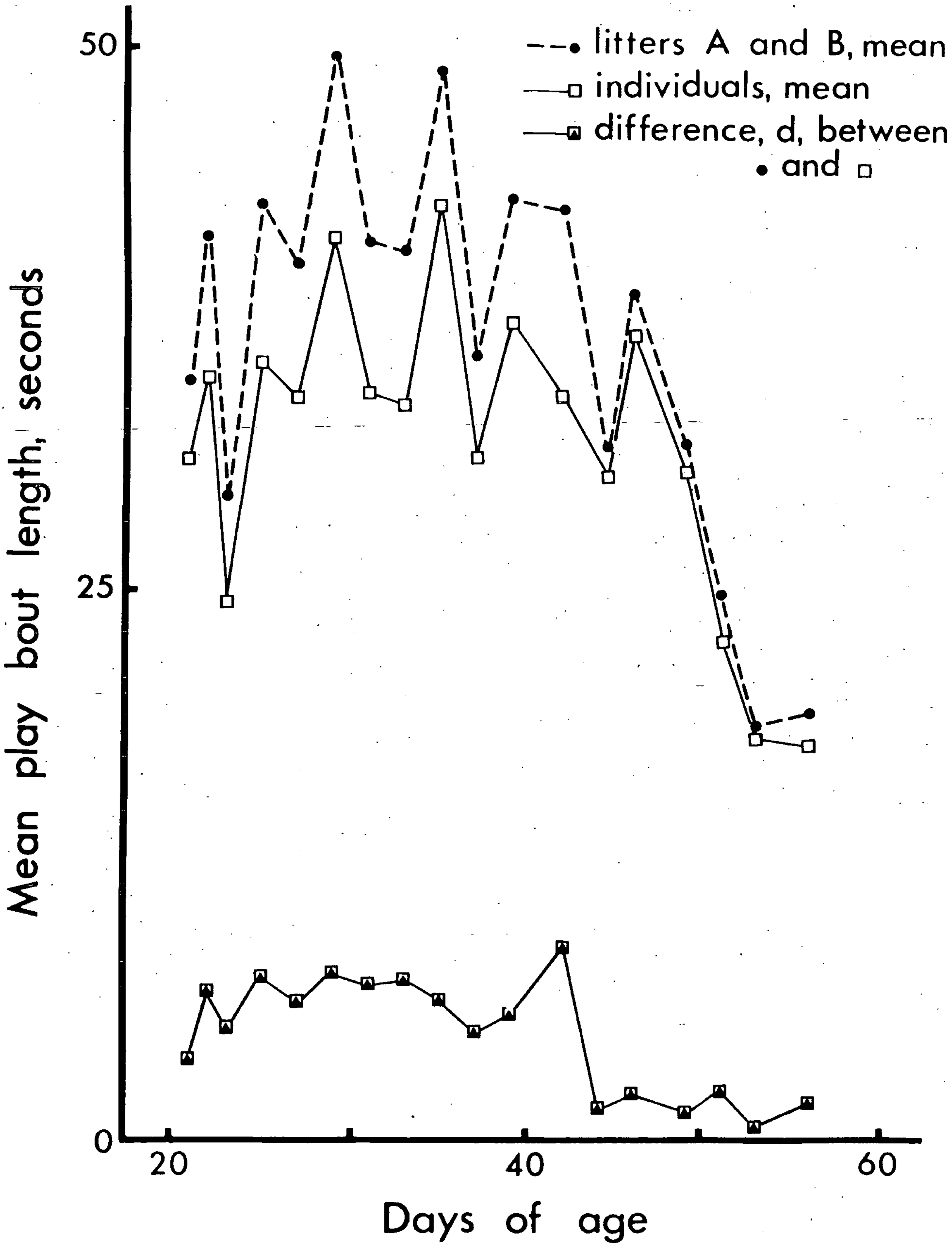


Fig. 3.3

Mean play bout lengths for litters A and B and individuals, and the difference, d, between them.

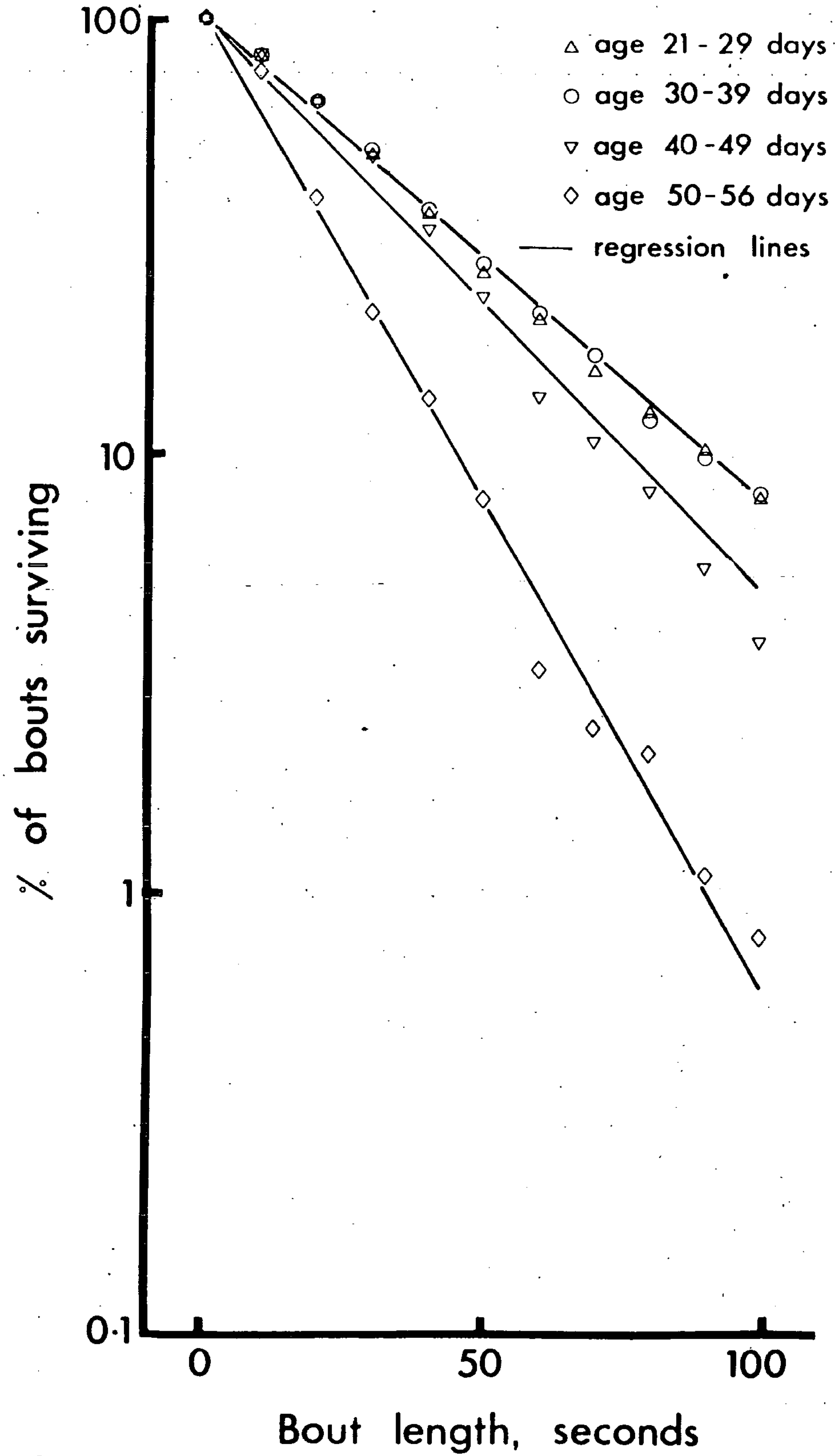


Fig. 3.4a

Log survivorship plot of play bout lengths for litters A and B with regression lines for each age-group. Those for the 20 - 29 and 30 - 39 day old groups are identical.

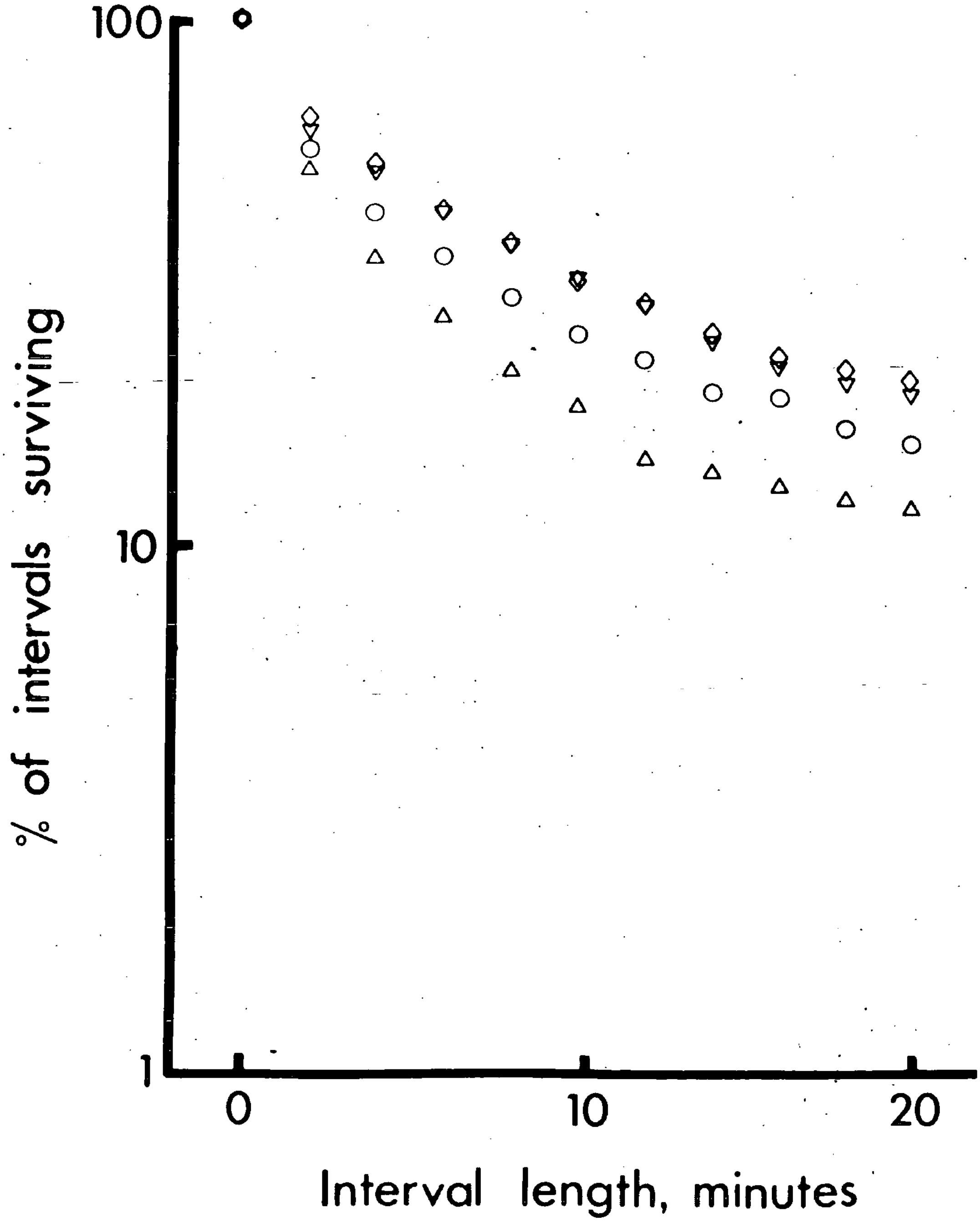


Fig. 3.4b

Log survivorship plot of interbout intervals for litters A and B. Age-groups are represented as in Fig. 3.4a.

4. Interbout interval lengths.

Log survivorship plots of interbout interval lengths give curves (Fig. 3.4b). These show the opposite age trends to bout length log survivorship plots: they become shallower with age at first, but remain the same for the two older groups.

5. Play group size.

Fig. 3.5 shows the proportions of total litter play at each age which occur in groups of two, three and four individuals. This shows that, up to 40 days of age, about a third of total play occurs in groups larger than two. Above this age, play becomes an increasingly dyadic activity until at 56 days over 95% occurs in pairs. Proportion of play occurring in pairs increases significantly with age ($r = 0.85$, $p<0.001$), while proportions in threes and fours decrease significantly (threes: $r = -0.73$, $p<0.01$; fours: $r = -0.77$, $p<0.01$). The increase in the proportion of play occurring in pairs is the result of simultaneous, if somewhat irregular, increases in the proportions of play in both mixed and single-sex pairs.

6. Observer consistency.

Concordances between the two analyses of one 19hr tape for the basic litter scores were: total play: 90.1%, total bouts: 94.4%, mean bout length: 96.7%. All concordances for each individual's scores exceded 80%, and approximately three quarters of these exceded 90%.

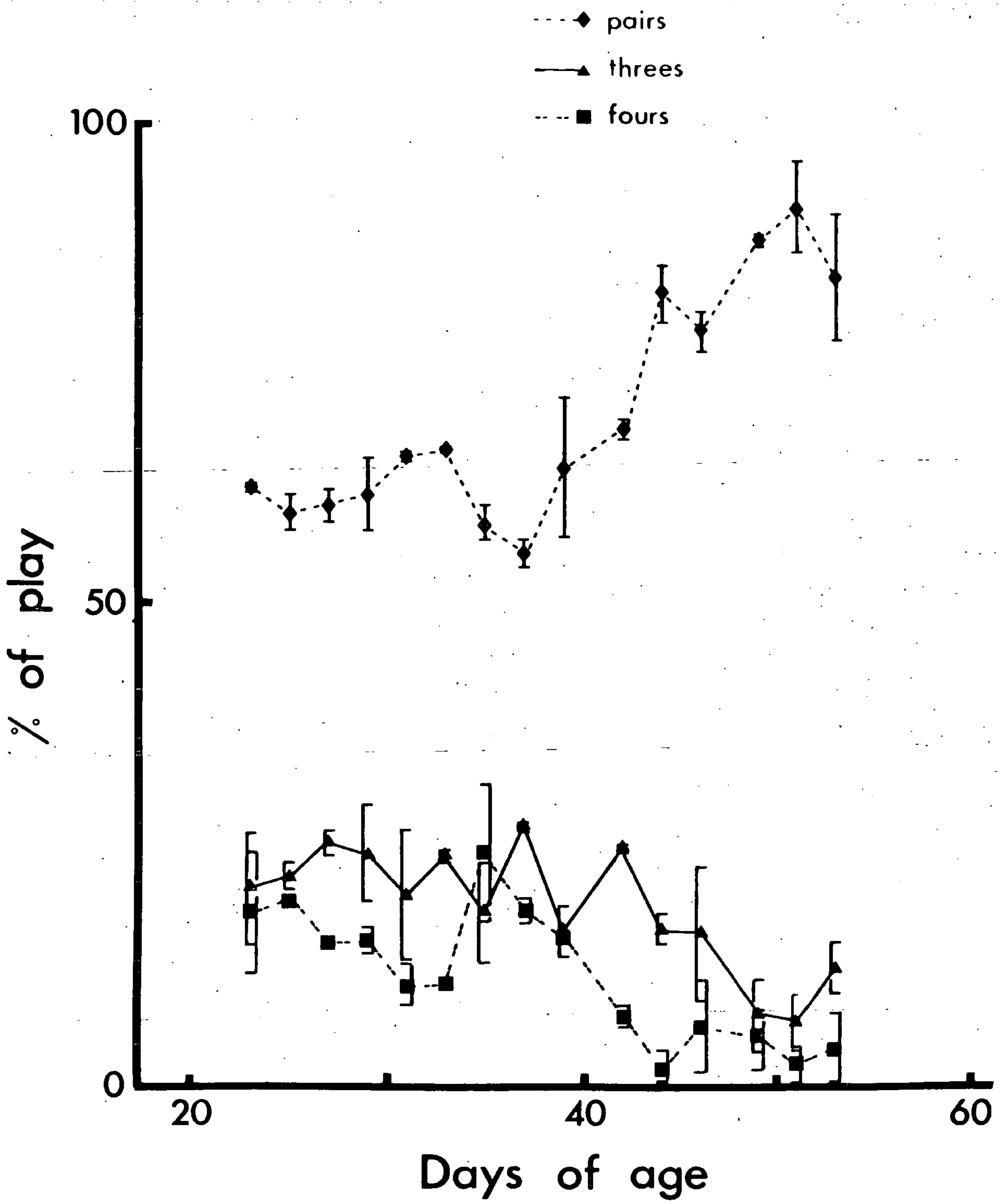


Fig. 3.5

Play group size: proportions of total litter play occurring in groups of two, three and four at different ages.

3.1.4

Discussion.

These results show that, overall, the amount of time which the rats spent in play decreased between 21 and 56 days, although it did not reach its peak until about 30 days. The seven litters whose results have not been quoted also showed this trend. If play carries the same unit cost in terms of energy and risk over this age range, then investment in play is highest at around 30 days. Assuming that investment in play is highest when the benefits to be gained are greatest, some property of the animal's surroundings at 30 days must make play most advantageous then. This peak in play occurs at the stage corresponding to that in the wild between weaning and emergence from the burrow, when the salient features of the young rat's environment are its siblings and its mother. That social play is maximal then suggests that maximum use is being made of the available resource - siblings - to achieve certain gains which social play can best provide.

In the absence of data from independent litters, it is impossible to say whether the smaller rise in total play at 40 days results from developmental changes or environmental variations, since litters A and B were reared simultaneously. Although it failed to constitute a significant trend, behavioural changes of some sort might be expected at this age, coinciding with the onset of puberty. Meaney and Stewart (1981) cite reports of an increase in male plasma testosterone at about 35 days (Sachs and Meisel 1979), and of vaginal opening and onset of ovulation in females at about 40 days (Kragt and Ganong

1968). Play at this stage could have some role in the learning of sexual characteristics, particularly since it is becoming increasingly dyadic and would therefore provide exposure to single sets of such properties. However, this would not explain the vigorous nature of play. Possible relationships between play and sexual behaviour are discussed further in 3.3 in the light of more detailed behaviour observations.

Investment in play at any age depends on the number of bouts initiated and the length of time for which each bout lasts. The log survivor functions indicate how these aspects of play vary grossly with age and thus how play investment is controlled. The curved functions for interbout intervals (Fig. 3.4b) show that at any age, a new play bout is most likely to begin immediately after the previous one has ended. This may in part be the result of the arbitrary choice of 10 sec as the bout criterion. Ideally, a pilot examination should have been carried out to see if any natural discontinuity existed in the log survivor plot of lengths of gaps in play indicating a change in the basis of these intervals. The bout criterion could then have been set at this level with some natural justification. Bout length log survivor functions (Fig. 3.4a), however, are straight lines, which indicates that bout termination is a random process and is independent of the time elapsed since the bout was initiated. This means that bouts are not terminated because of physical exhaustion. If this had been the case, the probability of termination would have increased with increasing bout length producing a convex log survivor function.

McDonald (1977) reported a similar straight line log survivor function for play bout lengths in the California ground squirrel, which he interpreted as evidence of the low priority of play. However, Fagen and Young (1978) have pointed out that this type of bout length distribution is found for a wide variety of behaviours including many, such as feeding, which would be seen as relatively high priority activities. While it is possible that play bout lengths are random because each is ended by interruption from a randomly occurring external event (it is an accepted characteristic of play that it is easily interrupted, e.g. Loizos 1966), it is also possible that the nature of the costs and benefits involved make random termination the optimal strategy for the animal to adopt. Maynard Smith (1974) has shown that such a strategy is optimal for an animal engaging in display conflict. Similarly, grazing animals would do best to break off at random intervals to check their surroundings for predators.

Although each set of log survivor functions retains the same basic shape throughout, indicating that the processes do not change fundamentally with age, there are age-related changes in slope which reflect overall probability changes. The flattening of the interbout interval curves indicates an overall decrease in the probability of play being initiated, while the steepening of the bout length functions from 30 days indicates an increase in the probability of bout termination. Control is thus exerted over play investment from both ends of the bout. These two types of control appear to be effective over different but overlapping age-ranges, initiations becoming less likely right from the start while termination becomes more likely from 40 - 56 days. Mean bout number and bout length scores reflect these changes in the log survivor functions: both decrease significantly over the course of the study, although Figs. 3.2 and 3.3 indicate that the decreases occur at different times.

Initially, therefore, total play increases because bouts become longer, a factor which outweighs their gradual decrease in number. However, from around 30 days play begins to decline because bout length stabilizes while bouts continue to become sparser. This early part of the decline is thus characterised by considerable enthusiasm for play once it has been initiated as shown by the greater mean bout length and the popularity of large play groups, but a decreasing tendency to initiate play which may reflect the increasing relevance of other aspects of the environment to the rat as it grows older. During the second phase of the decline play appears to become less "enjoyable". Animals break off their play sooner and become less likely to join in the play of others, as shown by the drop-in play group size and the closing of the gap between group and individual mean bout lengths. It appears that the average play bout begins to change at about 40 days from a group activity which may be perpetuated by successive individuals joining in and dropping out to a shorter interaction involving a single dyad.

3.2

ACTIVITY PATTERNS

3.2.1

Introduction

Adult rats are well known to be most active at night (Barnett 1975), particularly during the periods shortly after dusk and before dawn. Calhoun (1962) has reported that a captive population of rats in a large outdoor enclosure showed greatest feeding activity at night, with peaks 2 - 3 hr after sunset and before sunrise. The urban population studied by Takahashi and Lore (1980) showed similar activity patterns despite regular human activity in their habitat, indicating that these peaks of activity are not readily shifted by environmental disturbance.

Infant rats show a pattern of feeding activity which is appropriate to their own way of life and therefore very different from the adult pattern. Since milk is only available to them when the mother is present, infants feed more during the day, the mother's least active time, than the night (Levin and Stern 1975). Young rats appear to change from infant to adult feeding patterns over the weaning period when their diet is also changing. Levin and Stern reported that young rats first took more food at night than during the day at 19 days of age. This remained the lower limit for the emergence of the adult feeding pattern even in animals weaned as early as 15 days of age, suggesting that this is a developmental effect and not the result of other changes occurring.

In the present study, activity patterns were examined over the whole weanling-to-adult age range using the timelapse videotapes to follow the development of independent rhythmicity. Sleep bout times were obtained so that the characteristics of sleep during the light and dark phases could be compared and changes in total daily sleep could be monitored. The patterning of play activity throughout this period was also examined using play bout data from the analysis in section 3.1 in a comparison of play between the light and dark phases.

3.2.2

Method

Times at which each litter awoke and went to sleep were recorded. Previous observation had shown that littermates housed together tended to sleep and wake at approximately the same times, so the activity patterns of the litter as a unit were of most interest. The litter was classified as asleep if all individuals had lain still (often in a heap) for 2 min, and as awake if at least two individuals were active for 5 min. (These criteria were based on informal observations of the extent of activity which appeared to be necessary to awaken animals, and to prevent them from going to sleep.)

Treatment of results

Bouts were summed to give total times spent asleep and playing in the light and dark phases. Total sleep data were examined for age-related trends, as were play data in 3.1, by calculating Pearson product moment correlation coefficients between the mean score for the two litters and age. Light and dark scores were compared in Wilcoxon tests which, while they do not allow generalisation from these litters to the population as a whole, help to give an idea of the stability maintained in light/dark differences.

3.2.3

Results

(i) Age Changes

(i)1. Total sleep per day.

There is a small but significant decrease in daily sleep with age ($r = -0.51$, $p<0.05$) although there is considerable day-to-day fluctuation.

(i)2. Sleep bouts per day.

There is no apparent age-related change in number of sleep bouts per day ($r = -0.06$) and none in mean sleep bout length.

(ii) Diurnal fluctuations.

(ii)1. Total sleep in light and dark phases.

Fig. 3.6 shows that considerably more of the light phase than of the dark phase is spent in sleep ($p<0.01$). This difference increases up to about 30 days of age and then remains stable, the increase resulting mainly from a decrease in dark phase sleep.

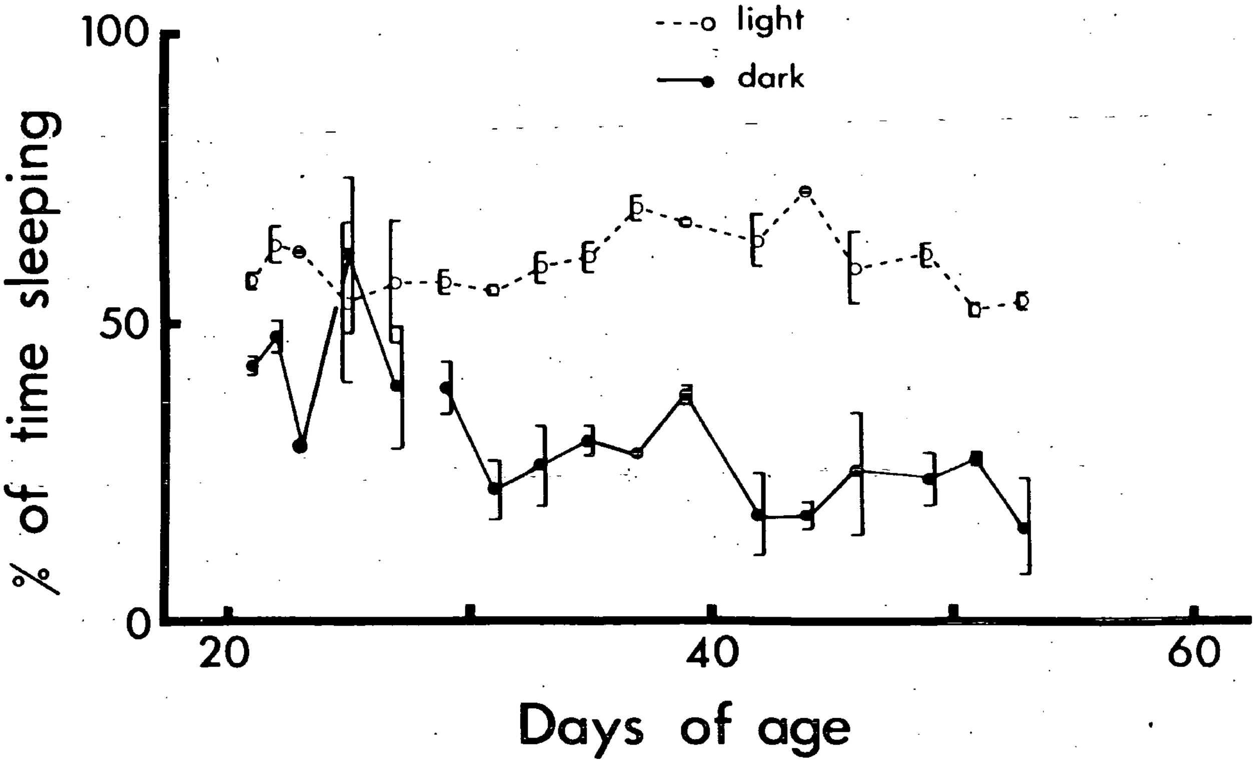


Fig. 3.6

Proportions of light and dark periods spent sleeping, means for litters A and B. Ends of bars show separate litters' scores.

(ii)2. Sleep bouts in light and dark phases.

Numbers of sleep bouts do not differ significantly between the two phases. However, sleep bouts are signifiantly longer during the light phase than the dark phase ($p<0.01$, see Fig. 3.7).

(ii)3.Total play in light and dark phases.

Although there is considerable variability between days, Fig. 3.8 shows that total play for both litters in the dark phase exceeds that for either litter in the light phase ($p<0.01$). This difference lessens by 45 - 50 days of age.

(ii)4. Play bouts in light and dark phases.

More play bouts occur in the dark than the light phase (Fig. 3.9, $p<0.01$). This difference is consistent, without overlap, between about 30 and 50 days of age. As Fig. 3.10 indicates, there is no difference in length between light phase and dark phase play bouts, and therefore the difference in total play time is the direct result of the observed difference in bout number: less play is initiated in the light phase. If total play is represented as a proportion of the time in that phase spent awake, Fig. 3.11, it can be seen that amounts of waking time allotted to play in the light and dark phases do not differ. Therefore, the differences in total play time and bout number are due solely to the different amounts of waking time available.

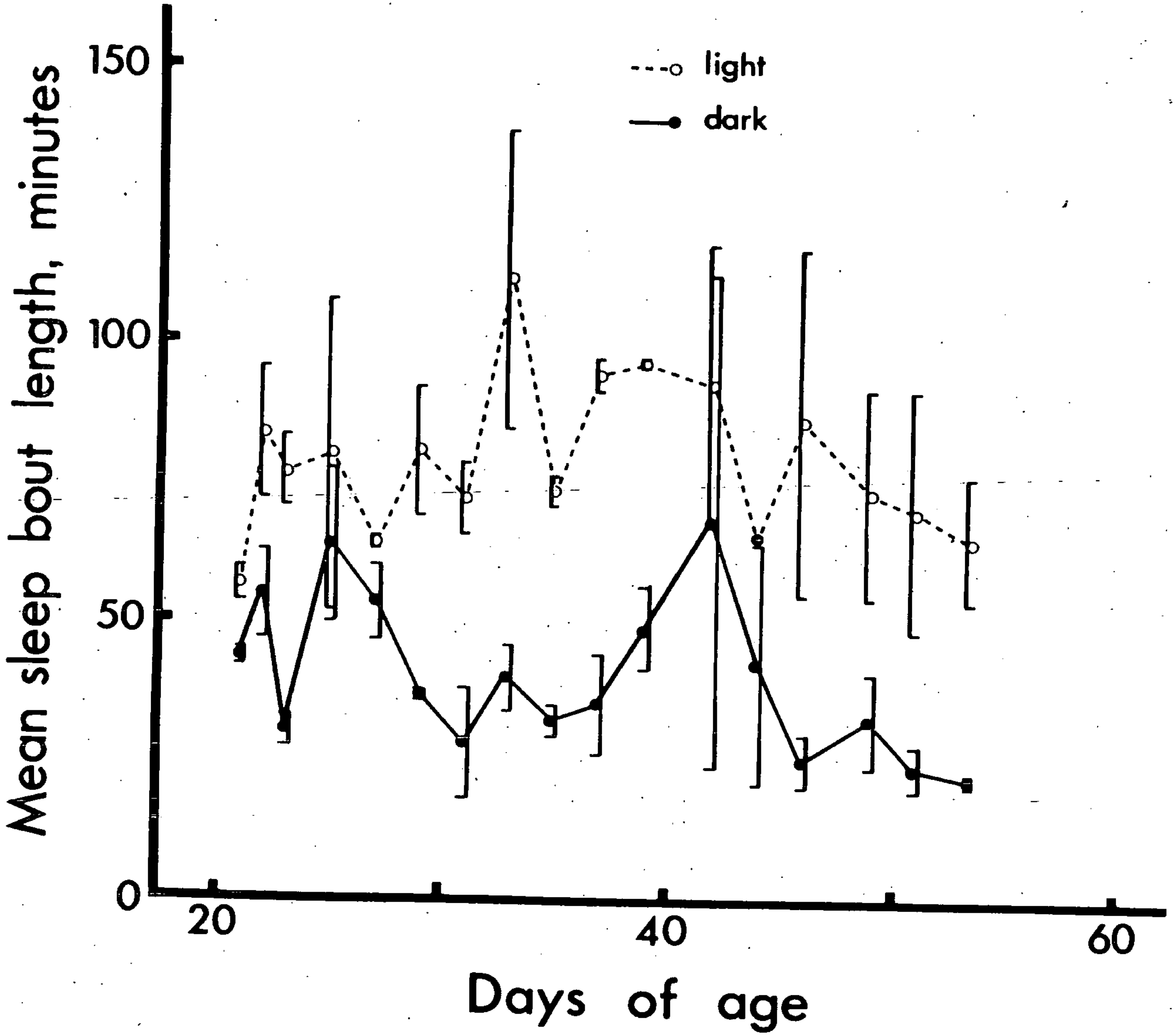


Fig. 3.7

Mean sleep bout lengths in light and dark periods, plotted as Fig. 3.6.

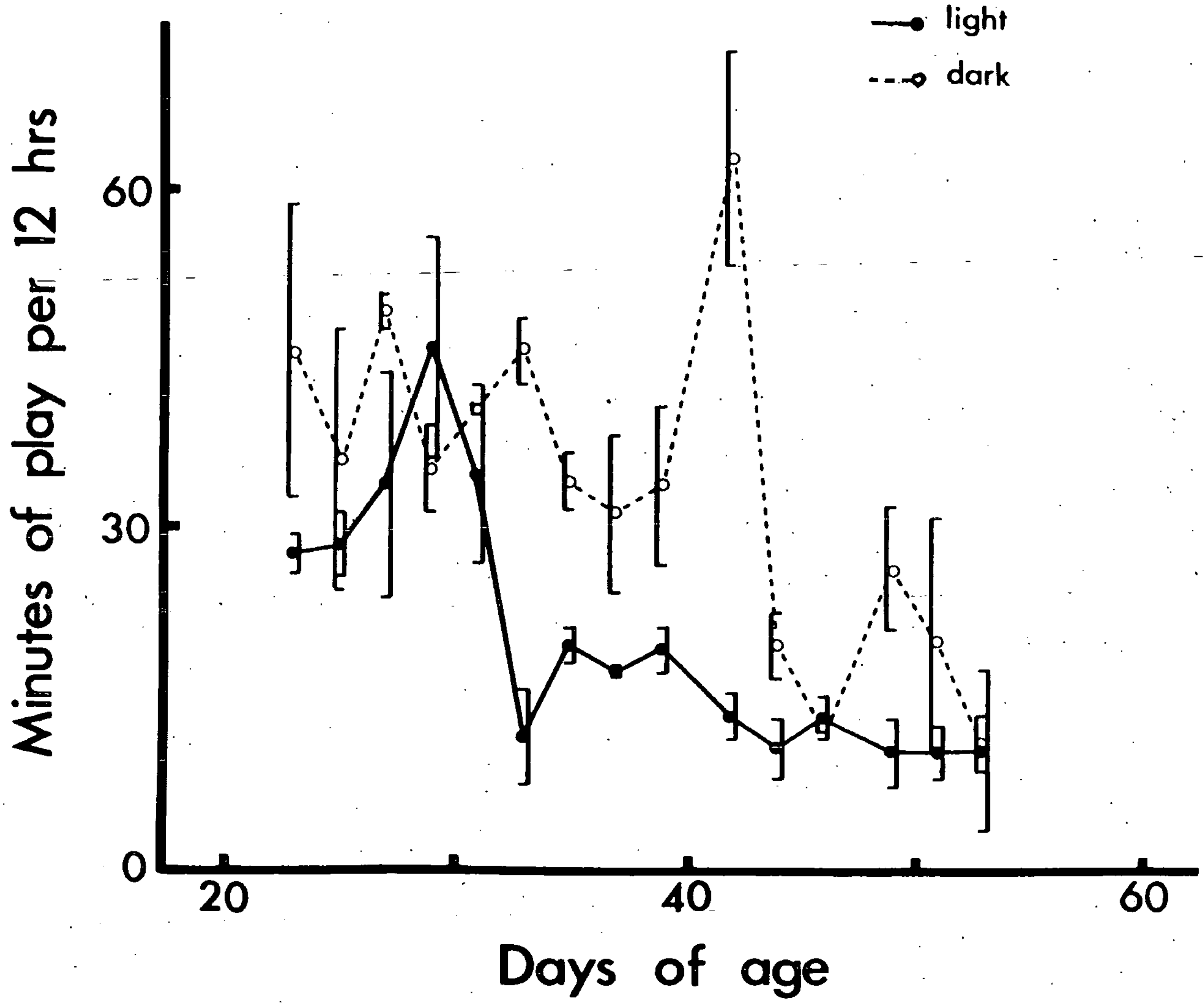


Fig. 3.8

Time spent playing per 12hrs in light and dark periods, plotted as Fig. 3.6.

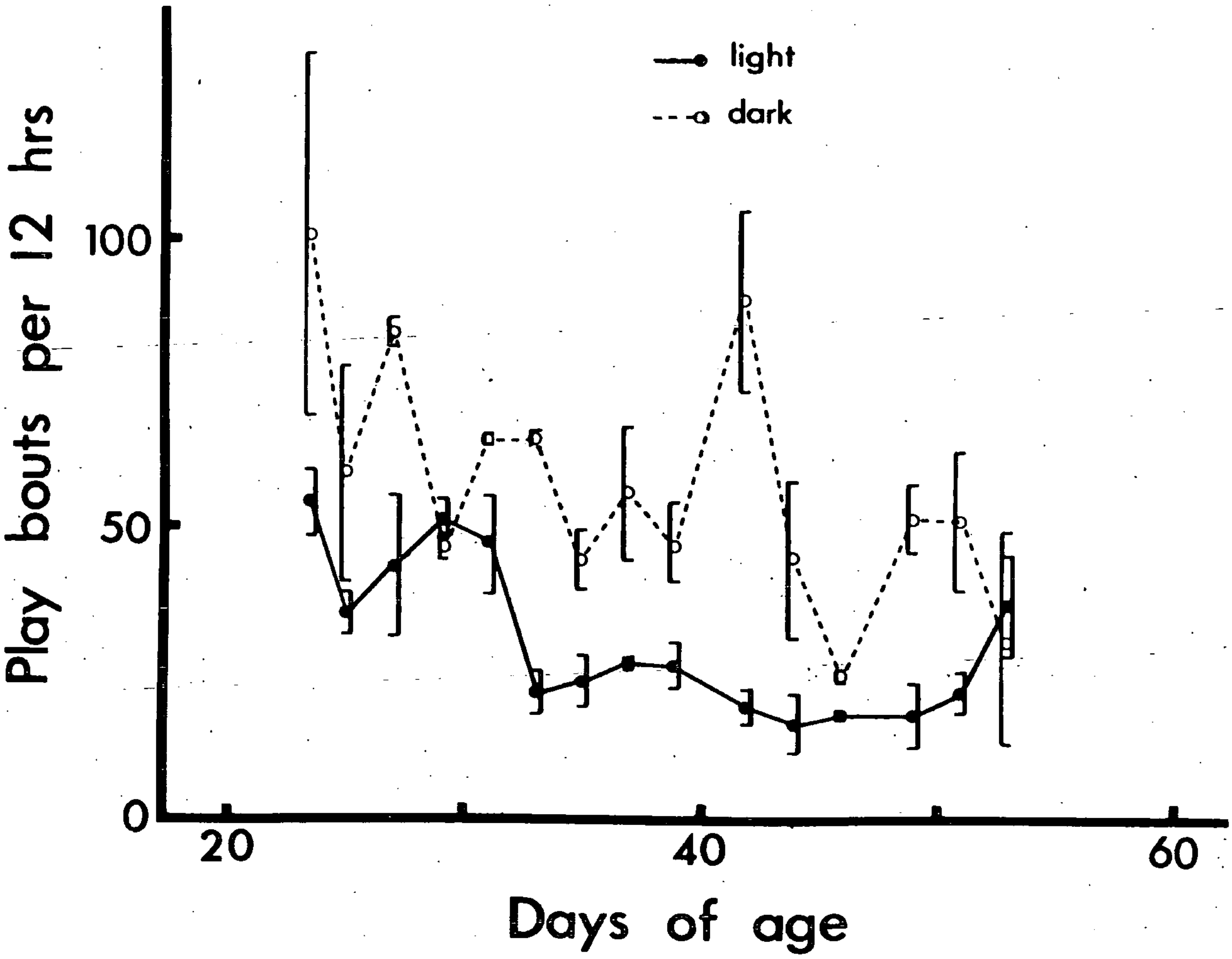


Fig. 3.9

Play bouts per 12hrs in light and dark periods, plotted as Fig. 3.6.

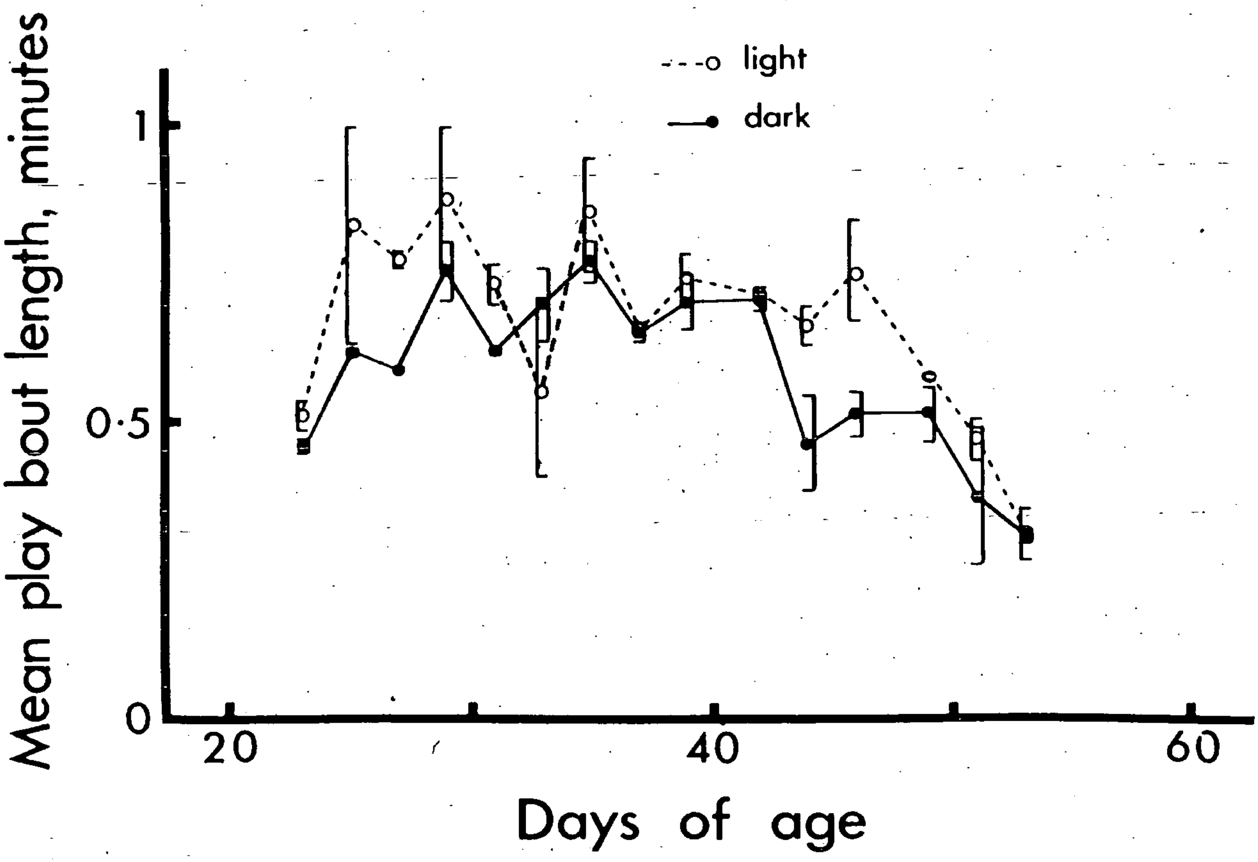


Fig. 3.10

Mean litter play bout lengths in light and dark periods, plotted as Fig. 3.6.

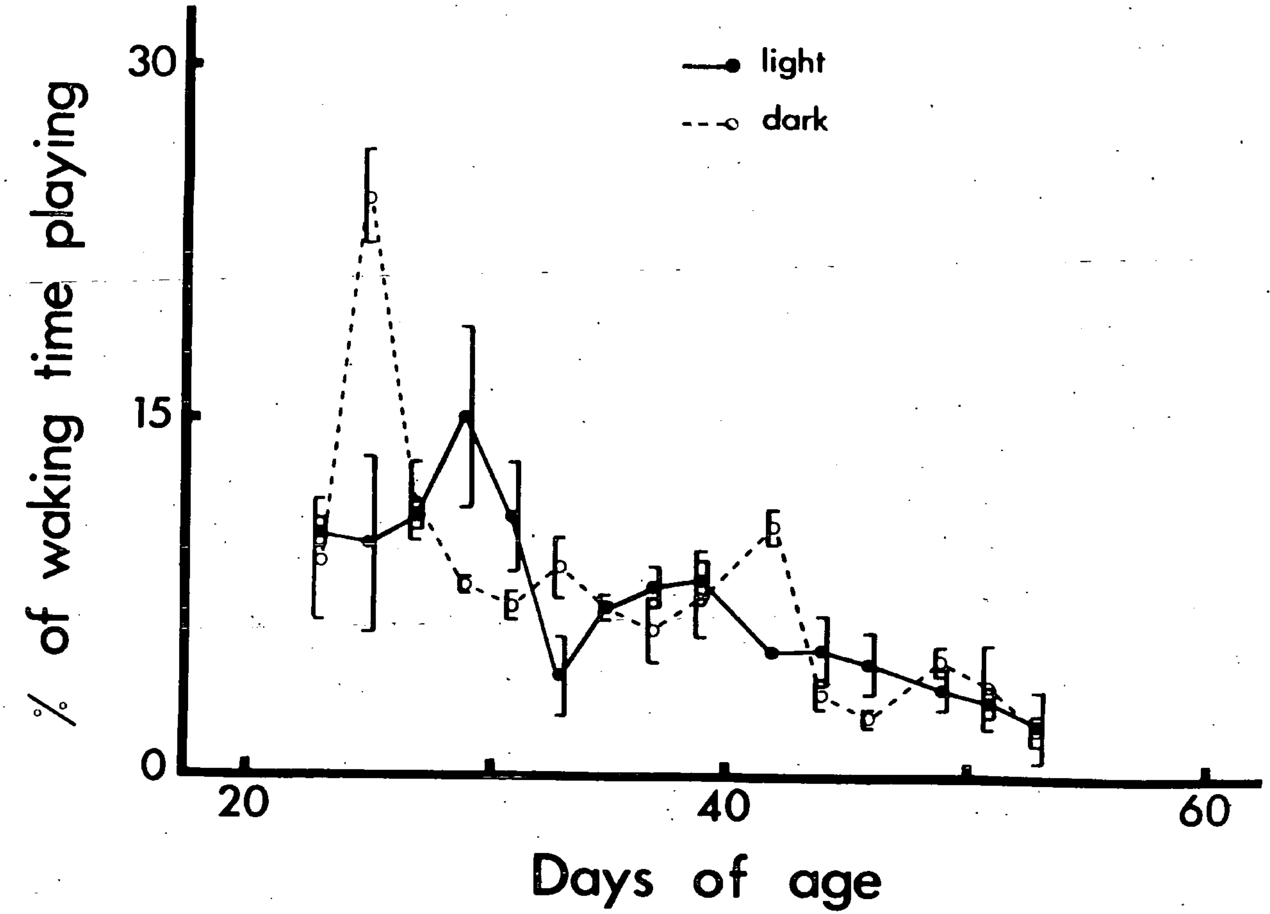


Fig. 3.11

Proportion of waking time spent in play during light and dark periods, plotted as Fig. 3.6.

3.2.4

Discussion

The total time each day which is devoted to sleep shows an overall decrease between 21 and 56 days, although this is probably slight compared to the decrease which occurs prior to weaning, accompanying eye-opening and the general increase in mobility. However, the nocturnal activity pattern characteristic of adulthood begins to emerge at weaning, and was already beginning to affect sleep at 21 days when this study began, as Fig. 3.6 shows. Sleep becomes concentrated into the light phase, the light/dark difference growing steadily up to about 30 days when stability is reached. From this age animals sleep more than twice as much in the light phase as in the dark phase. This difference appears to result from animals' comparative reluctance to wake up during the light phase: sleep bouts are significantly longer during this half of the day, the difference again stabilizing at around 30 days.

Play goes through the converse process, becoming concentrated into the dark phase, and achieving a stable light/dark difference by about 33 days. However, there is no light/dark difference in the proportion of waking time spent in play at any age, or in play bout length, indicating that an animal's tendency to play does not vary between night and day provided it is awake, and that the play which does occur at these times does not differ in general structure. (The overall difference in play becomes less reliable above 45 days as play becomes progressively more sparse.)

Adult-type nocturnal activity patterns thus begin to emerge at or just before weaning, as Levin and Stern (1975) reported for adult feeding rhythms. These new activity patterns then develop over the next 1 - 2 weeks into their more stable adult forms, with the result that older juvenile and young adult rats sleep for approximately 60% of the light phase and 20% of the dark phase, in bouts of mean length approximately 80 mins and 30 mins respectively.

3.3

BEHAVIOUR PATTERNS: FREQUENCY AND ORDER

3.3.1

Introduction

The two previous sections have shown that behaviour undergoes a number of changes during the period between 21 and 56 days as the animal's way of life changes from that of dependent infant to independent adult. The analysis described below examines individuals' behaviour in greater detail to show how its structure changed with age. Behaviour was recorded continuously, providing data on the frequencies of individual behavioural elements and the sequences in which they tended to occur in interacting animals.

Frequency data show which behaviours were most common at different ages in the litters observed, but do not show how they were related to each other. Using sequence data, however, it is possible to compare the quality of interactions at different ages by noting which behaviours occurred as common responses to which other behaviours. Since social play involves closely-meshed interaction sequences, particular attention was paid to the quality of play interactions to see what changes might be related to the decline in play reported in section 3.1.

Sequence data were also used to test the validity of some common assertions made about play. It is generally assumed, for example, that there are certain gestures e.g. 'bow' in canids (Bekoff 1974), which act as play signals or invitations, and set the tone of any subsequent interaction. (See discussion of play signals in 1.2(c).) Meaney and Stewart (1981) suggested that the movement which they called ´Pouncing´ (equivalent to the category Paws-on used here) served as a play invitation as it tended to occur at the beginning of play bouts. A similar assumption has also been made by Humphreys and Einon (1981) on the basis of informal observations. The validity of the assumption was tested using sequence data to show what proportion of Paws-on preceded play bouts and conversely what proportion of play was preceded by Paws-on.

A property which is described as a characteristic of play in a wide variety of species is that of frequent and rapid role reversal (e.g. Loizos 1966, Steiner 1971), where roles are defined according to the rules applicable to tha adult behaviours, usually agonistic, to which play is structurally similar. The rough-and-tumble wrestling play of rats resembles adult fighting in some respects, the behaviours Wrestle-top and Wrestle-under being similar in structure to those of the dominant and submissive animals respectively. These two behaviours were therefore taken to represent complementary roles and the frequency with which they were exchanged within bouts was examined.

3.3.2

Method

A method of focal animal sampling (Altmann 1974) was used in which the behaviour of the focal animal, and of others towards it, was recorded continuously to gain information on the frequencies of certain behaviour patterns, and on the sequences in which they tended to occur. Extracts from 14 of the 36 videotapes of litters A and B used in the studies described in 3.1 and 3.2 (taken at approximately five day intervals and representing seven ages) were subjected to this type of analysis. Each of the four animals in each litter was the focal individual for 15 min and animals were always observed in the same order. These 15 min sections were taken from the period between 20.00 and 24.00 hrs and were chosen with reference to the results quoted in 3.1 and 3.2 to ensure that the focal animal was active (i.e. not asleep) throughout. A total of one hour's worth of continuous behaviour recording was thus obtained from each litter on each day represented.

As in 3.1, observations were entered on the keyboard of a microcomputer. Entries were made in "sentence" format, the identity of the agent, the behaviour code and the identity of the recipient being recorded at each change of behaviour by or towards the focal animal. From preliminary observations, 19 behaviour categories were initially defined, but some proved to occur so rarely that they have been combined with others for calculation, and results are quoted in the final 13 categories which are listed in Table 3.1, and in the seven (also listed in

Categories for initial behaviour analysis	Combined categories for statistical tests
Approach-fast Flee-fast	Fast locomotion
Wrestle-top Wrestle-under	Wrestle
Paws-on	Paws-on
Sniff	Sniff
Groom Passive contact Sexual advance	Amicable contact
Approach-slow Flee-slow	Slow locomotion
Eat/drink Other	Solitary

Table 3.1

Behaviour categories used for initial analysis of videotapes, and combined categories used in statistical tests.

Table 3.1) into which these were combined for statistical analysis.

Since many interactions, especially playful ones, involved more than two animals, it was found necessary to allow simultaneous recording of pairs of dyadic interactions. This meant that the observer was not forced to decide which of two acts happened first. It was hoped that the provision of this extra option would exclude arbitrary decisions and allow more confidence to be placed in sequence data.

Treatment of results

Behaviour frequency and sequence scores were recorded for each focal individual. Frequencies were counted from the total number of occasions on which the focal animal was seen to carry out each behaviour. Sequence pairs of behaviours were occasions on which individual A directed a behaviour at individual B, and B changed its behaviour within one second. Sequence pair scores were tabulated for individuals in preceding/following matrices (see Appendix C). These data were then tested to show whether specific behaviour sequence pairs tended to occur more often than chance would allow (i.e. for a first order Markov relationship, Altmann 1965, Chatfield and Lemon 1970, Fagen and Young 1978). Because of the small sample sizes for individuals, expected values were too low to allow the use of Chi-squared tests, as suggested by Fagen and Young (1978), to test for a relationship. Instead, data were subjected to a logarithmic transformation producing a value, x'_{ij}, for each cell:

$$x'_{ij} = x_{ij} - \bar{x}_{i.} - \bar{x}_{.j} + \bar{x}_{..}$$

where x_{ij} = log. observed value, $\bar{x}_{i.}$ = log. row mean, $\bar{x}_{.j}$ = log. column mean and $\bar{x}_{..}$ = log. total mean. (Where the observed value was zero, x_{ij} was taken as log. 0.5.) This gave an interaction table for each individual in which column and row totals were zero, and positive and negative cell values indicated sequences which occurred more and less often, respectively, than would be expected by chance. An analysis of variance was then carried out on all individuals' interaction tables, in both age-groups.

Individual one-sample t-tests were then carried out on the eight animals' scores for each interaction. The interactions occurring more often than expected in six or more of the eight individuals' records are representd pictorially in ethograms (Fig. 3.13) in which arrow thickness corresponds to the level of significance given by the t-test.

Age-related changes in behaviour were examined by comparing combined sores for younger (under 40 days) and older (40 days and over) animals, since a number of major behavioural and physiological changes are known to occur at or around 40 days of age (see 3.1). Individuals' frequency scores were compared in Wilcoxon tests. Sex differences were examined by means of Mann-Whitney U tests, since only four individuals of each sex contributed to the analysis. (See Siegel, 1956, for non-parametric statistical tests.)

3.3.3

Results

(a) Frequencies

Figs. 3.12a and b show the ways in which the frequencies of the different behaviour categories change with age. (Fig. 3.12a refers to playful and b to nonplayful behaviours.) From this it appears that playful behaviours decrease in frequency from 25 - 30 days onwards. From around 40 days, however, Fast locomotion and Paws-on increase again, while Wrestle continues to decline. Of the nonplayful behaviours, Sniff, Slow locomotion and Amicable contact show no appreciable change in frequency, and Sexual approaches (separated from the other Amicable contact categories to show the onset of sexual behaviour) increase slowly from 30 - 40 days. (Since the behaviours involved are predominantly male sexual behaviours the increase is muffled in the calculation of means, and in statistical treatments, by females.) Statistical comparison of behaviour frequencies in the two age-groups (under and over 40 days) yielded only one significant change: Wrestle decreased ($p<0.01$) with age.

Mann Whitney U tests revealed few sex differences in the frequencies of behaviours. When scores for all ages were combined, the only significant sex differences were in the frequency of Fast locomotion, which occurred more in females ($p<0.05$) and of Sexual approach, which occurred more in males ($p<0.02$). Tests within the two age groups produced similar results. Animals below 40 days of age differed only in Slow locomotion, which was more common in males ($p<0.05$). In the older age range,

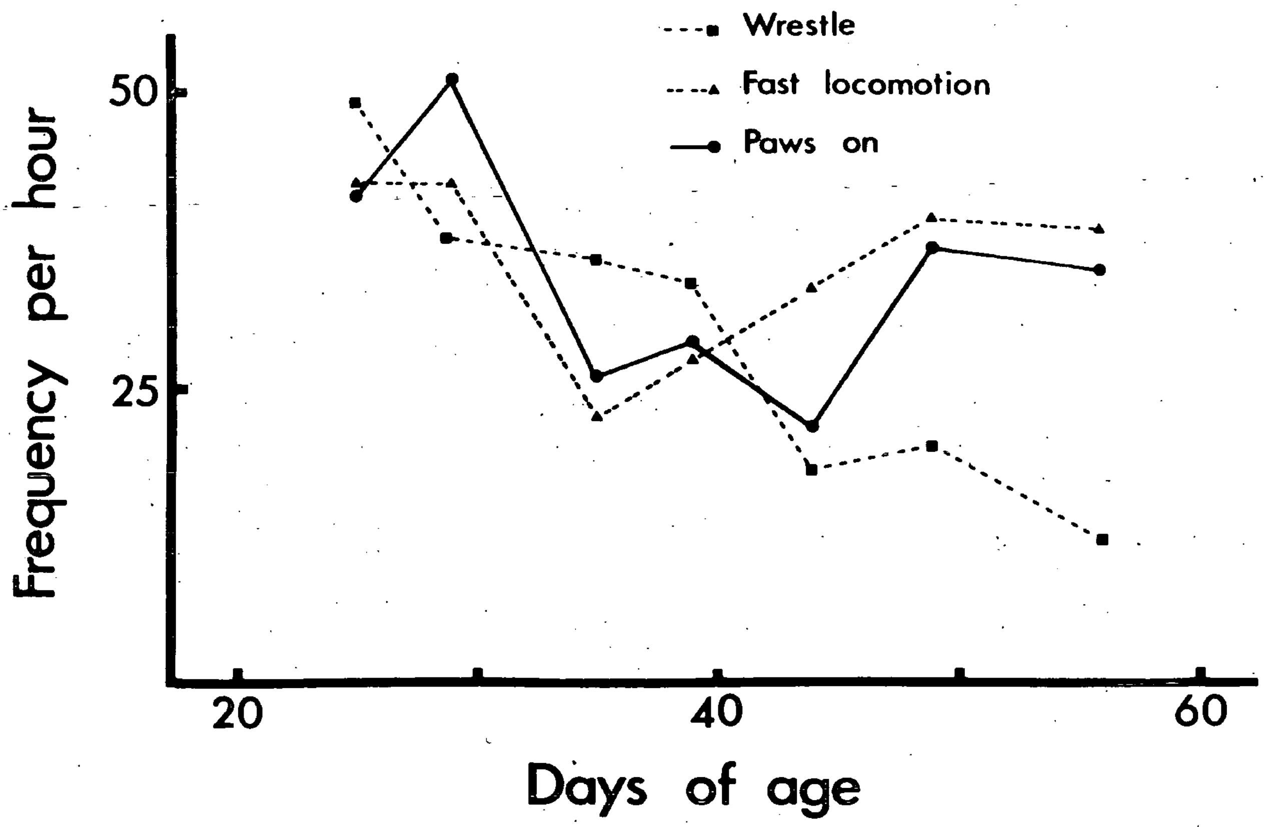


Fig. 3.12a

Frequencies of playful behaviours: number of occurrences of the behaviour per animal per hour (mean for all animals).

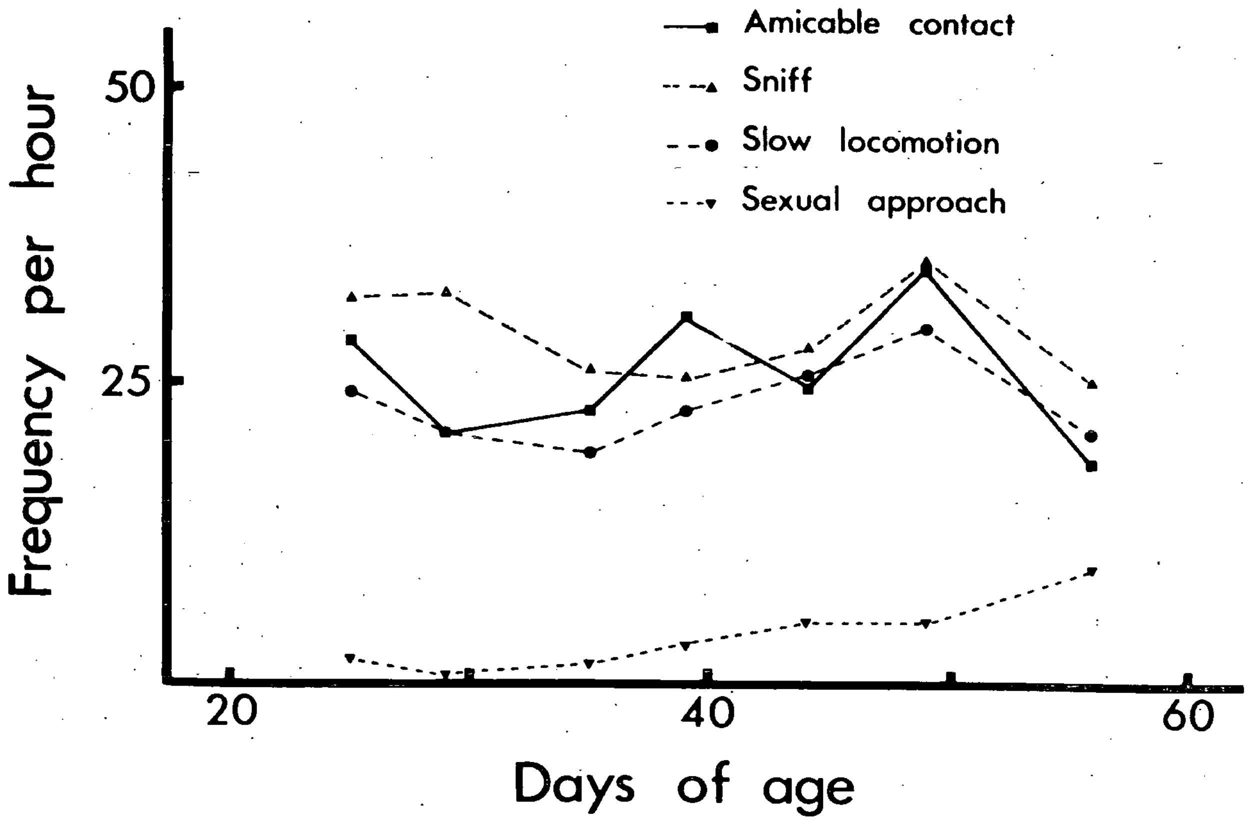


Fig. 3.12b

Frequencies of non-playful behaviours: defined as for Fig. 3.12a.

males made more Sexual approaches ($p<0.02$) and the asymmetry in Fast locomotion approached significance ($p<0.057$).

(b) Sequences

The log. transformations produced interaction tables for all individuals in both age-groups which were subjected to analysis of variance. A significant effect of cells ($F(30,420) = 6.34$, $p<0.01$) indicated that, overall, following behaviours did not occur randomly with respect to preceding behaviours but were related in predictable ways. The pattern of these relationships did not change significantly with age, as was indicated by the non-significant age-group by cells interaction ($F(30,420) = 1.04$, $p>0.05$).

Specific sequence pairs occurring more commonly than expected for six or more focal individuals are shown in diagrammatic form for younger animals in Fig. 3.13a. Arrow thickness represents the level of significance of the difference from chance as indicated by a t-test, i.e. the thicker the arrow the more likely it is that the second behaviour will follow the first. A smaller proportion of interactions reach the specified levels of significance in older animals, possibly because interactions of all types were less frequent. A lower criterion was therefore invoked for the ethogram for this age-group (Fig. 3.13b) in order to increase its sensitivity to any pattern which might be present. Thin arrows in this diagram represent interactions occurring more commonly than expected in five focal records out of eight. The majority of these sequence pairs are common to both age-groups,

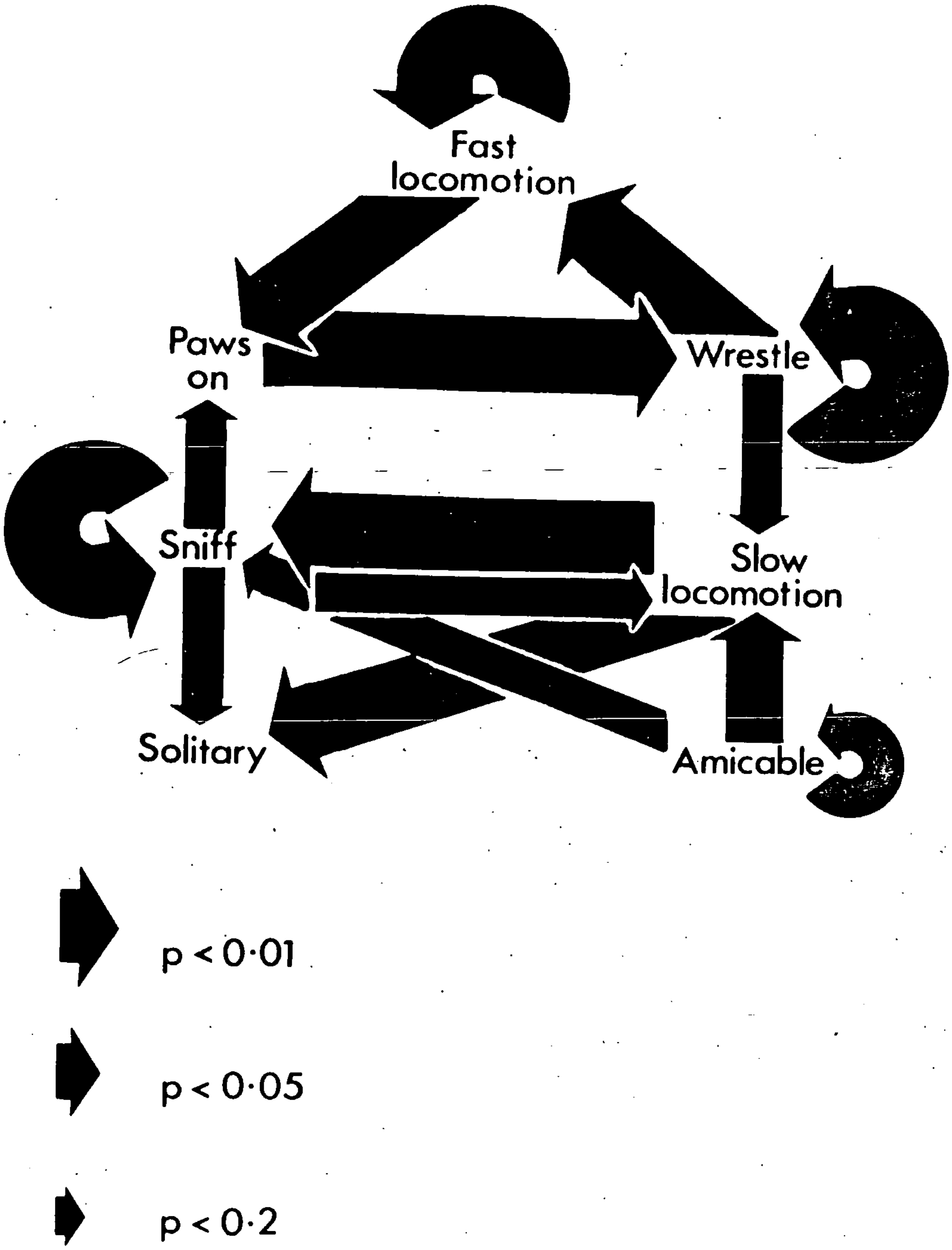


Fig. 3.13a

Common response sequence pairs between younger rats (25 - 39 days of age). Arrows represent sequences occurring more often than expected for 6 or more focal individuals, and arrow thickness denotes level of significance of t indicated by one-sample t-test.

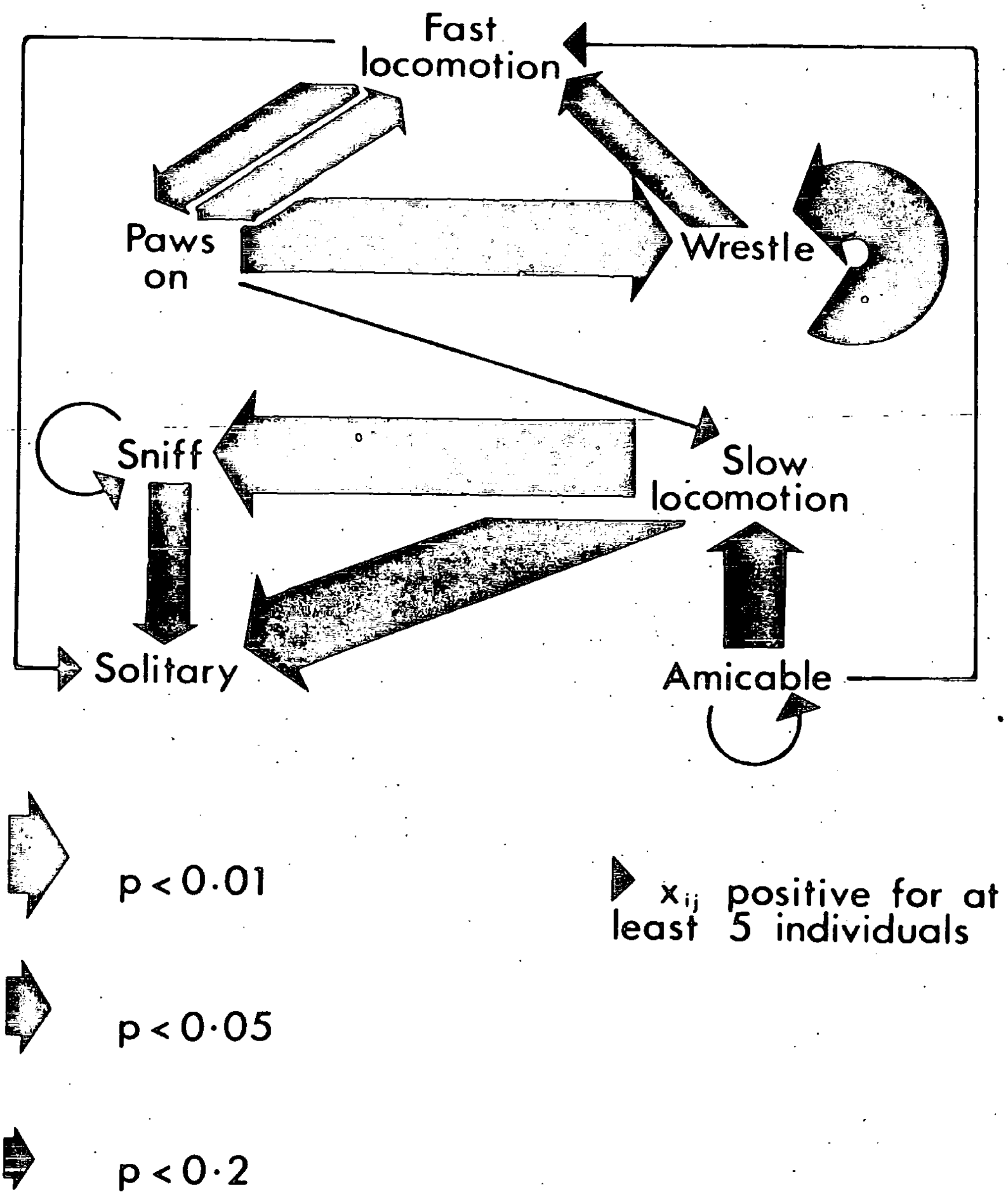


Fig. 3.13b

Common response sequence pairs between older rats (40 - 56 days of age). Arrows are coded as for Fig.3.13a, with additional thin arrows representing sequences occurring more often than expected in 5 focal individuals.

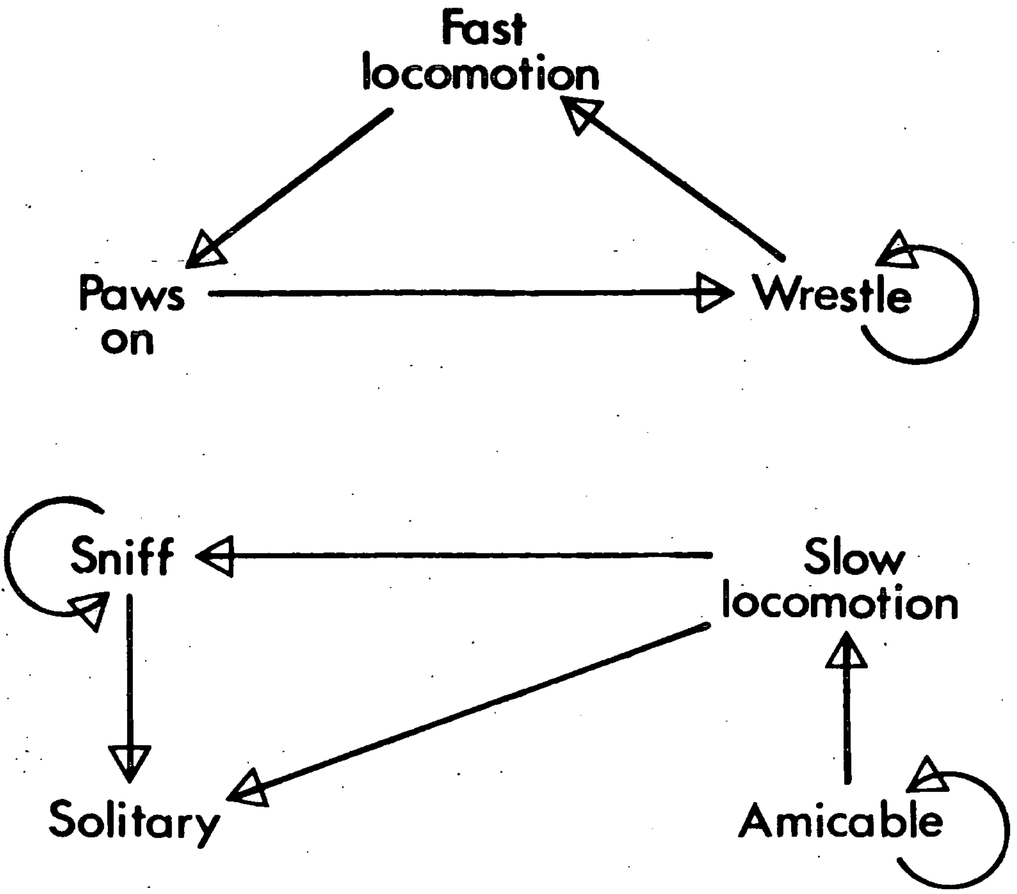


Fig. 3.13c

Response sequences occurring more often than expected in both younger and older rats, i.e. sequences arrowed in Figs. 3.13a and b.

forming a core of shared pairs whose ethogram, Fig. 3.13c, divides into two separate groups of behaviours, playful (Paws-on, Wrestle and Fast locomotion) and non-playful (Slow locomotion, Sniff, Amicable contact and Solitary). The two age-groups thus appear to differ in the ways in which these behaviour groups are linked. In older animals, Fast locomotion is no longer self-perpetuating, and is more closely linked to non-playful behaviours than in younger animals. Also, the early links between Sniff and Paws-on, and Wrestle and Slow locomotion, are not apparent later.

(c) Assumptions concerning play

(i) Paws-on acts as a play invitation.

The ethograms (Fig. 3.13) show that Paws-on is followed by Wrestle (i.e. rough and tumble play) much more often than chance would predict, but only leads to Fast locomotion (which includes chase/flee play) in older animals. The proportions of the total of the other two play behaviours, Wrestle and Fast locomotion, which are preceded by the different behaviours are shown in Table 3.2a. This indicates that over 80% of all play is preceded either by Paws-on (39.3%) or by other play (27.5% Wrestle and 16.1% Fast locomotion), and therefore that, of the occasions on which play was initiated rather than continued, 70% were preceded by Paws-on. Comparison of the proportions of play preceded by the different behaviours in the two age-groups, Table 3.2a, shows that there are only two significant age-related changes: more play is preceded by Amicable contact ($p<0.05$) and less by Wrestle ($p<0.01$) in older than in younger animals.

The behaviours following Paws-on are shown in

Behaviour	25-39 days of Age	40-56 days of age	All ages	Age difference
Fast loco.	18.1	13.6	16.1	NS
Wrestle	32.0	19.8	27.5	0.01
Paws on	36.0	43.5	39.3	NS
Sniff	5.5	7.3	6.6	NS
Amicable	3.2	12.4	6.0	0.05
Slow loco.	5.1	3.4	4.4	NS

Table 3.2a

Percent of play for which a preceding behaviour was recorded that was preceded by each behaviour in an interacting individual. Proportions are shown for the two age-groups and for play at all ages, and levels of significance of age differences indicated by Wilcoxon tests are given (NS = not significant).

Behaviour	25-39 days of age	40-56 days of age	All ages	Age difference
Fast loco.	16.3	16.0	16.2	NS
Wrestle	43.7	26.0	36.9	0.01
Paws on	8.5	12.4	10.0	NS
Sniff	2.6	3.0	2.7	NS
Amicable	8.1	10.7	9.1	NS
Slow loco.	7.4	19.5	12.1	0.05
Solitary	13.3	12.4	13.0	NS

Table 3.2b

Percent of Paws on for which a response was recorded that was followed by each behaviour in an interacting individual. Proportions for different age groups and significance of age differences are shown as in Table 3.2a.

Table 3.2b. On 36.9% of occasions it is followed by Wrestle, and on 16.2% by Fast locomotion, making a total of 53.1% of Paws-on followed by play. When the two age-groups are compared, Table 3.2b, less Paws-on is shown to be followed by Wrestle ($p<0.01$) and more by Slow locomotion ($p<0.05$) in older animals.

(ii) Rat play involves role reversals.

The examination of behaviours preceding play (Table 3.2a) showed that over 40% of all play was preceded by play in the same or some other form. While this suggests that role reversals were occurring, a more detailed examination was needed to separate these from the other sequences which could cause such a result. In this analysis, an exchange of roles in wrestling is indicated by a response sequence consisting of two consecutive occurrences of the same behaviour in interacting individuals, e.g. individual A Wrestle-top individual B ⟶ B Wrestle-top A. When Wrestle was examined for such role-reversals it was found that 25.4% of all Wrestle resulted in continuation of the interaction with roles reversed. Comparison of the two age-groups showed that this property decreased significantly with age ($p<0.05$) from 29.8% in young animals to 11.8% in older animals.

3.3.4

Discussion

Detailed behaviour analysis thus shows that the overall pattern of the rats' behaviour did not alter significantly with age, although changes occurred in the quality of certain types of interaction. Only Wrestle changed significantly in frequency, declining with age. The other two playful behaviours, Paws-on and Fast locomotion, declined with Wrestle initially, but began to increase again at 35 - 40 days and thus showed no significant age-related change in frequency when the two age-groups' scores were compared. Play behaviours did not differ in frequency between the sexes in younger animals. In older animals, however, there is an indication that Fast locomotion has become more common in females and that male sexual behaviour has become distinct.

Such a pattern could result if the behavioural elements first seen in play became incorporated into some adult activity whose frequency increased with age. The only behaviour seen to increase with age is Sexual approach, which includes anogenital sniffing and mounting. (Meaney and Stewart (1981) reported a more dramatic increase in sexual behaviour than that seen here, probably because their more frequent observations meant that more of their samples covered periods of oestrus.) These behaviours, as was noted above, are predominantly male sexual behaviours, the female counterparts being lordosis and short darting runs. Lordosis was not seen to occur, indicating that no females were observed in oestrus and therefore that any female sexual behaviour seen would be evasive rather than receptive. The increases in Paws-on and Fast locomotion, and the sex difference in the frequency of Fast locomotion in older animals, could therefore represent an increase in male attempts at mounting and anogenital sniffing which the non-receptive female attempts to avoid by moving rapidly away. If such an interpretation were correct, these two behaviours would be expected to become part of new sequences as their roles in the behavioural repertoire changed. Specifically the sequence Paws-on ⟶ Fast locomotion should become more common and, assuming such evasive tactics were successful, so should Fast locomotion ⟶ Solitary. Figs. 3.13a and b support such an interpretation. They show that both these sequences occur more often than expected in older animals, but not in younger animals. Behaviours which were identified as playful in younger animals (see Chapter 2) thus begin to re-emerge in new contexts with increasing age as has been reported for other species (see 1.2).

Although the gesture Paws-on begins to appear in different contexts among older animals, it was nevertheless shown to serve as a play invitation. As the ethograms show, it precedes Wrestle in both age-groups on a large proportion of occasions. Closer examination of the behaviours preceding play and following Paws-on indicated that 70% of initiated play (i.e.excluding play which was being continued) was preceded by Paws-on, and that 53.1% of Paws-on was followed by play. The differences between the age-groups highlight the change which occurs in the social relevance of Paws-on. While the proportion of play preceded by this gesture does not change, the proportion of Paws-on followed by play falls significantly (from 60% in young to 42% in older animals). Paws-on thus becomes increasingly associated with other behaviours while retaining some power to initiate play.

Within bouts of rough-and-tumble play,

examination of behaviour sequences showed that roles (as defined by posture) were exchanged during interactions on an appreciable number of occasions, and therefore that role-reversal is a characteristic of rat play as it is of the play of other species. Comparison of the age-groups revealed that roles were exchanged less between older than between younger animals, indicating that, although the behavioural context of Wrestle appears to change comparatively little with age, rough-and-tumble play nevertheless changes in quality. This change reflects the emergence of dominance relations reported by Meaney and Stewart (1981) for this age-range: roles are exchanged less as individuals' relative positions become better defined.

As young rats approach adulthood, therefore, their play undergoes certain changes in quality as well as decreasing in quantity, and the behaviours which were identified in younger animals as playful occur increasingly in new and non-playful contexts. However, the overall pattern of interactions did not change significantly with age, indicating that the major structural features of adult behaviour are present in young animals.

3d

Summary

This longitudinal study shows that behaviour undergoes considerable though gradual change over the period between weaning and maturity. At first the young rats showed no signs of a nocturnal activity pattern, did not demonstrate anything recognisable as sexual behaviour and spent large amounts of time playing. This they did in long and frequent bouts, often in large groups. By 50 days of age, however, when they had reached puberty, they had developed a regular nocturnal activity cycle and shown sexual behaviour in its adult form. They spent less time in play, and the activity itself appeared less playful, less distinct and more closely associated with other behaviours than juvenile play.

In the earlier stages, when play was at its most distinct, it could be seen to possess a number of the characteristics discussed in Chapter 1. It employed behaviour patterns seen in other contexts in older animals and had no apparent goal or tangible result. Any biting which occurred during wrestling bouts appeared to be inhibited as recipients did not show distress and no wounds were seen. A gesture was identified which communicated play intention and play bouts were found to include exchanges of role. The play of older animals was less distinct in terms of characteristics as well as behaviours. The decrease in role reversals suggests that dominance struggles may have been influencing the play of older animals, as was noted by Meaney and Stewart (1981) for animals over 45 days of age and by Panksepp (1981) for animals over 35 days of age. This would mean that play had a goal, namely the domination of a partner. The play invitation appeared to take on additional functions in older animals and thus became less distinct in its meaning.

Further properties of play at its most frequent and distinct (i.e. around 30 days) are explored in Chapters 4 and 5, in which experimental procedures are used to manipulate young animals' play experience.

Similar experimental treatments are required to show what functions play may serve. However, examination of the behaviour itself, its properties and the conditions necessary for its occurrence allows us to make tentative suggestions as to its functions which may be useful for guiding further work. Its social nature suggests a social function, although, as has been discussed (Chapter 1 and 3.1) probably at a very basic level since specific rules learnt in play would not be applicable to other behaviours (Einon, 1980). There is also evidence to suggest that social play may have a non-social function in the development of behavioural flexibility (Einon et al., 1978), and the experience may therefore be social only because other animals provide the most unpredictable play objects.

The developmental context of play at 35 - 45 days suggests that it is involved in sexual discovery, a hypothesis which is supported by its behavioural context. If this were the case, an animal deprived of play at this stage should be less competent sexually than one with normal experience. Rearing in social isolation from 14 days of age has been shown to have deleterious effects on the sexual abilities of male rats (Gerall, Ward and Gerall, 1967), but the effect of isolation from 1 day of age was not significantly different from that of isolation from 30 days (Gruendel and Arnold, 1969). From these results it seems that isolation has its effect on sexual behaviour at some age greater than 30 days. Animals reared with one hour of social experience per day between 25 and 45 days and then isolated up to 60 days were found to be as slow to copulate, by comparison with socially reared peers, as were animals reared in isolation for the whole 25 - 60 day period (Einon, personal communication). However, they mounted as quickly and as often as socially reared animals, although with a lack of accuracy in positioning which accounted for their corresponding lack of success. This suggests that play may be important for the development of the tendency to mount, but further experience between 45 and 60 days appears to be necessary for the correct construction of the whole behaviour pattern. Experiments manipulating social experience over the 30 - 60 day age range would be required to tease apart the effects of play and other forms of social experience, and to see at which ages the different forms of experience were most effective. Methods of manipulating play and social experience are used and discussed in the following two chapters.

CHAPTER 4

EFFECTS OF RECENT SOCIAL EXPERIENCE ON AMOUNTS OF PLAY

4.1

Introduction

Panksepp and Beatty (1980) showed that isolation for periods of several hours´ duration caused young rats to play intensely when they were subsequently returned to their companions. This effect died away if the young animals remained together, as they became satiated with the activity. These phenomena, although they were not quantified, had also been noticed by Einon et al. (1978) who made use of the play-intensifying effect of isolation to concentrate animals´ daily play into a single social hour during which little other social behaviour occurred. This effect is also used in the experiments described in Chapter 5 as a means of inducing play to order under experimental conditions.

The present experiment examines the effects of isolation and subsequent social experience on the behaviour profiles of young rats and goes on to look at the behaviour of pairs of animals of different social history. Each pair was made up of an animal fresh from isolation and a partial isolate (with one hour of social experience per day as in the experiments of Einon et al.) immediately after its social hour. Panksepp and Beatty´s results suggested that the latter would be socially satiated and thus less disposed to play than its isolate partner. If this were the case, such animals could be used in studies similar to that of Einon et al. to manipulate the play and social experience of a partner. The potential of animals in different social states for use in rearing experiments is discussed.

4.2

Method

Subjects

Subjects were 16 male Lister hooded rats bred in this laboratory from stock obtained from Olac, Bicester. They were weaned at 23 days of age and housed singly in white plastic cages 35 x 15 x 12 cm, with access to food and water ad lib. Their light/dark cycle of 12L:12D was half-reversed, with lights on between midnight and noon. All observations were made during the first half of the dark phase.

Apparatus

Animals were observed in cube-shaped metal boxes of side 30cm. Behaviour was recorded with a Hitachi high density VTR and low-light camera. Recordings were made in dim diffuse light, from an Anglepoise lamp directed at the white ceiling.

Procedure

The 16 animals were assigned randomly to two groups of eight, groups A and B, which differed in the amounts of social experience they received. Each individual was identifiable by its markings and was given an identity number.

On days 2-4, taking day of weaning as day 1, animals spent one hour each day in the company of another member of their group. They passed this hour in the home-cage of a third animal. On day 5 they were introduced to the apparatus. Four animals at a time, taken randomly from both groups, were placed in an observation box for an hour. After a brief initial investigation of these new surroundings, they spent most of this period in intense rough-and-tumble play.

The experimental social experience regime was implemented on days 6-9 inclusive (when the animals were aged 28-31 days). On these days each member of group A received an hour in the company of a fellow group A member, followed immediately by 10 mins in the company of a member of group B. The animals in group B, however, received only this 10 min period of companionship. Behaviour was recorded during the first and last 10 mins of group A's social hour, and during the following 10 mins which each member of group A spent with a group B animal. All animals were paired with the same partners on all four days of recording. A diagrammatic account of the procedure is given in Fig. 4.1.

The behaviour recorded on videotape was analysed by instantaneous sampling (Altmann 1974) at five second intervals. The behaviour categories used were:

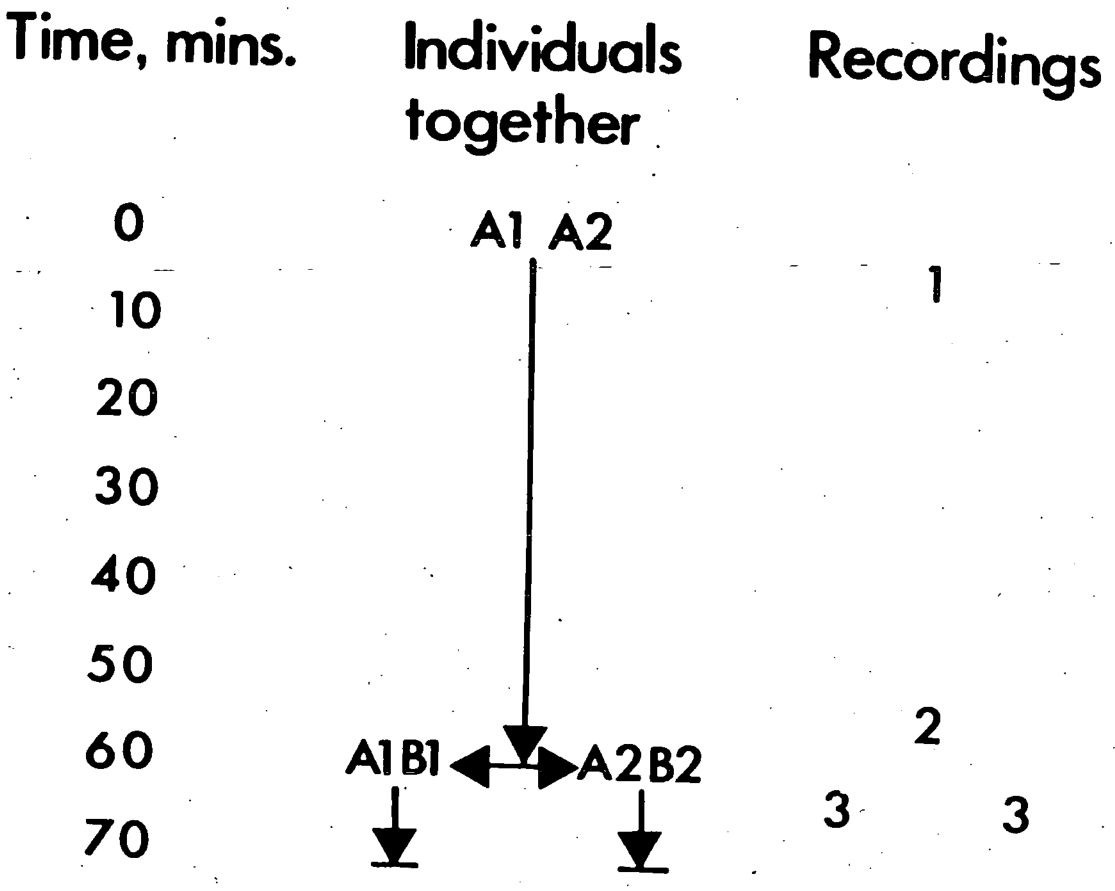


Fig. 4.1

Experimental design: social experience received by a sample set of four animals (individuals A1, A2, B1 and B2) on each of days 6 - 9, and the recordings made of their behaviour.

Wrestle

Chase

Paws-on

Sniff

Active amicable

Passive amicable

Solitary

This inventory is similar to the shortened version used for statistical treatment in 3.3, with the category Amicable contact subdivided into Active (where behaviour is directed at another individual) and Passive (where two animals are merely in bodily contact), since it was of interest to know whether these varied in different ways with time and partner. The category Chase, in which one animal runs after another who is running at high speed, replaces Fast locomotion.

This analysis gave numbers of samples on which each animal was seen carrying out each behaviour, for every 10 min record. From these the proportion of samples occupied by each behaviour could be calculated, which gave an approximation to the proportions of time spent in the different behaviours overall.

4.3

Results

Total scores were calculated for each behaviour by each animal in each observation period over the four days. The means of these, expressed as observations per 10 mins per individual, with standard deviations, are shown in histogram form in Fig. 4.2. Since the eight animals in group A spent the first hour in pairs, they yielded only four sets of independent behaviour scores (pair means). These scores were therefore compared between observation intervals using Mann-Whitney U tests. (If a further eight animals had been available, individuals' scores could have been compared in Wilcoxon matched pairs tests, which would have reduced the effect of individual variation on the results.) The levels of significance of the differences between observation intervals 1 and 2, 2 and 3 and 1 and 3 are shown in Table 4.1. These and Fig. 4.2 indicate that behaviour changes quite markedly between intervals 1 and 2, with play decreasing and amicable behaviour increasing, and that the behaviours return towards their original (interval 1) levels when a new partner, fresh from isolation, is introduced.

The behaviour of members of pairs during interval 3 (indicated by the two types of hatching in the third columns in Fig. 4.2) was compared using Wilcoxon tests. (The categories Wrestle and Passive amicable could not be compared because members of a pair necessarily scored the same.) The levels of significance of the differences are again listed in Table 4.1 from which it can be seen that the only activity to show a significant asymmetry was Paws-on, which occurred more in group B than group A animals ($p<0.05$).

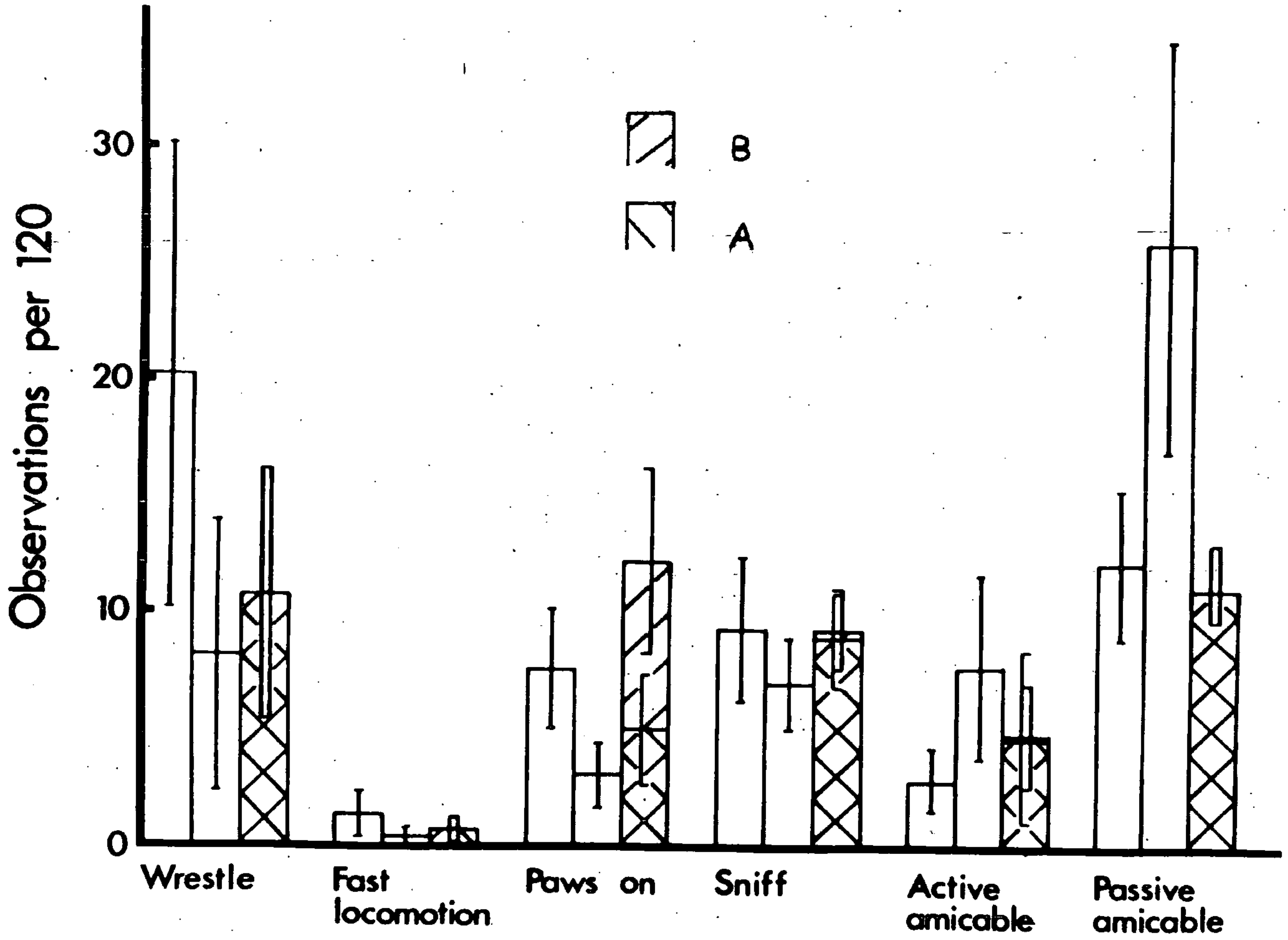


Fig. 4.2

Number of samples at which each behaviour was seen during each recording interval. The three columns for each behaviour represent its occurrence in recording intervals 1, 2 and 3 respectively. Scores plotted are group means over all days and bars represent S.D. Column 3 shows scores for groups A and B, distinguished by hatching.

Behaviour	Recording Intervals			
	1/2	2/3	1/3	3A/B
Wrestle	0.057	NS	NS	
Chase	NS	NS	NS	NS
Paws on	0.014	0.01	NS	0.05
Sniff	0.057	NS	NS	NS
Amic. active	0.05	NS	NS	NS
Amic. passive	0.05	0.01	NS	

Table 4.1

Levels of significance of differences between behaviour scores in different recording intervals from Mann Whitney U tests and, where possible, Wilcoxon tests.

4.4

Discussion

The differences between behaviour during intervals 1 and 2, at the beginning and end of the social hour, support the findings of Panksepp and Beatty (1980) that temporary social isolation increases subsequent play, and that play satiates with continued exposure to company. Play occupies 29/120 of the observations made in the first 10 mins of the social hour, which, if taken as a proportion of waking time spent playing, would approximate to a nightly level of 2hrs in 12, considerably more than was seen among socially housed animals (3.1 and 3.2). By the last 10 mins of the hour, play has declined to 11/120 observations, which is eqivalent to approximately 45 mins in 12 hrs and thus nearer the normal range. (Panksepp and Beatty´s results suggest that, with continued exposure to companions, play would continue to decrease over the next 24 hrs.)

Of the non-playful behaviours, both Active and Passive amicable behaviour increase during the hour, taking over the time relinquished by play. The quality of the experience thus changes with time. Isolation appears to increase the young animal´s tendency to play as soon as it finds a companion. This tendency decreases with continued access to company as animals become "satiated" with play and fill their time with other forms of social behaviour.

Introduction of isolates to aimals who have already had one hour´s opportunity to become satiated with play shows how the discrepancy in their recent histories affects their behaviour together. Fig. 4.2 indicates that the behaviour of the AB pairs is intermediate between that of group A pairs in interval 1 and interval 2. No behaviour scores are significantly different from those in interval 1, and only two (Paws-on, owing to the group B animal, and Passive amicable) are significantly different from those in interval 2. When the behaviour of members of AB pairs was compared statistically, isolates were found to show a higher incidence of Paws-on than their satiated partners. This supports the finding reported in 3.3 that this gesture serves as a play invitation, its use being increased in the animal who might be expected to have the greatest play tendency, and therefore to make the most effort to persuade its partner to play.

As might be expected, therefore, the mixture of high and low play tendencies produces an intermediate amount of play accompanied by intense efforts on the part of the isolate to initiate more. A socially satiated animal thus provides an isolate partner with slightly different social experience during a short period of time from that provided by another isolate. This effect could be of use for manipulating animals' social experience in experiments. Chapter 5 describes the use of animals treated with the drugs chlorpromazine and amphetamine as partners providing different forms of social experience for undrugged experimental animals. This technique was originally used by Einon et al. (1978) to provide different forms of daily social experience to otherwise isolated rats throughout rearing in order to separate the effects of different juvenile experiences on later abilities. A play-satiated partner could provide a more subtle form of play deprivation, without the other abnormalities which drugs may cause, and could thus be used in such experiments to separate further the effects of different forms of social experience.

CHAPTER 5

THE REINFORCING VALUE OF PLAY

5a

Introduction

One of the characteristics listed in 1.2 most often ascribed to play is that it is done for fun or for its own sake and is therefore reinforcing. While it is difficult to verify that an animal is enjoying an activity, properties of reinforcement can be tested by objective means. A positive reinforcer is defined as a result which increases the probability that an animal will repeat the behaviour which led to this result. If play is a reinforcer, therefore, it should increase the probability of whatever chain of behaviour brought it about. Thus an experiment examining this property should only allow play after a certain definable behaviour has been executed, just as food reinforcement experiments provide food only after the performance of a specific task. Young chimpanzees in the experiments of Mason, Saxon and Sharpe (1963) had to carry out a standard lever-pressing task to obtain a choice of food or a limited period of play. They performed the task readily, and, under certain circumstances, chose play more often than food. Play thus appeared to be acting as a reinforcer for lever-pressing, increasing the probability of its occurrence.

In the experiments described here, young rats were required to run to the appropriate side of a T-maze for the opportunity to play. Each animal was offered the choice of a limited period with a social partner who would play or with an otherwise similar animal who would not. The initial choice was between a free partner who could interact normally and one who was confined and therefore prevented from playing. If play was reinforcing, the rate of turning towards the free partner should increase, but since this result could also be caused by an attraction to some other property of the free animal, other alternative partners were offered in further tests to separate the reinforcing powers of different forms of social experience. As in the rearing experiments of Einon et al. (1978), the drugs amphetamine and chlorpromazine were used to alter the social behaviour of potential partners in such a way as to reduce play while affecting other forms of social behaviour differently.

The behaviour of the experimental animals and their chosen partners is analysed and the results are considered in conjunction with preferences shown in the T-maze tests to see which forms of social experience were valued most highly. Since Einon at al.(1978) have shown that play experience during the juvenile period is necessary for the normal development of certain adult abilities, these results should tell us whether animals take an active part in the development of their own abilities by seeking out the experience which will be of long term benefit to them. The animals' rate of learning in these tests is compared with that in a food/no food discrimination in the same T-maze, in which they are assumed to demonstrate optimal performance.

5b

General Method

In each of the experiments described, young rats were required to choose between the alternative experiences offered to them in the goal boxes attached to the two arms of a T-maze. The apparatus and basic design were the same in all the experiments and are described below.

Subjects

Subjects in all cases were juvenile Lister hooded rats obtained at weaning (21 - 23 days of age) and kept in a 12L:12D light cycle with lights on between midnight and noon. Testing was carried out during the dark phase, between 13.00 and 18.00 hours.

Apparatus

The apparatus was a T-maze made from Perspex tubing 5cm in diameter. The arms were 25cm long and led to cube-shaped goal boxes, 30 x 30 x 30 cm. A small metal start box, 15 x 10 x 10 cm, was attached to the stem. All entrances to the maze could be closed off with guillotine doors, which could be operated from a distance by means of pulleys. To aid discrimination, the two sides of the maze were decorated differently: the left side had vertically striped walls and a smooth black floor while the right side had horizontally striped walls and was carpeted with rough black emery paper. Testing was carried out in dim diffuse light from an Anglepoise lamp placed directly above the apparatus and pointed at the white ceiling.

Procedure

Over the three days following weaning, each group of rats spent 1hr per day in the apparatus so that all were thoroughly familiar with the surroundings when testing began. During these pretraining sessions all the doors between maze and boxes were left open and the rats explored and played freely throughout the apparatus.

Testing began on day 5 (taking day of arrival as day 1) and continued for four to seven days, after which the contents of the two goal boxes were reversed and testing was continued until the initial preference reversed.

Each experimental rat received blocks of 10 consecutive trials. The rat began each trial in the start box. The doors to both goal boxes were held open while it was released into the maze and were closed when it indicated its choice by entering one of the goal boxes. It was left in the chosen goal box for a predetermined period before being replaced in the start box for its next trial.

For each experimental group, goal box contents were counterbalanced so that, given the choice of experience A and experience B, half the group found A on the left and the other half found A on the right.

Treatment of results

Side choice was recorded for each trial. The progress of groups over time is presented graphically as the mean number of choices of A per rat on each day of testing.

Two-way analysis of variance (Winer 1971) was carried out on the daily choice scores of the left-hand

(L) and right-hand (R) groups. Between-subjects variable was the side of experience A and within-subjects variable was day of testing. In order to separate choice of a particular experience from choice of side only, the scores compared were the number of trials in which rats chose the left-hand side on each day. Since experience A was in the left-hand box for only half the rats, a difference in the number of trials in which each group chose that side (as indicated by a significant effect of groups) meant that the contents of the goal boxes, rather than other maze properties, were affecting side choice. A significant interaction between groups and days indicated that the preference of both L and R groups for a particular goal experience was changing over days. Any significant effect of days alone meant that, over days, the experimental group as a whole was developing a preference for a particular side irrespective of the experience found there.

In two experiments (5.1 and 5.2), the time taken to enter a goal box at each trial was recorded on the final day of testing (5.1) or on all days (5.2). Trials were not timed in the social choice experiments as it was not possible to operate videorecorder, apparatus and timer simultaneously.

EXPERIMENT 5.1

This experiment was carried out to test the learning abilities of young rats in the T-maze under known motivational conditions in order to provide a yardstick against which performance in other choice experiments could be compared. Subjects were offered the choice of food or no food in trials following a period of food deprivation.

5.1.1

Method

Subjects

Six male and six female rats, obtained from Olac, Bicester, at 23+/-2 days of age, were housed socially in single-sex groups in white plastic cages 40 x 30 x 15 cm. Initially the rats were allowed access to food and water ad lib, but from day 2 onwards food supply was limited.

Procedure

To ensure that the choice of food or no food was relevant to the rats´ internal state they were subjected to moderate food deprivation. Over days 2 to 4 deprivation time was increased by daily stages, times being 2hr, 6hr and 12hr on successive days. Each deprivation period was followed immediately by a 1hr pretraining session during which the reward food (Boot´s Vita Food, a milk-based food readily taken by young rats, sweetened with glucose) was offered in both goal boxes.

Subjects were thus familiar with the reward food when trials began on day 5, and food was present in only one goal-box. Rats took part in 10-trial blocks immediately after undergoing 12hr of food deprivation, half (the L-group) receiving food in the left-hand goal box and the other half (the R-group) receiving food in the right-hand goal box. The L and R groups each consisted of three males and three females.

Inter-trial interval was approximately 45sec. Testing continued for 7 days initially, and for a further 5 days after reversal, with food in the opposite goal box. Trial times (between release from the start box and entry into a goal box) were recorded on the final day of testing.

5.1.2

Results

The rats' mean daily scores (represented as mean number of trials in which the food side was chosen each day) both before and after reversal show that they learnt the location of the food and reversed this initial preference when the food was moved (Fig. 5.1). The results of the analysis of variance are shown in Table 5.1. This showed significant effects of groups and groups/days interaction, indicating that a preference was developed over time for the food side. The non-significant effect of days shows that neither side of the maze became inherently preferable. Performance after reversal gave similar results.

Mean trial time over all animals and all trials in which the food side was chosen was 7.66sec, with a standard deviation of 5.85.

This experiment therefore showed that young rats in a state of food deprivation were capable of rapid learning when faced with the "all-or-none" choice of food or no food, choosing the food side in over 90% of trials.

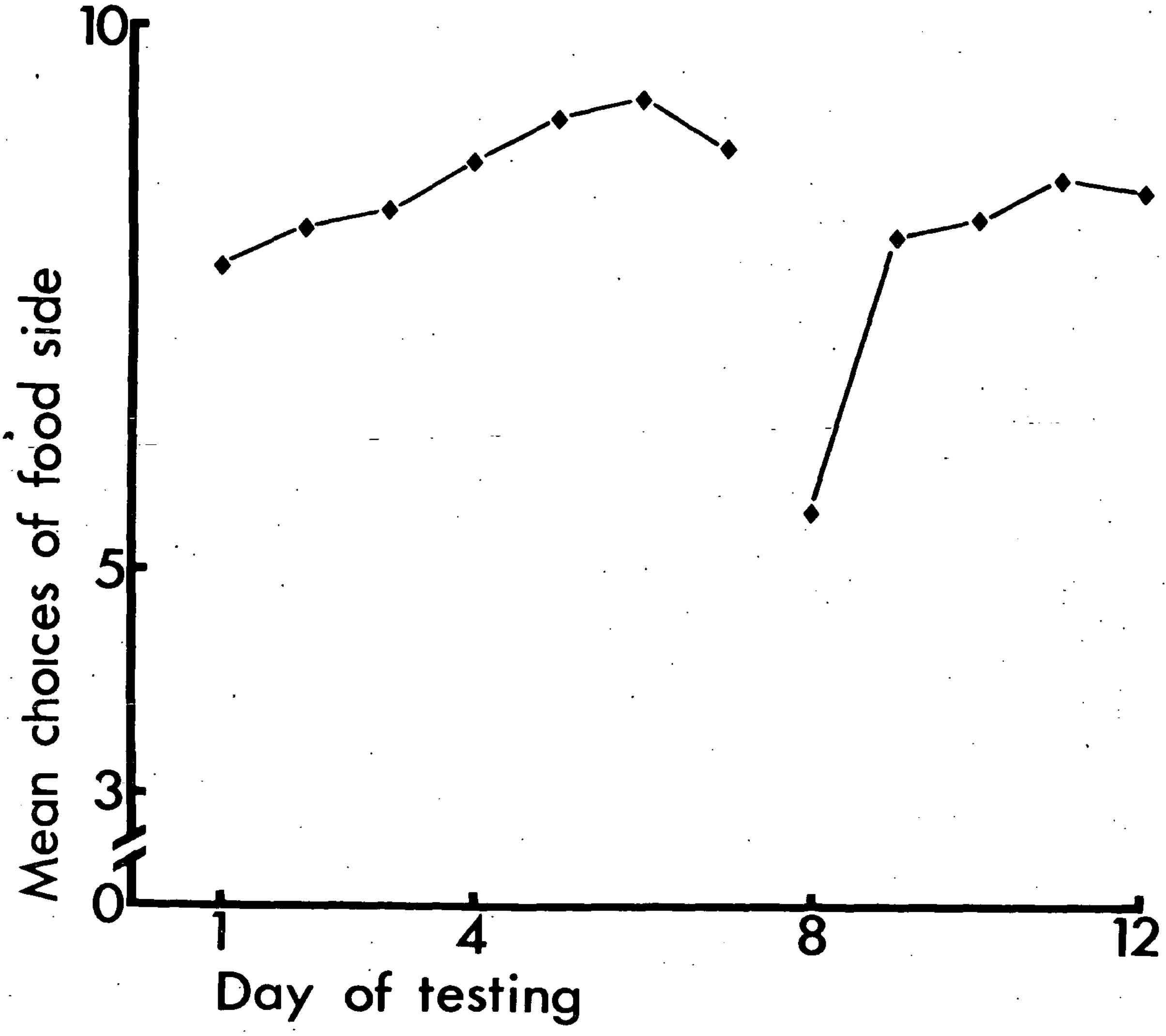


Fig. 5.1

Learning in experiment 5.1 (food/no food) by males and females, expressed as mean number of choices of food side per rat per day. Food was transferred to the opposite side on day 8, as indicated by the break in the line.

Experiment	Choice offered	Groups effect			Groups/days interaction			Days effect		
		df	F	p	df	F	p	df	F	p
1A	Food/no food	1,10	2022.51	0.001	6,60	8.52	0.001	6,60	1.27	0.282
1B		1,10	555.66	0.001	4,40	16.94	0.001	4,40	0.26	0.904
2A	Caged/free	1,10	195.27	0.001	3,30	8.49	0.001	3,30	2.39	0.088
	- females	1,10	13.71	0.01	2,20	3.82	0.05	2,20	0.08	0.920
2A	Caged/free	1,8	33.62	0.001	4,32	9.52	0.001	4,32	1.07	0.388
2B	- males	1,8	71.18	0.001	2,20	18.78	0.001	2,16	0.02	0.981
3A	Amphetamine/	1,10	28.35	0.001	6,60	2.56	0.05	6,60	1.10	0.374
3B	normal	1,10	6.46	0.05	4,40	2.39	0.066	4,40	0.88	0.512
4(i)A	Chlorpromazine (8mg)	1,10	52.55	0.001	3,30	0.38	0.770	3,30	0.89	0.538
4(i)B	/normal	1,10	75.24	0.001	3,30	3.67	0.05	3,30	0.76	0.530
4(ii)A	Chlorpromazine (4mg)	1,8	25.47	0.01	3,24	0.67	0.581	3,24	1.45	0.251
4(ii)B	/normal	1,8	25.19	0.001	3,24	1.66	0.200	3,24	1.66	0.200
4(iii)	Chlorpromazine (2mg) /normal	1,10	0.57	0.529	4,40	0.90	0.526	4,40	2.06	0.103

Table 5.1

Analysis of variance of side choice in all experiments.
"A" refers to results in initial arrangement and "B" to results after reversal.

5 c

Social Choice Experiments: General Method

In the following series of experiments, young rats were required to choose between two different companions of whom one behaved normally and the other was rendered abnormal in some way. A number of features, in addition to those described in the General Method section, were shared by all these experiments and are described below.

Subjects

The number of rats obtained for each experiment was sufficient to make up three equal groups of the same age and sex. On day 1, rats were randomly assigned to the experimental group and to two groups of partners for the experimental rats to choose between. Each experimental always chose between the same two individuals, and each of the partners served only one experimental.

From day 1 the rats were housed singly in white plastic cages 35 x 15 x 12 cm, with access to food and water ad lib. Their situation was thus analogous to that of the rats in experiment 5.1. Both groups were deprived of a commodity - food in experiment 5.1 and company in the social choice experiments - and were subsequently offered it in the T-maze. All rats spent a limited period immediately after each day's trials in the company of another member of their group. It was hoped that this social experience would counteract any short-term effects of isolation housing.

Procedure

During trials, the two alternative partners were confined in their respective goal boxes under wire mesh containers (19 x 12 x 7 cm) while the experimental rat made its choice. After the goal box door had been closed, the chosen partner was released from its confinement (except for one condition in experiment 5.2) and allowed to interact freely with the experimental rat for one minute. After this both rats were replaced in their starting positions for the next trial. The inter-trial interval was approximately 90 sec.

In all except experiment 5.2, the behaviour of experimentals in the goal boxes with their chosen partners was videotaped. The tapes were analysed by instantaneous sampling at 5 sec intervals, as in Chapter 4, to give a quantitative measure of the differences between the two types of experience offered to experimentals. The behaviour categories used in this analysis were as in Chapter 4 except that Active amicable was represented by Anogenital sniff (A-g Sniff) and Walk-over (W-o).

Alternate goal boxes were videotaped on successive days, so that the behaviour of all possible combinations of rats contributed to the final scores for all groups. Records were made over days 5 to 9 inclusive (the first five days of testing).

Results

The results of these behaviour analyses are presented as histograms showing the proportions of time each group of animals spent with a particular type of partner in each activity. Each experiment thereofre yielded four such behaviour profiles: one for each type of partner, and two (one for each partner condition) for the experimental group. The results were subjected to analysis of variance to test for differences between these conditions.

The preference level attained in each experiment (as indicated by the animals' choice scores on the last days of testing before and after reversal) was used to give a measure of the attractiveness of the abnormal partner relative to that of a normal partner. This will be referred to as relative attractiveness, R.A., and was calculated from the number of trials in which the abnormal partner was chosen, N, and the number of trials in which it would be expected to be chosen by chance, E, such that:

$$\text{R.A.} = \frac{N - E}{E}$$

R.A. scores could thus fall between -1 (never chosen) and +1 (always chosen), with R.A. for a normal animal falling at zero.

EXPERIMENT 5.2

Rats chose between a normal, free companion and one who remained confined under its wire mesh container throughout the interaction period, and was therefore unable to play. The experiment was first performed using female rats, and repeated using males.

5.2.1

Method

Subjects

Thirty-six female and 30 male rats were obtained from Olac, Bicester, at 21 days of age. Twelve females and 10 males were randomly assigned to each of the three groups: experimentals, free partners and confined partners.

Procedure.

Testing was carried out as described, with the experimental groups subdivided into L and R groups of six and five rats for females and males respectively. Trials in which the animal designated the confined partner was chosen resulted in the experimental spending 1 min in the goal box with the partner, the two remaining separated by the wire mesh container. During this time the rats could see, hear, smell and, to a limited extent, touch each other, but could not indulge in physical interaction involving the whole body. When the "free" partner was chosen, it was released, and could therefore interact freely.

Trial times of females were recorded throughout, as on the final day of experiment 5.1. In the initial arrangement, testing continued for five days (males) and four days (females). After reversal, both sexes were tested for a further three days.

5.2.2

Results

Figure 2 shows the mean choice scores for males and females expressed as mean number of trials each day in which the free rat was chosen. This indicates that young rats developed a preference for the free partner and maintained this preference after reversal by learning to run to the opposite side.

Analysis of variance gave significant effects of groups and groups/days interactions (Table 5.1), but days effects were not significant. The results of testing after reversal followed a similar pattern.

Relative attractiveness was calculated from group mean choice scores on the final days of testing in both conditions. These gave mean N for females as 1.85 trials, and for males as 1.95 trials, out of 10. RA was thus -0.63 for caged females and -0.61 for caged males.

The mean trial times for females are shown in Table 5.2. These indicate that running speed increased as the task was learned, reaching a maximum when maximum preference level was reached and decreasing temporarily when reversal of the partners presented a new task to be learnt.

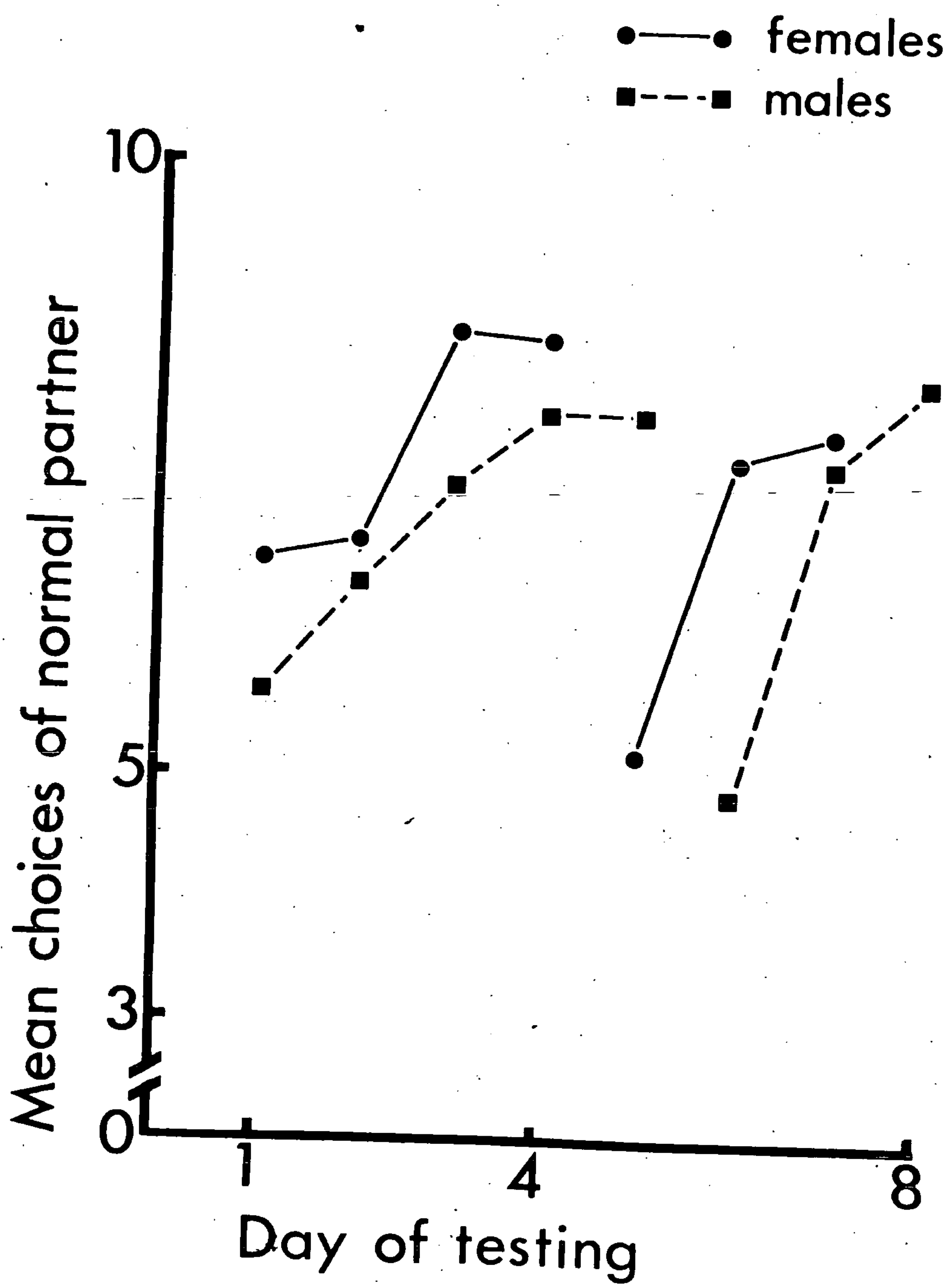


Fig. 5.2

Learning in experiment 5.2 (caged/free partner), expressed as mean number of choices of free partner per rat per day. Partners were reversed on day 5 (females) and day 6 (males).

Day	Mean trial time, sec	SD
1	10.79	14.86
2	5.60	4.07
3	4.25	3.08
4	4.21	5.28
	Partners reversed	
5	5.79	5.20
6	4.72	5.14
7	4.23	3.56

Table 5.2

Mean trial times for females in experiment 5.2 (caged/free partner) on successive days, over all trials in which the free partner was chosen.

5.2.3

Discussion

These results indicated that a free rat was a more desirable companion than a confined rat, whose social behaviour was restricted by its cage. Although this result is in agreement with the hypothesis that play is reinforcing, since the free partner played while the caged one could not, it remains equally possible that some other aspect of physical interaction was the major attractive element of the experience.

Further choice experiments were therefore carried out in which the behaviour of potential partners was modified with drugs in order to separate the different forms of social experience and so assess the value of play to young rats.

EXPERIMENT 5.3

Young rats chose between normal and amphetamine-treated companions.

5.3.1

Method

Subjects

Thirty-six female rats were bred in this laboratory from stock obtained from Olac, Bicester, and weaned at 21 days of age.

Procedure

Fifteen minutes before the start of each 10-trial block, one of the two partners received an injection of d-amphetamine sulphate (Smith, Kline and French Ltd.) at a dose of 2 mg/kg body weight. The drug was dissolved in 0.9% saline solution to give a volumetric dose of 1 ml/kg body weight. The other partner received a control injection of 0.9% saline solution only, also at a dose of 1 ml/kg. All injections were intra-peritoneal.

During trials, both partners were released when they were chosen, and the periods which experimentals spent with their chosen partners were videotaped.

Training comprised seven days in the initial arrangement and five days following reversal of the two partners.

5.3.2

Results

The group's learning performance is illustrated in Fig.5.3. This shows that the rats developed a preference for the normal over the amphetamine-treated partner, both before and after reversal. Both groups effect and groups/days interaction were significant in analysis of variance of the rats' initial choice scores (see Table 5.1), but days effect was not significant. After reversal only the groups effect was significant. RA for amphetamine-treated rats was -0.28.

A number of behavioural differences were apparent between the amphetamine and normal conditions: drugged partners played much less than normal partners, but spent more time in other social behaviours such as sniffing and crawling under and over. Although they appeared to be highly socially attentive, they did not respond to the repeated play invitations of the experimental rats with active rough-and-tumble play, as normal animals did, and showed no inclination to initiate play themselves.

Behaviour profiles for amphetamine-treated and normal partners, and for experimentals in their company, are shown in Fig. 5.4. (Columns represent the mean proportion of observations in which each group showed each behaviour, and bars represent standard deviations above and below the means.) Analysis of variance showed that behaviour was significantly different under the two conditions (Table 5.3). The behaviour profiles show that all three play categories - Wrestle, Chase and Paws-on - were

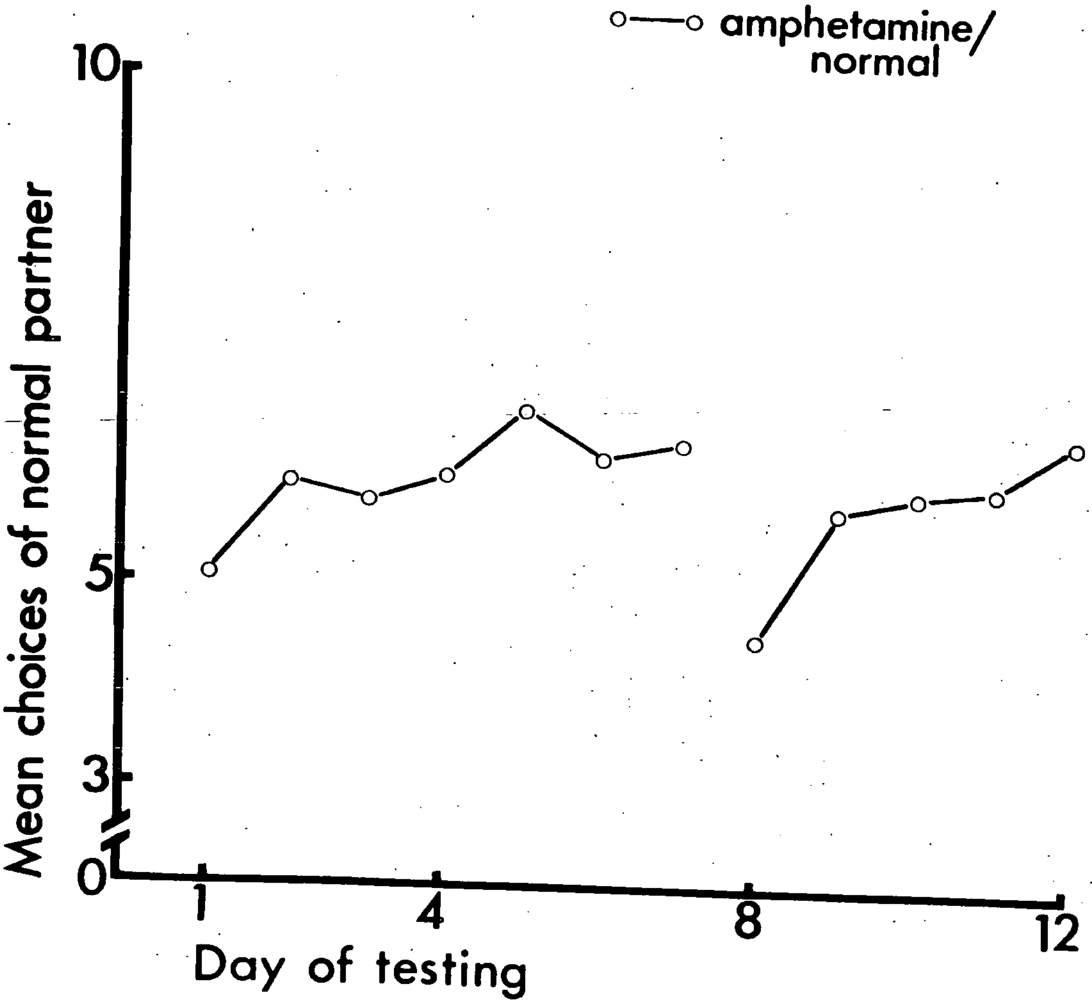


Fig. 5.3

Learning in experiment 5.3 (amphetamine-treated/normal partner) by females, expressed as mean choices of normal partner per rat per day. Partners were reversed on day 8.

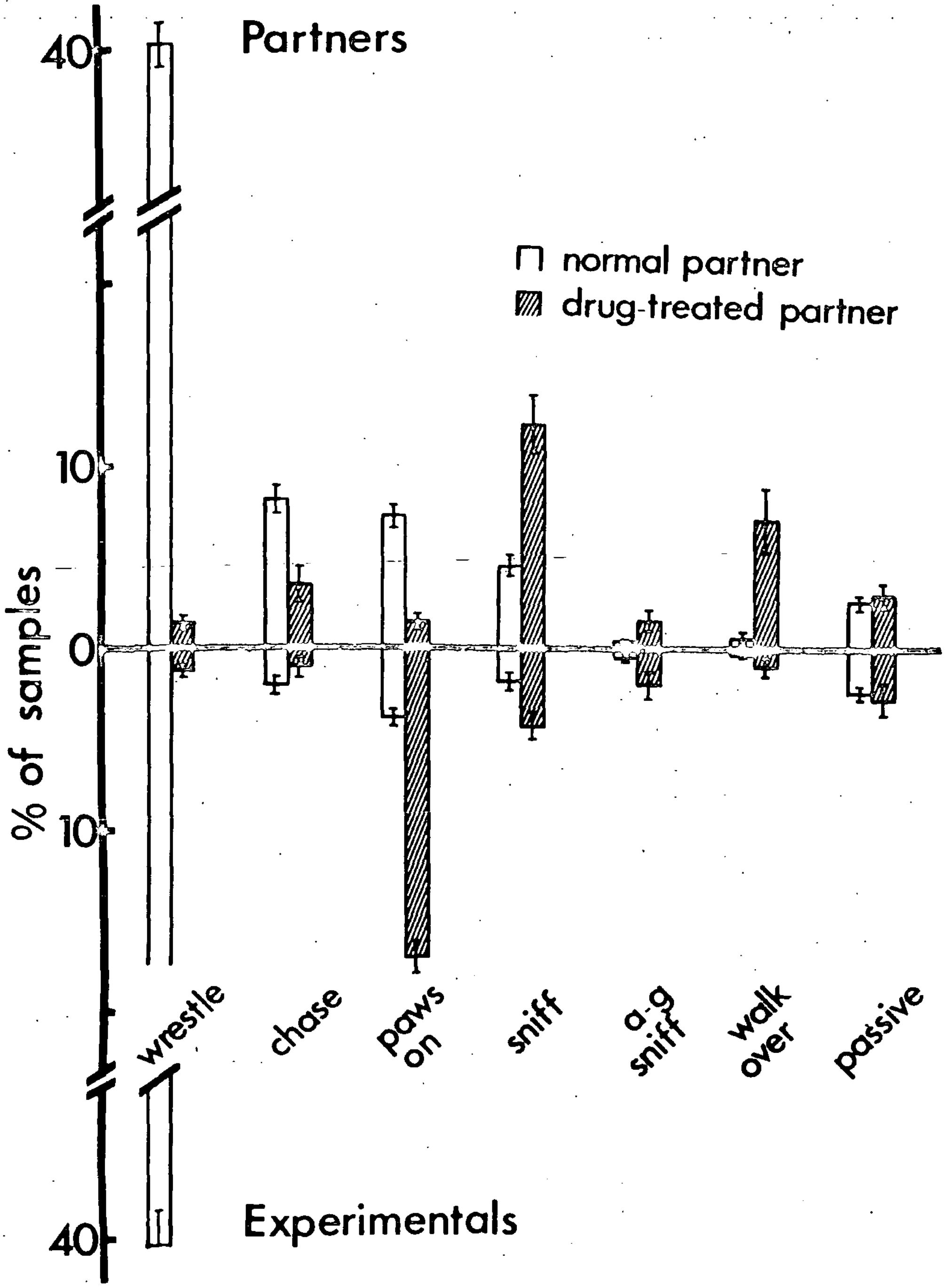


Fig. 5.4

Behaviour profiles for rats in experiment 5.3 (amphetamine-treated/normal partner). Top columns represent amounts of time spent in the different activities by drug-treated (hatched) and normal partners, and lower columns represent time spent in these activities by experimentals in their company. Vertical bars represent one S.D. above and below the mean.

Experiment	Choice offered	Groups effect			Groups/behaviours interaction			Behaviours effect		
		df	F	p	df	F	p	df	F	p
3e	Amphetamine/	1,22	74.02	0.001	6,132	336.18	0.001	6,132	423.36	0.001
3p	normal	1,22	118.04	0.001	6,132	123.56	0.001	6,132	175.96	0.001
4(i) e	Chlorpromazine (8mg)	1,20	60.20	0.001	6,120	109.77	0.001	6,120	149.02	0.001
4(i) p	/normal	1,20	417.62	0.001	6,120	228.88	0.001	6,120	226.40	0.001
4(ii)e	Chlorpromazine (4mg)	1,18	3.72	0.07	6,108	58.47	0.001	6,108	13.30	0.001
4(ii)p	/normal	1,18	9.06	0.008	6,108	67.02	0.001	6,108	12.87	0.001
4(iii)e	Chlorpromazine (2mg)	1,20	5.70	0.026	6,120	104.80	0.001	6,120	4.43	0.001
4(iii)p	/normal	1,20	3.19	0.09	6,120	112.88	0.001	6,120	4.60	0.001

Table 5.3

Analysis of variance of behaviour scores in experiments 5.3 and 5.4. "e" results refer to the behaviour of experimentals and "p" results to that of partners.

reduced in the amphetamine-treated partners, but that three of the four amicable behaviours - Sniff, Ano-genital sniff and Walk-over - were simultaneously increased. Experimentals showed lower levels of Wrestle with amphetamine-treated partners but gave more play invitations (Paws-on). They also showed slight increases in the amicable behaviours Sniff and Ano-genital sniff in the drug condition.

5.3.3

Discussion

Experiment 5.1 showed that some aspect of whole-body interaction is reinforcing to young rats. In this experiment, the choice offered was between two types of physical interaction, one involving large amounts of active play and the other involving little play but much social attention of other kinds. Faced with this choice, the young rats showed a significant preference for the company of the normal partner. Such a preference could result either from an attraction to the experiences offered only by the normal partner (play and reciprocation) or from an aversion to the experiences offered only by the amphetamine-treated partner (abnormally large amounts of amicable behaviour). In order to separate these possibilities, different combinations of social partners were offered to further groups of young rats.

EXPERIMENT 5.4

The rats were offered the choice of chlorpromazine-treated or normal partners. Three separate experiments were carried out (referred to as experiments 5.4(i),(ii) and (iii)) using different doses of chlorpromazine.

5.4.1

Method

Subjects

Subjects for all three experiments were male rats bred in this laboratory from Olac stock and weaned at 21 days of age. Experiments 5.4(i) and (iii) each used 36 rats, and experiment 5.4(ii) used 30.

Procedure

A chlorpromazine injection was given to one of the two partners 15 min before each block of trials. The chlorpromazine (Largactil; May and Baker Ltd) was diluted with sterile distilled water so that doses of 8 mg/kg body weight (experiment 5.4(i)), 4 mg/kg (experiment 5.4(ii)) and 2 mg/kg (experiment 5.4(iii)) could be given, as before, in volumes of 1 ml/kg. All injections were intraperitoneal. Control injections of equivalent volumes of solvent only were given to the other partners.

Initial training in experiments 5.4(i) and (ii) continued for four and five days respectively, after which the partners were reversed and trials continued for a further four days. Animals in experiment 5.4(iii) received training for five days in the initial condition only.

5.4.2

Results

The learning performances of the three experimental groups are shown in Fig. 5.5. This indicates that animals in experiments 5.4(i) and (ii) developed a preference for the normal over the chlorpromazine-treated partner, while animals in experiment 5.4(iii) showed no preference for either.

Analysis of variance carried out on the side choice results (see Table 5.1) showed significant groups effects in experiments 5.4(i) and (ii) but not in experiment 5.4(iii). Groups/days interactions and days effects were not significant in any of the experiments. In the two experiments in which the partners were reversed, performance after reversal was similar to that before. Groups effects were significant in both 5.4(i) and (ii), and groups/days interaction was also significant in experiment 5.4(i). Other effects were not significant.

R.A.´s for chlorpromazine-treated rats were as follows: 8 mg/kg: -0.62; 4 mg/kg: -0.43; 2 mg/kg: +0.05.

The behaviour of rats given chlorpromazine at 8 mg/kg, and to a lesser extent that of those given 4 mg/kg, differed noticeably from normal. Animals receiving the high dose were generally inactive, but despite this passivity, experimentals behaved socially towards them.

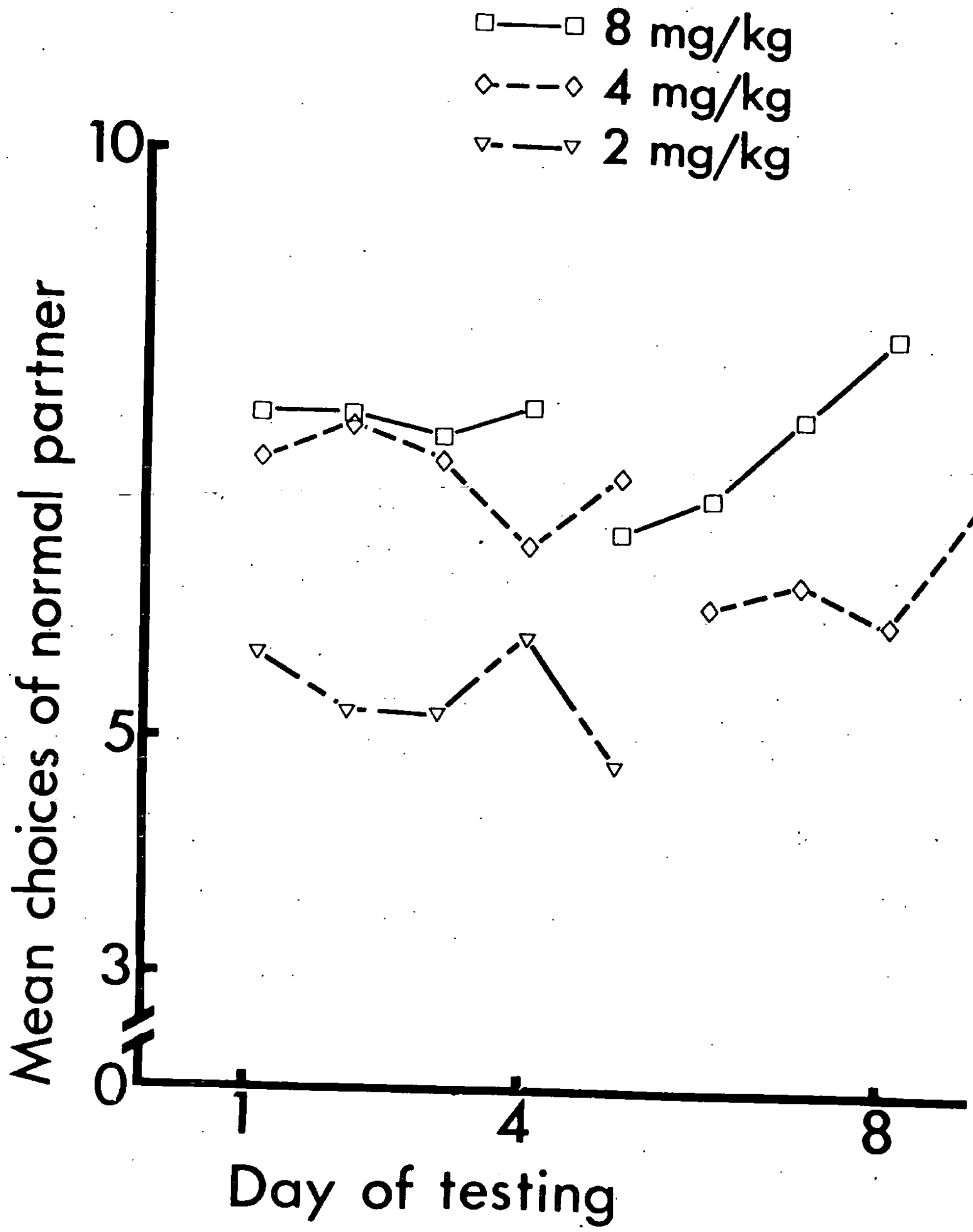


Fig. 5.5

Learning in experiments 5.4(i), (ii) and (iii) (chlorpromazine-treated/normal partner) by males, expressed as mean choices of normal partner per rat per day. Partners were reversed on day 5 (5.4(i)) and day 6 (5.4(ii)).

Animals given 4 mg/kg appeared active and initiated a certain amount of contact, but their play was conspicuously sluggish. Rats who received chlorpromazine at 2 mg/kg showed no apparent behavioural abnormalities except a slight slowing and lack of co-ordination during rapid rough-and-tumble play.

Behaviour profiles from the three experiments are shown in Figs. 5.7, 5.8 and 5.9. Analysis of variance (see Table 5.3) showed that drug-treated animals behaved significantly differently from normal only at the two higher doses, while experimentals behaved abnormally with partners given the 2 mg/kg and 8 mg/kg doses, but were not significantly different from normal with partners given the 4 mg/kg dose.

At the 8 mg/kg dose (Fig. 5.6), partners showed decreases in all active behaviours. Experimentals in their company showed decreases in active play and increases in play invitations and amicable behaviours. The 4 mg/kg dose (Fig. 5.7) had similar but less drastic effects: treated partners showed a reduction in active play but their levels of amicable behaviour did not differ from those of normal partners. When with them, experimentals showed a reduction in active play and a slight increase in the contact-making behaviours Paws-on and Sniff. At the lowest dose (Fig. 5.8) both partners and experimentals showed only a decrease in wrestling (equivalent to approximately 7 sec/min less than normal).

The relationship between attractiveness of drug-treated animals and behaviour scores (both their own and those of experimentals in their company) was examined

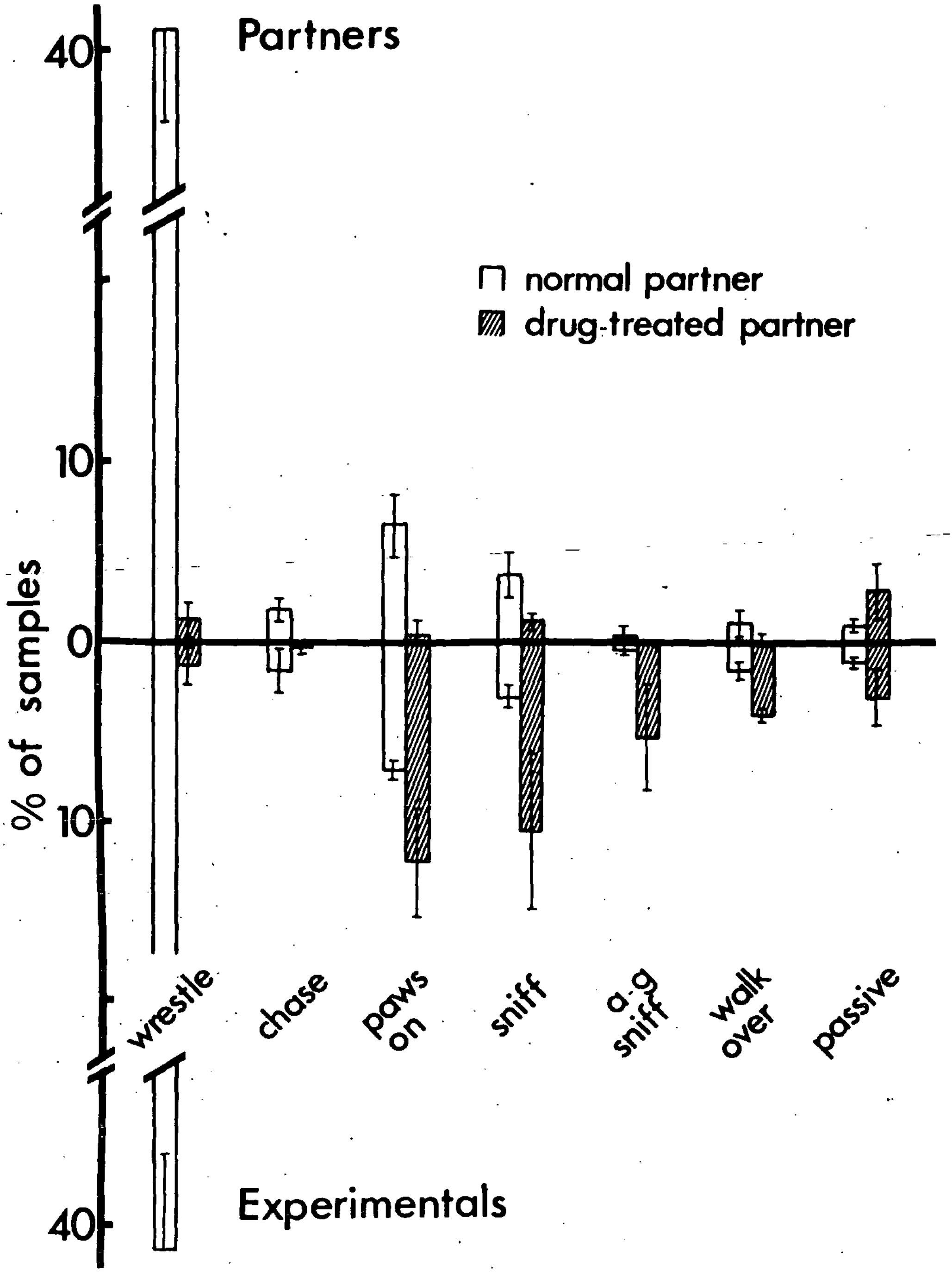


Fig. 5.6

Behaviour profiles for rats in experiment 5.4(i) (chlorpromazine (8 mg/kg)/normal partner). Top columns represent behaviour of partners and lower columns represent behaviour of experimentals. Hatched columns refer to the drug condition and blank columns to the normal condition, as in Fig. 5.4. Bars indicate S.D.

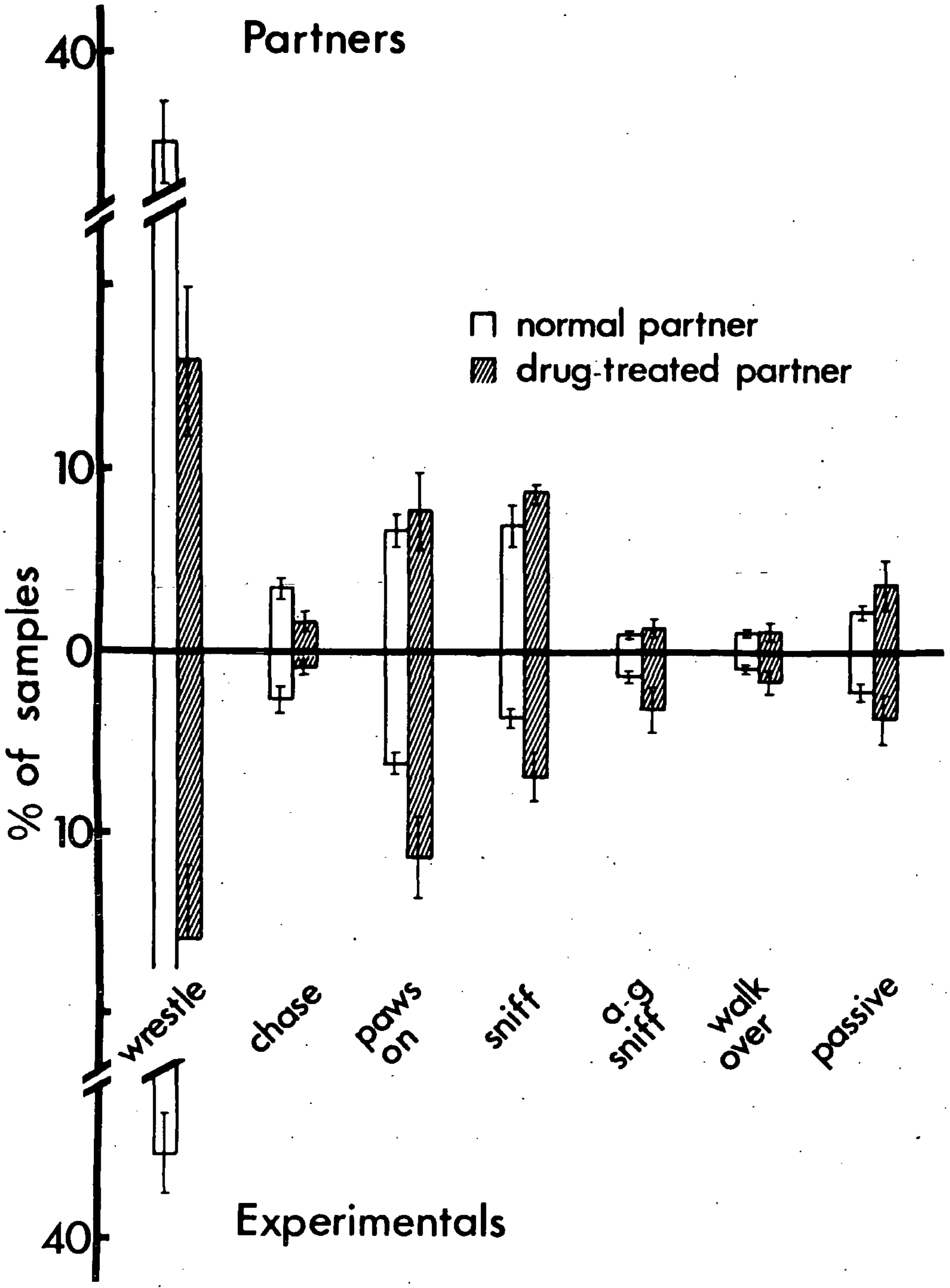


Fig. 5.7

Behaviour profiles for rats in experiment 5.4(ii) (chlorpromazine (4 mg/kg)/normal partner). As in Figs.5.4 and 5.6, top columns represent partners, lower columns represent experimentals, hatching refers to the drug condition and bars indicate S.D.

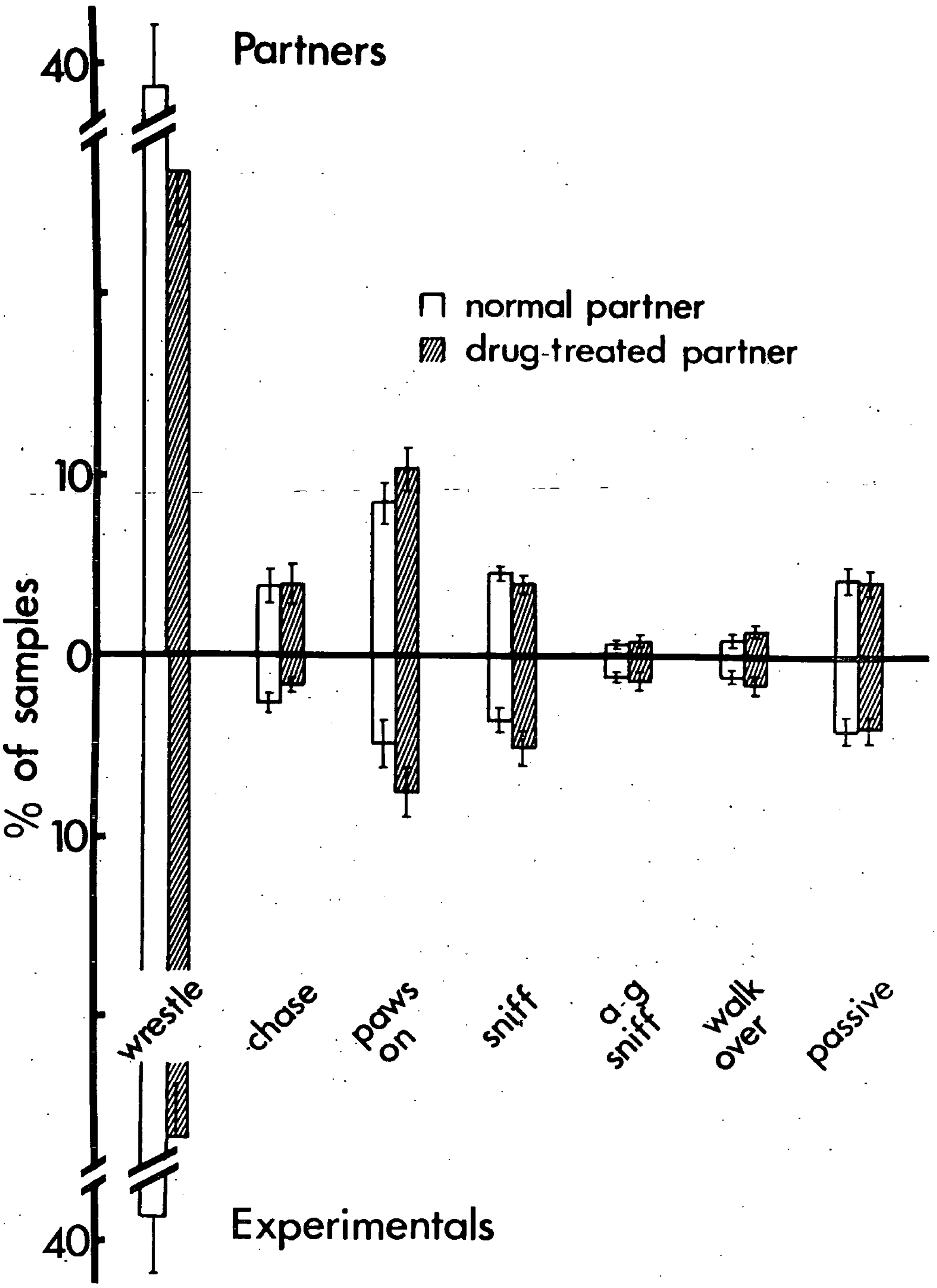


Fig. 5.8

Behaviour profiles for rats in experiment 5.4(iii) (chlorpromazine (2 mg/kg)/normal partner). As in Figs. 5.4, 5.6 and 5.7, top columns represent partners, lower columns represent experimentals, hatching refers to the drug condition and bars indicate S.D.

Behaviour	Correlation between R.A and: Experimental's behaviour	Partner's behaviour
Wrestle	0.554**	0.554**
Chase	0.370*	0.140
Paws on	0.012	0.216
Sniff	-0.216	-0.084
A/g sniff	0.081	0.030
Walk over	-0.223	0.094
Passive contact	-0.134	-0.134

** $p<0.01$
* $p<0.02$

Table 5.4

Pearson product-moment correlation coefficients between R.A. of drugged partners and behaviour scores associated with them (i.e. their own behaviour and that of experimentals in their company) over experiments 5.3 and 5.4(i), (ii) and (iii).

over all experiments in which behaviour was recorded. Correlation coefficients (Pearson product moment correlation, Ferguson 1959) were calculated between individual partners´ R.A. scores and the levels of behaviours associated with them. Two sets of coefficients were thus obtained from the two sets of behaviour scores (partner and experimental), and are shown in Table 5.4. R.A. was found to be significantly correlated with time spent wrestling (r = 0.554, P<0.01) and with the amount of time which experimentals spent in chasing the drug-treated partners (r = 0.370, P<0.02).

5.4.3

Discussion

The three experiments using chlorpromazine show how different levels of behavioural abnormality affect young rats´ social attractiveness. The 8 mg/kg dose depressed all active behaviours, thus affecting play as amphetamine did but having an effect opposite to that of the stimulant on amicable behaviours. Experimental rats showed a preference for normal partners over partners treated with chlorpromazine at 8 mg/kg, as they did for normal over amphetamine-treated partners, suggesting that play was a major factor influencing their choice. Normal partners were also preferred, though to a smaller extent, over partners given chlorpromazine at 4 mg/kg. These animals showed reduced play but no abnormalities in amicable behaviour, suggesting that play was again governing partner choice. Partners given chlorpromazine at 2 mg/kg, who did not show any significant overall abnormality in behaviour, were treated as normal by experimentals.

5d

Discussion

Experiment 5.1 showed that this discrimination was well within the learning capabilities of rats aged between 25 and 30 days who were appropriately motivated. It was therefore assumed that the extent to which they chose particular partners in the subsequent social choice experiments reflected definite preferences rather than random behaviour.

Experiment 5.2 showed that a partner who could interact freely was strongly preferred over one who could not, suggesting that some aspect of physical interaction with a free animal reinforced learning. The speed at which the rats ran towards free partners (mean trial time = 4.23 sec) also indicates the importance of social interaction to them. Animals running towards food took almost twice as long to reach the goal box (mean trial time = 7.66 sec) either because they were less highly motivated, or, as informal observation suggested, because the absence of other rats made the apparatus a more frightening place.

The subsequent social choice experiments separated out the different aspects of the experience of free physical interaction to see how highly play was valued by comparison with other forms of social interaction. Animals treated with amphetamine, or chlorpromazine at one of three doses, were offered as alternative social partners to normal individuals, since these drugs were known to inhibit play while affecting other behaviour differently. By recording simultaneously the preferences of experimentals as indicated by their choices of partner on successive trials, and their behaviour with their chosen partners, it was possible to see in more detail which social behaviours were preferred.

Both amphetamine and chlorpromazine decreased play, but while chlorpromazine also decreased (8 and 4 mg/kg) or did not affect (2 mg/kg) amicable behaviour, amphetamine increased it. Animals treated with either drug at the higher doses were less attractive than untreated individuals, suggesting that play, on which both drugs exerted similar effects, was most important in determining a partner´s attractiveness. However, a closer examination of the levels of preference expressed shows that partners were also attractive for other reasons. R.A. scores, being derived directly from preference levels, indicate the value placed on each type of abnormal partner relative to that placed on a normal companion, and can therefore be compared directly. In Fig. 5.9, the R.A. scores of the abnormal partners are ranked on a scale which runs from -1 (never chosen) to +1 (always chosen). The order in which they fall on this scale suggests that attractiveness is related to the extent and variety of an animal´s social behaviour. Confined animals were unable to use more than nose and paws in social interaction, and rats treated with chlorpromazine at 8 mg/kg, who were similarly unattractive, were physically available but inactive. Those treated with chlorpromazine at 4 mg/kg, who were more attractive than the heavily dosed group, engaged in some play and normal amounts of amicable behaviours, and amphetamine-treated animals, who were more

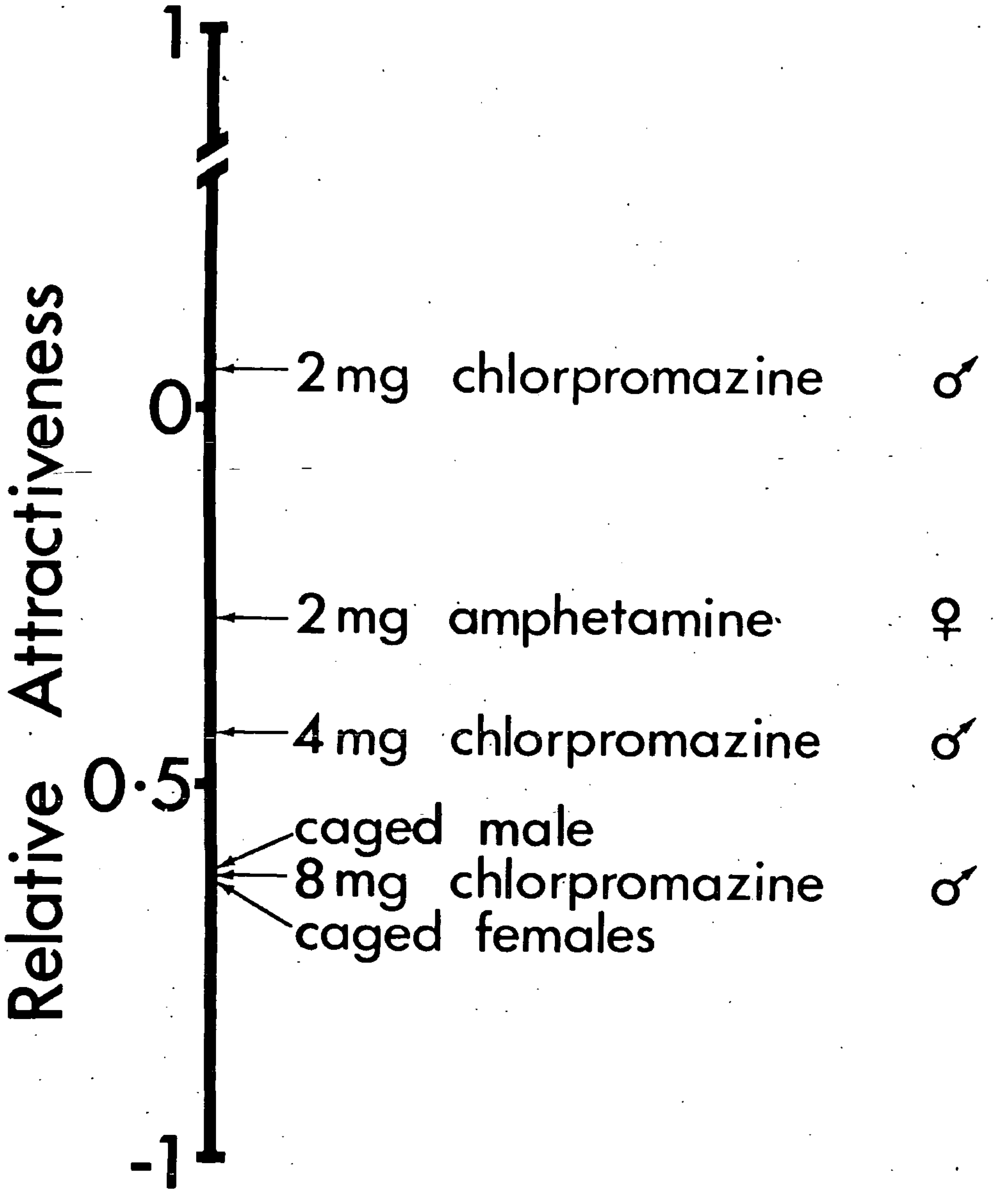


Fig. 5.9

Relative attractiveness of different abnormal partners in experiments 5.2, 5.3 and 5.4, as indicated by experimentals' partner choice (see text for calculation of R.A.).

attractive still, did not play but showed high levels of amicable behaviour. Thus while play is attractive, its absence may be compensated for to some extent by a large amount of non-playful attention.

The fact that even the virtually unconscious chlorpromazine-treated partners in experiment 5.4(i) were nevertheless chosen more often than was no food in experiment 5.1 indicates that a rat is also mildly attractive by virtue of its physical presence alone. Latané, Joy, Meltzer, Lubell and Cappell (1972) came to similar conclusions when testing the attractiveness of adult rats in an open field. While a normal, sociable rat was strongly attractive, an anaesthetized, and therefore totally inactive, animal was also mildly attractive.

The findings indicate that a number of factors contribute to the attractiveness of a rat as a social companion. However, when the relationship between behaviour and social attractiveness was examined across experiments 5.3, and 5.4(i), (ii) and (ii), the only behaviours whose incidence correlated significantly with R.A. were the active play behaviours Wrestle ($p<0.001$) and Chase by the experimental ($p<0.05$). The greater an animal's tendency to play, therefore, the more attractive it was as a partner.

Thus it seems that play is sufficiently reinforcing to young rats to make them take active steps to seek it out. This can be seen as a mechanism which has evolved to ensure that they undergo experience which will be to their long term benefit.

CHAPTER 6

DISCUSSION

In Chapter 1, a review of studies of play in many species showed that, while there is no generally accepted definition of play, observers found little difficulty in recognising this activity when they saw it, and agreed with other, independent workers on its identification. The activities which were described as playful in these studies varied widely, but were shown to be bound together into a "family" group (Wittgenstein 1953) by shared characteristics. Chapters 2 - 5 describe observational and experimental examinations of various aspects of the play of rats. This work gives quantitative information concerning the properties of rat play which allows comparison with the play of other species.

6.1 Properties of rat play.

6.1.1 Recognition by naive observers.

The experiments described in Chapter 2 established that observers with no experience of rats were nevertheless able to recognise play consistently, and to agree amongst themselves on what constituted play, even though they had not previously discussed their criteria. The behaviours which were agreed upon as play by the majority of these observers (wrestling, chasing and pouncing) formed the basis of a working definition of rat play which was used during the other studies described.

The observers' agreement thus indicated that play was a valid concept to apply to the behaviour of young rats, and constituted a natural behavioural entity.

6.1.2 Characteristics of the activities recognised as play.

Chapters 3 to 5 describe examinations of different aspects of the behaviours which the naïve observers identified as play. These behaviours were shown to share a number of the characteristics listed in Table 1.1 with the play of other species. These characteristics are listed again in Table 6.1 together with an assessment of their validity for rat play. Those found to be valid are discussed below, treated in the three categories previously used (Motor patterns, Motivation, outcomes and environmental effects and Social factors).

(a) Motor patterns

Behaviours seen in other contexts:

The positions taken up in play wrestling, in which one animal lies on its back beneath, facing and at right angles to its partner, are similar to those reported by Grant and Mackintosh (1963) for serious fighting between adult male rats, when the dominant animal takes the top position. The considerable structural similarity between play-fighting and serious fighting in rats led Poole and Fish (1975) to use Grant and Mackintosh's (1963) inventory of aggressive behaviours, with little modification other than the use of a "p-" prefix, to classify playful behaviour (e.g. "p-aggressive posture" and "p-submissive posture" correspond to the on-top and under positions in play wrestling, their serious counterparts being "Aggressive posture" and "Submissive posture").

Chasing, the other major type of playful

Characteristic	Valid for rat?
(a)Motor patterns	
Seen in other contexts	Yes
Play differs from non-play	Yes-informal observations
exaggerated	
loose muscle tone	
Fragmented and re-ordered	Yes-different results
Elements repeated	No evidence
Innovative	No
(b)Motivation, outcomes and environmental effects	
Reinforcing	Yes
Self-motivated	Yes
No goals/intrinsic goals	Appear intrinsic
Mainly in juveniles	Yes-decreases with age
Optimum conditions:	
relaxed, familiar	Yes
no physical needs	No evidence
Easily interrupted	No evidence
Influenced by weather	No evidence
(c)Social factors	
Involves signals	Yes
Injuries rarely inflicted	Yes
Roles exchanged	Yes below 40D, no when older
Self-handicapping	No evidence
Bouts longer	No evidence
May turn serious	No evidence

Table 6.1

Characteristics of play as listed in Table 1.1, and an assessment of their validity for rat play.

interaction among rats, involves a combination of motor patterns in two animals (running towards and running away simultaneously) which also occurs in sexual behaviour, when the oestrous female leads the male in a series of short darting runs which are interspersed with investigatory sniffing and attempted mounts. Meaney, Stewart and Beatty (in press) have also pointed out that chasing occurs in both play and sexual behaviour.

Playful and non-playful manifestations of behaviours differ:

Although quantitative data on non-playful manifestations of behaviour patterns seen in play were not obtained in this study, informal observations and the accounts of other workers (e.g. Poole and Fish 1975) have suggested that the above behaviours occur at a lower intensity in play. Play wrestling appears considerably more gentle than serious wrestling, possibly because a lower muscle tone is employed, and play chasing frequently involves bounding strides which could be termed exaggerated (see 1.2(a)).

Sequences fragmented and re-ordered:

Play and serious versions also differ in the behaviours they lead on to. The wrestling occurring in fights culminates in victory for one participant and may involve injuries to one or both animals. However, behaviour sequence analysis (3.3) showed that play wrestling is likely to lead either to more of the same activity with roles reversed, so that neither animal is victorious, or to some other form of play (see Figs. 3.13a and b).

Sequences highly variable:

It was impossible to assess the variability of play relative to other comparable behaviours because no quantitative data were collected concerning behaviour sequences in sexual or aggressive behaviour. However, analysis of the rats' play sequences (3.3) indicated that elements in rat play tend to occur in certain orders, so that if an animal directs a behaviour at a littermate, the recipient's likely response can be predicted from the probabilistic relationship demonstrated between acts and responses. Although the organisation of behaviour was found to change with age (Figs. 3.13a and b), play patterns had their own probable positions in chains of behavioural events at both ages.

(b) Motivation, outcomes and environmental effects.

Reinforcing:

The experiments described in Chapter 5 provide quantitative support for the generally held assumption that play is reinforcing. When offered the choice of a partner who would play, or another who was confined or had been treated with amphetamine or chlorpromazine and therefore would not, young rats demonstrated a preference for the playing partner by learning to run to the appropriate side of a T-maze. This learning was presumably reinforced by the experience of play, which was available only on the preferred side.

Motivation, results and goals:

Play produced no apparent immediate results, either in terms of changes in the environment or of changes in the animal itself. The fact that young rats would initiate play without external stimulation, and without attaining any immediate material advantage through doing so, suggests that they engaged in this activity purely for its own sake. They were also found to run through the T-maze consistently faster for play than for food reinforcement (5.5), which may indicate that they were even more highly motivated to seek out play than food when appropriately deprived, although it is more likely that this difference resulted from a difference in fear levels.

Specific goals, such as biting without being bitten (Symons 1978b), were not apparent in the play of rats. While it is possible that bouts of wrestling with reversal of roles resulted from both animals trying to gain the on-top ("dominant") position, there is no evidence to support this interpretation over the converse one that both partners compete for the under position.

Predominantly among juveniles:

The amount of time devoted daily to play rose to a maximum at 25 - 30 days, and then decreased with age. By 56 days, when the animals were assumed to have reached puberty and the study was terminated, individuals were only devoting 0.7% of their waking time to play, compared to 7.1% at 25 - 29 days.

Familiar relaxed environment most conducive to play:

Pilot studies were carried out for the experiments described in Chapter 5 to determine the conditions in which play was most likely to occur, so that apparatus, lighting, animals' experience and any other relevant factors could be manipulated to maximise the likelihood that play would occur when the willing partner was chosen. It was found that play was incompatible with behaviour indicative of fear, such as freezing and defaecating, and did not occur in new surroundings until they had been explored thoroughly. Play was also more likely to occur in dimly lit than in brightly lit surroundings, and was interrupted by sudden loud noises.

As has been reported for play in many other species, therefore, play is most likely among rats in familiar and non-frightening surroundings.

Low priority:

The log survivor function for rats' play bout lengths was a straight line (see Fig. 3.4a). McDonald (1977) obtained a similar shaped function for the play of Columbian ground squirrels, and took this as an indication that play was usually interrupted by other, randomly-occurring events before it could reach a conclusion of its own, and was therefore a low priority behaviour. However, as has been discussed above (3.1), log survivor functions of this shape are common among other behaviours, including some, such as feeding, that would otherwise be considered high priority.

Such an interpretation of the random distribution of play bout lengths may be contested on two counts. Firstly, it is unlikely that play was terminated by random external interrupting events, since, although bout length log survivor functions for individuals are of the same straight line shape as those for whole litters, litter bouts were on average longer than individual bouts, indicating that play tended to be continued by some individuals while others dropped out. Thus whatever caused part of the play group to stop did not affect the remainder. The log survivor functions also indicate that animals did not stop playing because of exhaustion, and therefore it seems likely that this bout length distribution has evolved as the best way to organise this behaviour in terms of immediate and ultimate results.

Secondly, the term "priority" has questionable value when applied to the short term organisation of behaviour, since so many different factors, both internal and external, contribute to deciding which behaviour an animal carries out at a given time. Any behaviour can be considered to have top priority when it occurs, and to have been superseded by the next activity when it finishes. However, it remains useful when applied to behaviour on a larger scale in relation to the prevailing conditions, e.g. Baldwin and Baldwin (1974) found that play took on extremely low priority among squirrel monkeys under conditions of food shortage.

(c) Social factors.

Signals:

Their observations of the behaviour of young rats led Meaney and Stewart (1981) to suggest that the behaviour they called "Pounce", which is equivalent to the category "Paws-on" used here (3.3), acted as a play invitation. This assumption was tested in 3.3, using behaviour sequence information to see to what extent Paws-on preceded play and play followed Paws-on. It was found that 70% of play initiations were preceded by Paws-on, and over 50% of Paws-on were followed by play, showing that the behaviours were closely linked and providing a numerical indication of the role of this gesture as a play invitation. The proportion of play preceded by Paws-on does not change with age but the proportion of Paws-on leading to play decreases. Since Paws-on does not decrease in absolute amount with age as play does, this suggests that the gesture begins to take on a different meaning among older animals while still serving to initiate play.

The consistent recognition of play in rats by naïve human observers may also indicate that all play activities had some signal properties, as West (1974) suggested when preferring to explain its exaggerated appearance as a typical intensity which enhanced its signal qualities. This signal must have been sufficiently powerful or universal to carry between the two species.

Injuries rare:

Animals did not appear to inflict injuries on their littermates in play. No marks were visible on their skin, and no animal was seen to show distress.

Roles exchanged:

It was shown in 3.3 that the roles of "dominant" and "subordinate" wrestler were exchanged during play wrestling. This was more common in younger animals, who exchanged roles on some 30% of occurrences of wrestling. Only about 12% of wrestling between older animals resulted in continuation with roles reversed.

Dominance relations not expressed:

The evidence of role reversals suggests that dominance relations did not influence the play of younger animals to any great extent, but may come to affect play more with age. This lends support to the findings of Meaney and Stewart (1981) and Panksepp (1981) that dominance relations begin to influence the play of rats from 35 - 40 days. Unfortunately, insufficient data were available on each individual dyad to permit examination of the stability of relations between individuals.

The statement that dominance does not affect play thus appears to be true for younger rats, over the age-range at which play is most frequent, but becomes progressively less accurate with increasing age.

Play may turn serious, especially among older individuals:

No instances of serious aggression were seen, either associated with play or independent of it. However, the fact that bouts tended to terminate sooner, and involve fewer role reversals, in older animals may indicate that subordinate individuals were quicker to accept their position and so avoided aggression.

The activities which were identified as play in rats (Chapter 2) have thus been shown to possess many of the characteristics commonly quoted for play in other species. These are summarised in Table 6.1. Naïve observers established these activities as part of a play concept by placing them consistently in this category, although they were unable to define it verbally. This showed that it is possible to use human observers to bioassay play behaviour, as Miller (1973) suggested, by making use of their inherent abilities to pick up play signals in other species. The properties listed in Table 6.1 provide a more objective, though perhaps less sensitive, means of identifying play among rats, or of supporting identifications made by observers.

The above discussion gives the human view of play in the rat, its recognition, appearance and properties. Its relevance for the animal itself will now be examined in terms of the costs and risks attached to it, and the benefits which may ultimately be gained from it.

6.2 Costs of play for rats.

Since energy expenditure in play was not measured directly in these experiments, the best available indicator of the energy costs incurred in this activity is the amount of time which was devoted to it. At its peak, between 25 and 30 days, this constituted a mean of 52 mins per 24 hr per individual, or 7.1% of waking time. This falls at the upper end of the 1 - 10% of waking time quoted by Fagen (1981) for various primates, but probably exceeds the value for wild rats because the animals under study were kept in what could be considered optimal social play conditions, confined together with ad lib food in familiar surroundings. These conditions minimised other costs in terms of risk of accidental injury and possible increased predation which could be incurred by wild rats in play.

Devoting 7.1% of waking time to play nevertheless represents a considerable investment with no readily apparent return. The way this investment is regulated may give some clues as to the ultimate gains.

6.3 Regulation of play in rats

6.3.1 Short-term:

The experiment described in Chapter 4 supported the views of Panksepp and Beatty (1979) that the amount of play occurring is controlled by homeostatic mechanisms which aim to regulate play to some specific level. These serve to produce the rebound effect seen following play deprivation, and the satiation effect following concentrated play experience, which were demonstrated in Chapter 4.

6.3.2 Long-term:

The levels of play for which these homeostatic mechanisms aim appear to be set differently at different ages. Evidence from other species suggests that they are also influenced by external conditions such as food availability. Baldwin and Baldwin´s (1976) experiments limiting the food supply of captive squirrel monkeys showed that play was depressed when food was harder to obtain, even though spare time still remained when play could have occurred. When food was again made freely available following these periods of deprivation, the monkeys´ play showed a rebound, as described above following play deprivation by other means, before returning to normal.

The amount of play thus appears to be rationed, through regulated homeostatic control, in relation to external conditions.

6.4 Benefits of play for rats

The work described here does not provide direct evidence to indicate how rats may benefit from play, but it can give support to certain of the theories quoted in 1.4.2. These theories are discussed below in relation to the support they receive.

1. Skills practise

The similarity of the behaviours seen in play to those seen in other contexts, which was discussed above (6.1.2) as a characteristic of rat play, supports a view of play as practise on grounds of design (Symons 1978b). Such a view is supported by the absence of any apparent difference in the frequency of playfighting between the sexes, since rats of both sexes fight in adulthood when the occasion demands it. Males may fight each other for oestrous females or attack strange males intruding into the group, and pregnant and lactating females defend their burrows against intruders of either sex (Calhoun 1962). (The more detailed studies of Meaney and Stewart, 1981, revealed that females showed less of the play-initiating behaviour "Pounce" and were seen less often in the "On-top Posture" than males. Such differences could also support the view that play is designed to provide practise for fighting skills, since sex differences in adult fighting circumstances require that female agonistic behaviour be mainly defensive while male agonistic behaviour is more offensive.)

The absence of injuries, or indeed any winner or loser in playfights, need not preclude a practise function as some have argued it should. If we consider practise for human passtimes whose serious versions may cause injury, such as boxing, it can be seen that it is possible to practice the necessary skills without damaging a sparring partner. This indicates that practise does not need to be identical in form to the real thing in order to perform its function and develop skills, and therefore that play-fighting may contribute to the development of fighting skills even though the two behaviours differ in some respects.

It is also possible that play makes some contribution to the acquisition of sexual skills. It has been pointed out that chasing play bears some similarity to sexual activities (6.1.2), and that the behaviour involved, Fast locomotion, increases in frequency against the general downward trend in play at the age at which other sexual behaviours begin to increase (3.3). Calhoun (1962) also noted that this behaviour could be directed towards the mother, and suggested a direct relationship to adult sexual following. Evidence from rearing studies has been reviewed (3.3) which suggests that social experience over the age-range at which play occurs is important for the development of normal male sexual behaviour. The experiments of Einon (personal communication), described in 3.4, point to play as being an important experience in the development of the tendency of males to approach and mount females, although other experience appears to be necessary for the correct orientation and coordination of the behaviours which leads to successful mating. Animals reared with only one hour of social experience per day, whose social interactions had consisted of an abnormally large proportion of play because of the isolation rebound effect, were normal in the extent to which they approached and mounted females, while peers reared in isolation showed a deficit.

These considerations apply to physical skills, which involve the successful carrying out of specific behaviour sequences. Play could also promote social skills by allowing the animal to learn which series of behaviours to carry out in the presence of which other animal. This possibility is considered below.

2. Physical training

Rat play involves vigorous physical activity which is likely to have a beneficial effect on bodily capacity, whether as a function or as a by-product. Fagen (1981, p.283) has cited evidence that training responses are often more dramatic in young animals, and some may occur only as a result of exercise before puberty. Play thus coincides with this period when exercise can have its greatest and most wide-ranging effects. The rat's play period also occurs when growth (in terms of weight gain per unit time) is at its fastest; the growth curves plotted by Widdowson and Kennedy (1962) are sigmoid, their steep central sections covering the 4 - 8 wk age range. Thus if exercise leads to training responses partly by influencing growth processes, as Fagen's reported evidence suggests, this would be the most effective age at which to devote energy to exercise in the form of play.

Rat play conforms to at least some of Fagen's (1976) predictions for the form of the ideal exercise play. It provides overload, high-intensity and endurance exercise which are required to develop the power and strength of specific muscle groups and the work capacity of the whole body respectively. Wrestling, in which the underneath animal bears some resemblance to a weight-lifter in training as it raises its partner on its hind feet, provides overload and high-intensity exercise, and

Fast locomotion provides endurance exercise. It is uncertain whether the play of rats has the predicted pattern of short strenuous bouts interspersed with lighter activity. Overall, no such patterning was apparent, but durations of the different types of play were not measured separately.

If play is to provide useful exercise, its form should be appropriate to the animal's requirements as an adult. The opportunistic lifestyle of the adult rat involves a wide range of varied activities for which it would be difficult to devise specific training because of their dependence on the environment. However, there is nevertheless a universal need for speed and stamina for escaping from danger, and a general improvement in static muscular strength brought about by overload exercise would facilitate such heavy tasks as digging, dragging large food items and, for females, retrieving pups.

3. Learning

Rat play is almost entirely social, involving few object-oriented or solitary activities. It could therefore allow learning about the actions and reactions of other individuals, but does not appear to be designed to gather information about the behaviour of objects or the environment, or about the individual's solitary abilities, in the way that the more experimental play of some other species is (e.g.chimpanzees: van Lawick Goodall 1968, badger: Eibl-Eibesfeldt 1950).

Since dominance relations begin to affect play at 35 - 40 days (Meaney and Stewart 1981) it seems likely that animals assess each other's strength in play. Panksepp (1981) has provided further evidence for such a process. He reared rats in isolation, placing them together in pairs for a 5 min test period every four days, and observed their interactions during these test periods up to 64 days of age. By 36 days, their dyadic relationships had reached a level of stable asymmetry which was maintained throughout testing. Because of the isolation rebound effect, these animals played almost continually throughout the 5 min test periods, and therefore play was effectively their only social experience. Thus any asymmetries expressed in their interactions must have developed through play.

However, as Symons (1978a) has pointed out, a hierarchy is not an entity in itself, but the nett result of the animals´ interactions, and therefore play cannot be considered to function to produce a hierarchy. Rather, it may function to reduce later aggressive competition, a result which would be advantageous to all individuals in a stable group, by making them aware which animals are stronger and weaker than they are. Individuals would then become sorted into a hierarchy as a result of this.

4. Innovation

Although it was not possible to assess the relative variability of rats´ play, the activity was found to have a moderately predictable structure, and is therefore unlikely to function to produce novel behaviour combinations.

5. Social functions

(a)Development of complex social behaviour:

The play of rats is itself a complex social behaviour, involving the meshing of rapidly changing behaviours between partners, and the correct sending and receiving of signals. It could thus help to prepare animals to cope with the complexities of adult interactions, although there would be no reason for behaviour serving such a function to be as energetic as play.

(b)Development of communicatory skills:

Signalling was shown to occur in rat play (3.3). It was also shown that the meaning of the signal gesture changed with age, indicating that play did not function to teach the young rats the meaning of signals used by the whole social group. However, it remains possible that they learnt some of the underlying principles of communication, or developed their sensitivity to signalling, in play.

(c) Social integration:

If young rats were to become integrated into the group directly through play, learning their own and other group members' relative roles, they would need to play with adults as well as peers. Meaney and Stewart (1981) noted that mothers played with their own young, but the adult males in Calhoun's (1962) study of a semi-wild colony tended to ignore juveniles, although they tolerated playing young in their vicinity. This suggests that play is not directly responsible for the development of stable relationships between young and old group members, although it may contribute indirectly by promoting social skills, as was suggested above ((a) and (b)).

However, there are indications that play contributes directly to the development of stable relationships between peers. The evidence from the decrease in role reversals (3.3) and from the observations of Meaney and Stewart (1981) and Panksepp (1981) indicates that dominance relationships are expressed in the play of older rats (over 35 days of age). This suggests that, since aggressive or threatening interactions were not seen among juvenile rats, these relationships were reached after animals had assessed each other's rank in play. Panksepp (1981) noted that dominance was not necessarily dependent on size, although dominant animals tended to be heavier on average, indicating that animals did not assess each other by appearance alone.

The development of such stable relationships in play can be seen as the development of a social skill, in that animals learn to behave appropriately towards other individuals. As has been pointed out, a dominance hierarchy is not an end in itself, but the result of the ways in which group members respond to one another. These responses, apparently developed at least partly through play and manifested as a dominance hierarchy, function to promote the welfare of both dominant and subordinate individuals by reducing overt aggression within the group. Thus although play is widely seen as promoting fighting skills (see 1. above), it also appears to contribute to a reduction in actual aggression. In a sense, therefore, it may be seen as developing the skills needed to refrain from fighting.

(d) Litter cohesion:

The litters observed here were unable to disperse even if they had wanted to, and therefore offer no information. Calhoun (1962) has reported that litters of wild rats disperse at about 60 days, which corresponds to the age at which play dies out, but that dispersal appears to be precipitated by threats from the mother, which suggests that the bonds uniting litters may outlast play, although they may be reinforced by play when it occurs.

6. Flexibility

Lorenz (1956) has suggested that "generalist species" such as the rat, which can exploit a wide range of niches through their ability to adapt their behaviour to the circumstances, acquire this flexibility in play. In support of this suggestion, the play deprivation experiments of Einon et al. (1978) have provided evidence suggesting that rats reared without play experience are slower to adapt their behaviour to a new task than others who have played.

The social play of rats is structurally well-suited to promoting behavioural flexibility. It involves rapid chains of interaction between animals for which both participants must monitor each other's behaviour continually so that they can react to changes as they arise. Although the behaviours involved are similar on most occasions, play is by no means stereotyped, and no two bouts will involve the same movement sequence. It is thus possible that young rats develop a general ability to react quickly and appropriately to changes in the environment through the experience of the rapid interaction sequences of rough and tumble play.

7. Functions: summary

The properties of the play of rats therefore indicate several possible functions. It could serve as practise for the adult activities it resembles, as training to enhance physical development or as experience to prepare the animal for life in a changing world, although it does not appear to be designed for the gathering of specific information about the environment. Being social it could provide information about the relative strengths of peers and thus form a basis for the development of dominance relations, and could help animals to learn certain basic principles of social behaviour and communication. However, it is unlikely that it promotes socialisation in any more direct way as it occurs mainly among juveniles and involves different behavioural conventions from other social interactions.

It is quite possible that the different forms of play function in all these areas simultaneously. If this were so, then the current form of play would be the result of the effects of selection pressures from several different directions. The resulting behaviour would therefore be a compromise between those most appropriate to serve the different component functions, and might be expected to have something of a committee-designed appearance. For example, chasing play could be built up from a number of different functional pathways. Fast movement in any direction would benefit the young animal by developing its physical work capacity. Co-ordinating this behaviour with similar behaviour in another individual would still provide endurance exercise, but would also necessitate reacting appropriately to the other individual's actions as they occurred, and could therefore help develop behavioural flexibility. The incorporation of specific sequences of behaviour, such as pouncing, into the interaction could promote the learning of potentially useful skills, with the fast, co-ordinated movement still serving the training and flexibility functions already mentioned. Wrestling play could be built up along similar lines, serving a combination of exercise, practise, flexibility and other functions, its different form resulting from differences in the types of exercise and practise.

It therefore seems likely that the social play of rats has not one but several functions, its design being the best compromise suited to serving all of them simultaneously. However, it must be stressed that this and the above suggestions concerning the functions of rat play are based almost entirely on indirect evidence. Possible ways of obtaining direct evidence for any species are discussed below (6.6) in relation to information obtained in the studies described above on some of the properties of play.

6.5 Implications for play as a whole: summary and speculations

6.5.1 Identification

The work described in Chapter 2 reinforces the views which many independent observers have expressed (e.g. Miller 1973) that recognition alone is a valid criterion for the identification of play, and therefore that the widespread use of this criterion as a basis for studies is justified. However, although the naïve observers agreed on play overall, they did not agree absolutely; certain behaviours were considered playful by some but not by others. Disagreements among experienced observers are also to be found in the literature, e.g. on the behaviour of young mice. Poole and Fish (1975) and Einon et al. (1981) were of the opinion that mice show little or no play, while Wolff (1981) has written a paper entitled

"Solitary and social play in wild *Mus musculus* " discussing behaviours which the above authors dismissed as non-playful. This indicates that recognition alone is not sufficiently constant between individuals to act as a criterion for identifying play, but should be used as a basis for objective description. Observers classifying behaviour into objectively agreed categories can achieve near-perfect levels of agreement on play and other behaviours, as Coelho and Bramblett's (1981) highly trained observers showed. A working definition of play in any species is therefore best achieved by initial recognition, or bioassay, by several observers followed by discussion to reach a concensus, and objective description of the agreed behaviours.

Comparison of the properties of activities recognised as play in different species provides the closest available approximation to a general definition, since this specifies the common ground uniting the class "play". The properties listed in Tables 1.1 and 6.1 have been quoted by several authors for a variety of species, and can therefore be considered to form the nucleus of such a definition.

It is likely that observers were judging behaviour by considering ther immediate impressions in the light of certain objective criteria. The signal features of play appear to be sufficiently generalised to cross species barriers, allowing play between widely different animals when circumstances bring them together (e.g. man and his pets: Beach 1945, chimpanzee and orang-utan: Maple and Zucker 1978, and other combinations listed in Fagen 1981, Table 7.4) and may therefore be expected to transmit the same message to a human observer. This communication is probably responsible for the immediate impression of play which observers report but cannot pin down. Motivation and results, or lack of results, may then be used as supporting evidence to verify the original impression. Animals are reported as appearing to be highly motivated to play, and to participate for no obvious reason beyond pure enjoyment, impressions which were supported by the experiments described in Chapter 5.

However, as Barash (1977, p.179) has pointed out, anything enjoyable must have a function, however obscure or distant in time, as purely hedonistic behaviour would constitute a drain on resources with no compensatory benefits and could not evolve. He saw enjoyment as having evolved to ensure that beneficial activities were carried out at the appropriate moment, even though their benefits might be delayed. Thus the fact that play is reinforcing can be considered to result from the benefits associated with the activity.

6.5.2 Functions

The life-history organisation of play (Fagen 1976) suggests that its beneficial effects are delayed, affecting the animal's fitness at some time well after the play has occurred. Although there is little direct evidence as to the nature of these functions, owing to the problems of dissociating the effects of play from those of other experiences, a number of possible functions have been proposed on the basis of the design of the behaviours (see 1.4). Thus the fact that much play is highly active and strenuous (e.g. horse: Fagen and George 1977) suggests that physical training is a widespread function. Similarly, the occurrence of species-specific aggressive behaviour patterns in play may be interpreted as indicating that play is designed to improve fighting skills.

Evidence from a number of sources allowed certain suggestions to be made concerning the functions of rat play. Observation of its design suggested that it could provide exercise, practise in fighting and sexual skills and increased behavioural flexibility. The experiments of Einon et al. (1978) indicated, by examining the effects of play deprivation, that play may contribute to the development of behavioural flexibility, and a similar technique (Einon, personal communication) suggested that play may facilitate the development of parts of the male sexual response. Play also appeared to contribute to the development of dominance relations in rats approaching puberty, indicating that it has a role in reducing aggression within the group. It was suggested that play could serve all these functions simultaneously. Such an explanation can be extended to other species, and can account for some of the characteristics which are common to their different types of play (Tables 1.1 and 6.1). Behaviour which has evolved under the opposing influences of several unrelated effects might be expected to look like a variable mixture of activities, and would be unlikely to have any readily apparent function.

The tendency to play is not universal among mammals, or within specific taxonomic groups. Although, within such groups, it appears to be more common in the longer-lived, more sociable species, it also occurs in carnivores, regardless of the sociability of their life-style. This suggests that play has evolved in parallel in many different cases to answer similar functional needs.

Consideration of the nature of the proposed functions (see 1.4) allows further speculation. These functions constitute improvements on an already viable plan rather than essential developments, e.g. an animal obtains a certain amount of exercise in maintenance activity alone, so that play would function to supplement this amount rather than to provide an entirely new experience. Thus if play did function in this way, as a developmental luxury, it would be expected to be one of the first activities to be sacrificed under adverse conditions, if survival were threatened. Martin (1982) has pointed out that, although the energy cost of play is small relative to that of overall survival, it could nevertheless become critical. If energy was in short supply, play could be a sufficient drain on resources to retard growth, or cause weight loss, and thus have an irreversible effect on the animal's physical development. Loy (1970) noted a drop in the play of rhesus monkeys in response to food shortage. The evidence of Baldwin and Baldwin (1974, 1976) indicated that squirrel monkeys stopped playing when food was scarce without appearing to suffer any major developmental deficits in consequence, although the behaviour of adults who had not played as juveniles was less complex than that of animals with normal play experience. This suggests that play had a refining effect on their basic behavioural development, but was not responsible for the total development of any one ability.

The somewhat tenuous evidence available

therefore suggests that play functions to sharpen and improve the animal´s existing capabilities, in the areas discussed in 1.4 and possibly also in others, provided that time and energy are available. It seems likely that it serves many or all of these functions simultaneously.

6.6 Conclusion

The work described and discussed here has therefore shown that, although play is a diverse and somewhat amorphous class of behaviour, the message transmitted in play signals can cross species boundaries, indicating a degree of homogeneity within the behaviour. The different forms of play are united in objective terms by a number of common structural, contextual and social features, e.g. most play involves behaviour patterns which are seen in other motivational contexts and occurs only in relaxed surroundings, and social playfighting is characterised by an absence of injury despite the aggressive nature of the patterns employed. In rats, play reaches its peak at 25 - 30 days of age, soon after weaning, and declines thereafter. Their play appears to undergo qualitative changes from the age of onset of puberty, becoming, for want of a better word, less playful in older animals.

The fact that play takes up time and energy (see 1.2 and 3.1), and that it is reinforcing and actively sought by the young animal (Chapter 5), indicate that it must be of some benefit, although the nature of the benefit is not immediately obvious. Play appears to be one of the first behaviours to be sacrificed in adverse conditions, which suggests that it is not essential for basic survival, but that it serves to improve the animal´s fitness when resources are available. The functions which have been suggested for play (see 1.4) agree with such an interpretation, emphasising improvement of properties which were already present (e.g. skills, physical capacity, flexibility) rather than development of entirely new abilities which were previously absent. Because of the absence of direct evidence, most of these functions have been proposed on the basis of design and contextual features. The highly active nature of much play suggests that physical training is an important function in many species, and its structural similarity to species aggressive behaviours (e.g. butting in horned ungulates, wrestling and play-biting in mustelids) indicates that practise in fighting skills may also be a widespread function. The number of plausible functions which have been proposed and the mixed, variable and apparently functionless nature of the behaviour suggest that it may serve several of these functions simultaneously, and so lead to an all-round improvement in the animal's abilities.

6.7 Suggestions for further work

As the above unfounded speculations indicate, the work described here does not lead to any definite conclusions concerning the real mystery of play, its functions. However, it provides a potentially useful basis for more specific studies by describing aspects of the behaviour under specified and easily duplicated conditions. Some of the questions suggested by this work are discussed below:

1. How does the play of wild rats compare with that of the laboratory populations studied here, under these

conditions and under natural conditions?

The answer to this question would reveal whether laboratory rats exhibit amounts and types of play which are similar to those of their wild counterparts, and therefore whether it is justifiable to apply interpretations in terms of selective advantage under natural conditions to the play of laboratory rats, despite strain differences. A study of the development of play in captive-born descendents of wild stock, using the methods described in Chapter 3, could reveal any strain differences by eliminating variation due to differences in surroundings, although strain differences in play itself could be masked by the greater sensitivity of the wild type to minor disturbances.

Examining the play of rats in natural conditions would present certain practical problems, as it is likely that a large proportion of this behaviour occurs in the animals' burrows. While fibre-optics would permit observation of litters in their burrows with minimum disturbance, the picture obtained would not be sufficiently detailed to identify behaviour with accuracy, although gross movement would be detectable, allowing examination of overall activity patterns. Detailed observations of underground behaviour would therefore have to be carried out on captive groups in transparent-sided burrows. Observations could be made of both laboratory and wild types in these conditions by means of time-lapse video recording, as described in Chapter 3, and the amounts and patterns of play could be compared directly with those of animals in the other conditions. Such comparisons should thus show whether laboratory rat play has remained sufficiently similar to that of the wild type, despite selective breeding for specific characteristics, and the absence of natural selection pressures on laboratory populations, to justify attempts at explanation in terms of selective advantage.

2. What is the cost of play?

Although it is generally assumed that play carries a fairly high cost in terms of energy and risk (see 1.3), this assumption is based on impressions rather than direct evidence. It would be extremely difficult to quantify all the costs of play, because of the enormous practical problems inherent in seeing occasions of predation on playing animals, or accidental injury during play, and of counting these and comparable non-play occurrences in wild populations. However, it is possible to measure energy expenditure in play, which is considered to constitute a significant proportion of the cost (Fagen 1981). Martin (personal communication) has recently measured energy expenditure in playing kittens by calorimetry, and his findings, which are summarised in 1.3, gave a value for energy expenditure in play which was lower than previous estimates had suggested. Similar measurements should therefore be made for other species, in relation to the type of play occurring, to see whether the energy costs of play are indeed being overestimated.

3. How does variation of environmental factors affecting energy availability, such as food supply and temperature, influence play and other activities?

Answers to this question have already been provided for some species under some conditions by "natural experiment" studies (see 1.5), and in controlled experiments on captive populations (e.g. Baldwin and Baldwin 1976). Their findings led to the suggestion that play is sacrificed in favour of other more crucial needs when energy is in short supply, and therefore that its functions are non-essential improvements rather than unique developments. Further experimental examinations, in which individual factors were precisely controlled, would show how play changes under their influence relative to other behaviours, and would therefore indicate its priority for the allocation of scarce resources. Further observational studies of wild populations, similar to those cited above, would also be informative if careful note were taken of the prevailing conditions.

4. How is adult ability correlated with play?

The greatest need in this area is for studies linking play with attributes of adult behaviour, which can suggest directly how the individual may benefit from this juvenile experience. Such studies should ideally be longitudinal, following individuals through the play period into adulthood and observing their behaviour throughout, although, as was pointed out in 1.5, comparative studies can also provide useful information on long-lived species. Play experience can be varied in a number of ways by manipulating conditions, partners etc. as has been discussed (1.5, Chapter 4, Chapter 5). Detailed examination of a wide range of adult behaviour may then be required to pick up the aspect related to the difference in play.

Longitudinal studies of play and adult behaviour have been carried out on rats by Einon et al. (1978), and on cats by Caro (1979, 1980). The former study used the simplest and most extreme manipulation of play available, total prevention, by supplying experimental animals with partners who would not play (as in Chapter 5, and see also 1.5 for a description of the method), while control animals were given partners who played with normal enthusiasm for the permitted 1 hr per day. When adult, the animals were subjected to a number of behavioural tests (e.g. emergence from an enclosed area, activity patterns in an open space and taking a novel food). Those who had not experienced play were found to be slower to habituate activity in an open space, and slower to reverse the learning of a previously learnt task, than those who had played. This difference was interpreted as indicating a difference in behavioural flexibility, but the tests were so far removed from the real-life problems which rats might encounter that the advantages of these skills were not immediately obvious. Similar studies, following rats from different rearing conditions into seminatural environments (c.f. Calhoun 1962) and observing their behaviour should provide information which was more easily interpreted in terms of individual success.

In the study on cats (Caro 1979,1980), individuals were observed as kittens and later as adults, and correlations were examined between aspects of object play and predatory behaviour, and between kittens' predatory behaviour patterns and their predatory success as adults. It was found that adult predatory success correlated highly with the frequency of predatory patterns that animals had shown as kittens in the presence of live mice, while only three object play behaviours were significantly correlated with predation. The fact that some play behaviours correlated in frequency with some predatory behaviours suggests that a limited relationship does exist which might be examined further by the use of similar techniques combined with manipulations of the amount of play occurring.

These methods could also be extended to other behaviours and other species to provide information on the adult correlates of play.

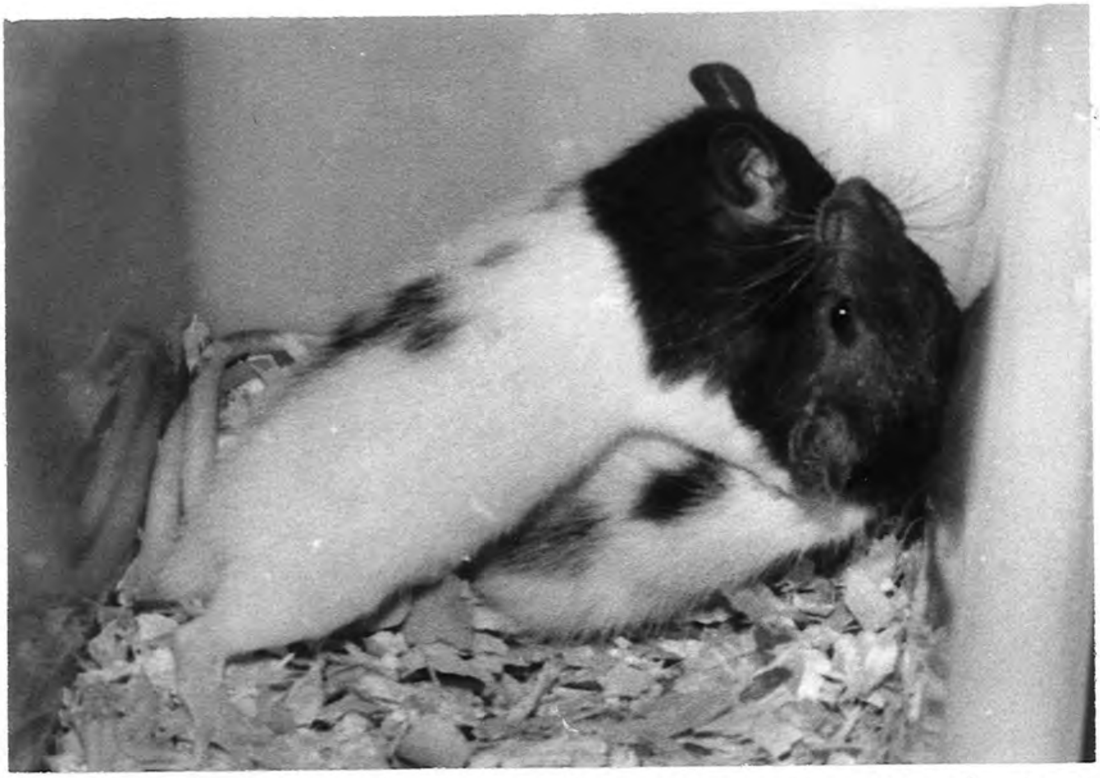
The contribution which the work described here provides may thus be seen as a few answers to questions concerning the nature of play, and a lot of questions with a basis of information from which to attempt to answer them.

APPENDIX A

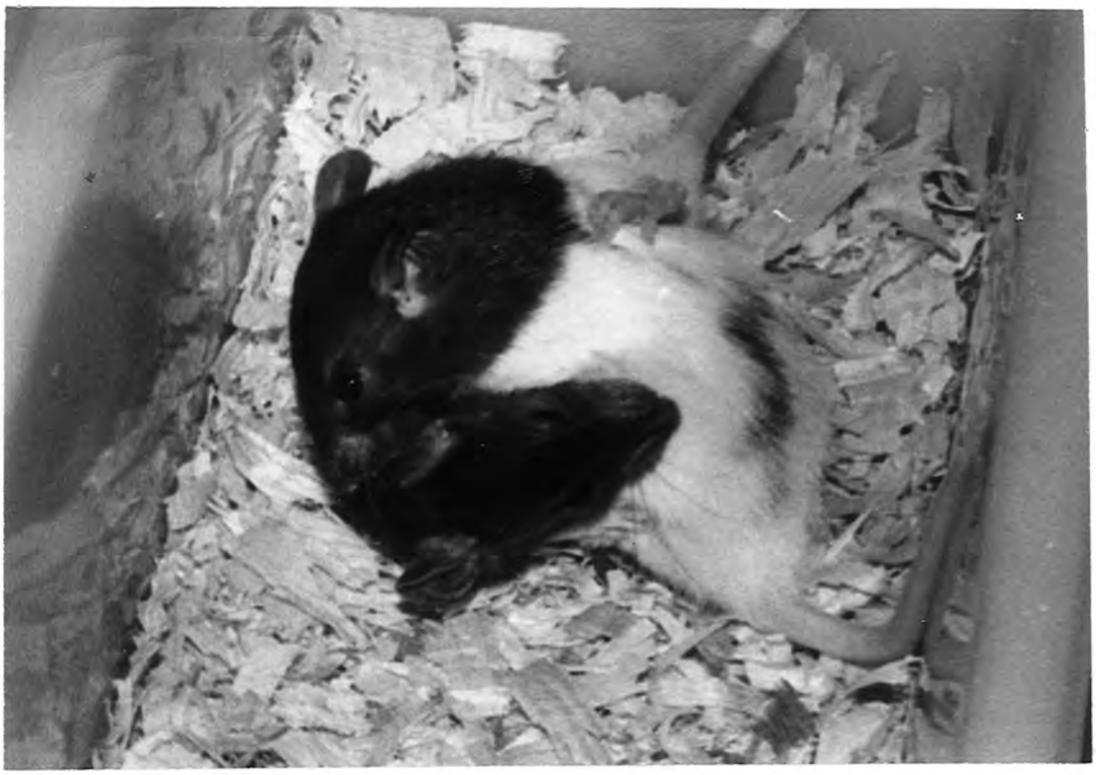
PHOTOGRAPHS OF PLAY

The photographs included below illustrate some of the postures adopted in play by 25 day old hooded rats (A1 - 3) and approximately 3 month old ferrets (A4 - 7). Because play is dynamic in nature, its most striking feature being the rapidity of movement involved, still photographs can only convey a limited amount of information, but they nevertheless serve to show the types of position which animals may take up in the course of play, and the types of "assault" they are liable to launch on playmates.

Rats



A1. Paws-on: one rat places its paws on the other's back. Play is frequently initiated with this gesture (see 3.3).



A2. Wrestle: two wrestling rats are typically in ventro-ventral contact at right angles to each other, the underneath animal being in the otherwise atypical position of lying on its back.

A3. Wrestle: the underneath animal rights itself without giving signs of submission, and with no apparent opposition from its partner.

Ferrets

A4. Chasing: both animals run fast, often with occasional high bounding strides. The chaser here shows a playface.

A5. Mutual tail-chasing: a form of chasing in which the circle has become so small that both animals are simultaneously chaser and chased. Each is playbiting the other´s tail.

A6. Wrestling: being longer and more flexible than rats, ferrets can adopt a wider variety of wrestling postures

A7. Play neck-bite: this seemingly aggressive act affords the biter no subsequent advantage in conflicts, causes the recipient no apparent distress and leaves no wound.

APPENDIX B

DESCRIPTION OF BEHAVIOUR CATEGORIES USED IN ANALYSES

1. Categories listed in Table 3.1 and used for detailed analysis in 2.2 and 3.3.

Approach-fast: fast movement towards another individual.
Flee-fast: fast movement away from another individual.
Wrestle-top, Wrestle-under: Wrestling dyad characteristically consists of one animal engaging in each of these behaviours. The pair cling ventro-ventrally, ´Top´ individual ventral side down and at right-angles to ´Under´ who has dorsal side down, though this behaviour involves much movement, struggling and position-changing.
Paws-on: One individual places its forepaws on its partner´s back or head.
Sniff: One individual touches its partner´s head or body (except the anogenital region) with its nose.
Groom: One individual picks through its partner´s fur with mouth and/or paws.
Passive contact: Two animals´ bodies are in contact at any point other than nose or paws.
Sexual advance: One individual sniffs partner´s anogenital region, or mounts.
Eat/drink: Self-explanatory.
Other: Any behaviour not included above.

For the general behavioural analyses in 3.1 and 3.2, play included Wrestle and Fast locomotion, and Paws-on provided it received a playful response in the form of one of these behaviours.

An animal was considered to be asleep if it was lying still in any position with its eyes shut.

APPENDIX C

BEHAVIOUR SEQUENCE PAIRS (3.3)

Behaviour sequence scores for individual animals in the age-ranges 21 - 39 days and 40 - 56 days are given in the preceding/following matrices below. Each cell represents a specific sequence pair for which the preceding behaviour is indicated by the column and the following behaviour by the row.

Key to behaviour abbreviations:

FL	Fast locomotion
SL	Slow locomotion
P-O	Paws-on
WRS	Wrestle
SNF	Sniff
AMI	Amicable
SOL	Solitary

	21 - 39 days						40 - 56 days					

Individual A

	FL	SL	P-O	WRS	SNF	AMI	FL	SL	P-O	WRS	SNF	AMI
FL	13	6	6	7	3	2	3	1	3	2	1	2
SL	0	1	2	5	2	6	1	1	4	2	0	6
P-O	8	2	0	0	9	1	7	3	3	2	2	2
WRS	5	0	12	19	0	0	2	0	11	4	0	0
SNF	1	3	0	0	3	3	1	0	0	0	2	0
AMI	2	2	3	1	5	0	0	1	3	6	2	3
SOL	6	4	2	2	4	1	3	8	3	0	10	2

Individual B

	FL	SL	P-O	WRS	SNF	AMI	FL	SL	P-O	WRS	SNF	AMI
FL	14	1	6	10	2	2	1	0	1	0	1	3
SL	0	1	3	5	3	0	1	2	5	1	7	2
P-O	11	2	6	1	3	3	0	1	4	0	3	1
WRS	4	0	18	11	0	0	0	0	1	2	1	0
SNF	1	2	1	0	5	4	3	4	1	0	0	0
AMI	1	0	1	3	0	2	4	6	2	0	1	0
SOL	6	9	7	0	11	2	1	3	2	1	6	3

Individual C

	FL	SL	P-O	WRS	SNF	AMI	FL	SL	P-O	WRS	SNF	AMI
FL	16	4	7	20	5	2	1	2	5	6	1	6
SL	4	1	1	6	1	5	1	1	0	4	1	2
P-O	11	1	9	2	5	2	4	0	3	3	5	3
WRS	5	3	22	9	0	1	4	0	9	5	1	2
SNF	2	3	0	0	4	2	0	2	1	0	1	2
AMI	6	2	2	2	3	4	2	1	4	6	5	6
SOL	7	10	4	1	9	2	5	4	6	1	9	4

Individual D

	FL	SL	P-O	WRS	SNF	AMI	FL	SL	P-O	WRS	SNF	AMI
FL	4	1	7	8	1	0	1	4	7	0	1	0
SL	1	3	4	8	7	6	1	2	6	3	2	6
P-O	11	6	6	1	2	0	2	1	0	0	1	1
WRS	4	1	27	32	0	1	2	0	5	1	0	0
SNF	1	1	1	1	1	1	1	2	0	0	1	2
AMI	1	2	4	4	0	3	1	3	3	0	1	2
SOL	4	8	8	1	10	1	6	9	4	10	1	0

21 - 39 days 40 - 56 days

Individual E

	FL	SL	P-O	WRS	SNF	AMI	FL	SL	P-O	WRS	SNF	AMI
FL	6	1	6	4	3	0	2	0	4	3	3	3
SL	0	2	3	1	9	4	0	4	1	1	3	5
P-O	8	3	0	1	4	1	1	0	1	2	3	1
WRS	0	0	15	8	0	2	0	0	5	3	0	1
SNF	0	3	1	0	8	2	0	3	1	0	1	1
AMI	0	1	4	3	7	8	3	1	3	5	1	5
SOL	6	12	2	1	11	4	2	7	1	0	1	2

Individual F

	FL	SL	P-O	WRS	SNF	AMI	FL	SL	P-O	WRS	SNF	AMI
FL	2	1	2	2	1	0	0	0	2	0	1	2
SL	1	0	2	1	9	3	2	0	5	0	0	5
P-O	3	3	3	0	7	0	1	1	2	1	0	0
WRS	2	0	13	7	2	2	0	0	1	0	0	0
SNF	0	3	0	2	9	0	2	2	1	0	2	2
AMI	1	1	3	3	2	2	1	0	1	0	4	1
SOL	4	6	7	3	9	4	2	12	1	0	11	0

Individual G

	FL	SL	P-O	WRS	SNF	AMI	FL	SL	P-O	WRS	SNF	AMI
FL	3	3	7	6	2	1	1	1	7	5	2	2
SL	1	1	0	3	8	1	2	0	6	1	2	2
P-O	5	3	0	1	2	1	7	0	7	0	2	3
WRS	0	3	8	3	1	0	0	0	8	1	0	0
SNF	1	1	2	0	2	0	1	3	9	0	1	1
AMI	0	1	0	0	2	6	0	0	1	2	3	1
SOL	6	7	1	0	3	0	3	6	2	0	8	3

Individual H

	FL	SL	P-O	WRS	SNF	AMI	FL	SL	P-O	WRS	SNF	AMI
FL	12	3	6	5	3	2	7	0	5	3	1	1
SL	0	2	3	4	5	2	1	0	6	2	4	1
P-O	4	1	2	1	5	1	3	1	2	2	2	2
WRS	1	0	15	5	4	1	0	0	4	0	0	1
SNF	1	3	2	0	2	2	3	2	1	0	5	2
AMI	2	0	5	1	2	2	0	2	2	0	1	1
SOL	4	9	6	4	7	2	7	6	4	0	5	4

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