INDIVIDUAL DIFFERENCES IN THE MOTHER-KITTEN

RELATIONSHIP IN THE DOMESTIC CAT *(Felis catus)*

by

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ABSTRACT

Anecdotal reports from other studies and previous observations by the author suggest that there are individual differences in the mother-kitten relationship in the domestic cat. This study set out to provide more substantial evidence for the existence of such individual differences, to describe the nature of these differences, and to develop ways of classifying types of mother-kitten relationship.

The basic features of maternal behaviour in the domestic cat are described, and comparisons made with other mammals, in particular carnivores. The literature on individual differences in mother-infant relations (which mainly concerns primate species) is reviewed.

Seventeen multiparous mothers, and their litters of 2, 3 or 4 kittens, were studied from birth to 6 weeks. Families were housed and observed in individual cages. Two types of behavioural data were collected: quantitative data on defined maternal and litter measures, and qualitative data on the observer's subjective impressions of each family (recorded in diary form).

The qualitative data were used to describe differences between mother-kitten relationships in individual families. On the basis of these differences mothers could be classified into various groups.

Using the quantitative data, statistical evidence is presented, from analyses of variance, which demonstrates that mothers differ significantly, and generally consistently, from one another, on a large number of maternal measures. Litters also differ significantly, and generally consistently, but on fewer measures. Litter size, sex ratio, and kitten death make minimal contributions to the above differences. Regression analysis and

factor analysis were among the statistical techniques used to describe the nature of the individual differences between mothers.

The two main differences found between families can be expressed in terms of the quality of care that mothers exhibit in weeks 1-3, and in the timing of weaning. It is argued that factors which may make major contributions to these types of differences include the nutritional state and milk yield of the mother, and her personality.

ACKNOWLEDGMENTS

CONTENTS

CHAPTER 1   MOTHER-INFANT RELATIONS IN THE DOMESTIC CAT (*Felis catus*)
AND THE STUDY OF INDIVIDUAL DIFFERENCES IN MOTHER-INFANT
RELATIONS

1.1 BACKGROUND AND AIMS

Individual differences in mother-infant relations have been the
subject of intense study in humans, and the research can perhaps be
thought of as falling into two broad categories: the work which has
concentrated on investigating disrupted mother-infant relationships,
such as when the mother and child have been separated for a time
(Bowlby, 1969; Clarke and Clarke, 1976), and work which has been
more concerned with understanding the variation that exists within
the range of 'normal' mother-infant relations (Escalona, 1968;
Ainsworth and Bell, 1969; Richards and Bernal, 1972; Ainsworth,
1979).   Both types of work however have often shared a common
interest in the effects that early differences in the mother-infant
relationship might have on the later development of the child (see
Hinde, 1974, and Dunn, 1976, for reviews).

Extensive research into the effects of early disruption of the
mother-infant bond, through temporary separation of infants from
mothers, has also been conducted on non-human primates (Hinde and
Spencer-Booth, 1971b) and some comparable work has been reported on
other mammalian species, eg cats (Guyot, Bennett and Cross, 1980).
However there are very few studies which provide quantitative
evidence on the extent and nature of 'naturally occurring' (ie not
created by experimental manipulation) individual differences in
mother-young relations in non-human species.   Although this lack has
been diminished considerably in recent years by a number of detailed
studies on baboons (Altmann, 1980) and rhesus monkeys (Hinde and

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Spencer-Booth, 1971a; Hinde and Simpson, 1975; Stevenson-Hinde, Stillwell-Barnes and Zunz, 1980), there is still very little quantitative information available on species of other mammalian orders.

The scope and depth of the research into individual differences in the normal human mother-infant relationship is vast when compared with the work on non-human primates since the latter is still in its very early stages, but similar issues are being tackled in both types of study, eg methods of describing the differences, the stability or consistency of the differences over the course of the relationship (Hinde and Spencer-Booth, 1971a; Dunn, 1975; Waters, 1978) and the consistency of mothers in their styles of mothering with different infants (Altmann, 1980), the variables which may be responsible for the differences, and the effects of the differences on infant development.   The non-primate research has tended to concentrate on describing the nature of the individual differences and investigating causal factors (Hinde and Spencer-Booth, 1971a) because the studies have been short-term rather than long-term. However, in her work on baboons, Altmann (1980) has applied herself to the problems concerning both the short and long-term effects on infants' social development of different types of mother-infant relationship.

The aim of the present study was to investigate individual differences in the mother-infant relationship in a non-primate species, the domestic cat *Felis catus*.   The cat is particularly suitable for a study of this nature both because the individuality in behaviour of members of the species is well known, and because much is already understood about the maternal behaviour of the species (Ewer, 1959; Rosenblatt, Turkewitz and Schneirla, 1961; Schneirla, Rosenblatt and Tobach, 1963; Rosenblatt, 1972; Haskins, 1975, 1977; Moelk,

1979). Although there is some evidence that individual differences in mother-kitten relations do exist in the cat (Schneirla *et al* 1963 and personal observations (see below)), no quantitative evidence has been collected. The first step in the present study was, therefore, to provide quantitative evidence for individual differences in the mother-kitten relationship; then to find ways of describing the differences if they did indeed exist; and finally it was hoped that a method for classifying different types of mother-kitten relationship might be developed.

It was during a study on social play in kittens from 5-15 weeks of age (Lawrence, in preparation) that individual differences in the mother-kitten relationship were first brought to the author's attention. It was observed that individual mothers behaved very differently towards their kittens when the latter were at a comparable age. In particular, mothers responded differently to playful approaches from their kittens. At one extreme there were mothers who tolerated their kittens' pawing and biting and sometimes responded by licking their kittens or even playing with them; at the other extreme were mothers who responded by leaving immediately or showing aggression; and in between were mothers who merely ignored their kittens.

The observations described above pointed to two possibilities for further work. (1) A more systematic and quantitative study of animals of the same age, or (2) a quantitative study of mother-kitten relations at an earlier stage in kitten development. The latter was chosen because it was felt that it would lead to a clearer understanding of the nature of individual differences in the mother-kitten relationship, not least because more fundamental aspects of maternal care would be examined.

Summary of aims

    1 To provide evidence for the existence of individual dif-
ferences in the mother-kitten relationship in the dom-
estic cat.

    2 To describe the nature of these differences.

    3 To develop a method for classifying types of mother-
kitten relationship.

In order that the results from this study should be seen in
proper perspective, the basic characteristics of the mother-kitten
relationship in the domestic cat are detailed (1.2 to 1.4). A
comparative approach is taken, with information from studies of other
mammalian species, and in particular carnivores, being used to help
illuminate many features of domestic cat maternal behaviour. As
further background information for the present study, in the sub-
sequent sections (1.5 to 1.7), a review is given of some of the
approaches taken, and findings made, in studies of individual dif-
ferences in mother-infant relations. As already explained, most of
the work, at least concerning naturally occurring individual dif-
ferences, has been on primate species.

1.2 PATTERNS OF MATERNAL CARE IN MAMMALS

1.2.1 <u>General Introduction</u>

Patterns of maternal care in mammals vary extensively from
species to species and range from only slight and brief care before
the young become independent, to intensive care and the development
of a complex social relationship between mother and offspring which
endures beyond weaning. The position of the cat in this range is
considered by describing the general characteristics of maternal
care in this species and comparing them with those of other

mammalian species.

Many factors contribute to the variability in patterns of maternal care that exists between species. One of these is the relative maturity of the young at birth: species typical maternal behaviour in the early weeks *post partum* tends to reflect the needs and abilities of the offspring. Walser (1977) described 4 stages of development at which the young of different species can be born: premature (as in marsupials and monotremes), altricial (as the naked and blind young of rabbits and mice), semi-altricial (where the young have hair and sometimes vision at birth, as in many carnivore and primate species), and precocial (where the young are well developed and can move around on their own, as in most ungulates and hystricomorph rodents). The cat is a semi-altricial species. In 1.2.2 various aspects of its maternal behaviour are described and compared with other semi-altricial and altricial species. In 1.2.3 a general comparision is made with precocial species. Premature species are not discussed further.

1.2.2 Maternal care in altricial and semi-altricial species
       including the domestic cat

1   Nesting behaviour

Nest building

Most altricial and semi-altricial species keep their young in a nest or den. The rabbit (Ross, Sawin, Zarrow and Denenberg, 1963), rat (Rosenblatt and Lehrman, 1963) and deer mouse (King, 1963) all build nests, and the semi-altricial coyote (Bekoff and Wells, 1980) and wolf keep their young in dens. The domestic cat does not build a nest as such. When living in close association with man, the female often chooses a dark sheltered corner of the house in

which to give birth and thus creates a nest-site.   Laboratory cats
who were given paper sacking on which to litter down sometimes tore
up the sacks and crawled inside them with their kittens (personal
observation).   Cats living on a farm choose a nest-site amongst
straw bales in a barn (MacDonald and Apps, 1978).   In free-ranging
cats living in a rural farming area on the island of North Uist,
Scotland, den sites for the young were usurped rabbit holes
(Corbett, 1979).   Feral cats living on the uninhabited Monach
Islands, Scotland, also used old rabbit holes or sometimes dense
clumps of tall marram grass through which they made passages
(Corbett, 1979).   Wild cats (*Felis sylvestris*), in France use no
nesting material and have their litters above ground (Conde and
Schauenberg, 1974).   Lionesses keep their cubs hidden in thickets,
and cheetah give birth to their young in areas overgrown with shrubs
and in tall grasses (Schaller, 1972).   From the evidence, it
appears that *Felis catus* and other members of the *Felidae* tend to
make use of natural, or at least available, cover for protection of
the young and do not build nests or dig out dens.   For convenience,
however, the place where the young are kept is referred to as the
'nest-site' in the text that follows.   The need for a proper nest,
of course, is greater in altricial species where the young are naked.

Function of the nest-site

Altricial and semi-altricial species which keep their young at
a nest-site tend also to give birth to litters of more than one or
two infants.   The nest-site or den therefore provides a way of
keeping the young together while the mother leaves them to find food.
The young of some species have also been found to have at least two
behavioural adaptations which result in their remaining at the

nest-site while their mother is absent.   When alone, young tend to
huddle together - such behaviour also serves the function of keeping
the infants warm where thermoregulation has not yet developed.
They also have an ability to orientate to the home site from an early
age and so are unlikely to stray far from it.   Home orientation has
been investigated in detail in the kitten (Freeman and Rosenblatt,
1978a,b), in hamster pups (Devor and Schneider, 1974) and in rat pups
(Gregory and Pfaff, 1971).   In some species the father or other
members of the social group stay with the young while their mother
goes away to forage, or they may bring food to her at the nest-site.
However such behaviour is discussed fully when the relationship
between maternal behaviour and social organisation is considered.

Retrieval of the young

Retrieval of young which have strayed from the nest-site is
common.   Noirot (1969) believed that mouse pups make specific
ultrasonic calls which elicit retrieval in the adult.   Leyhausen
(1979) explained that in the domestic cat the sight of a kitten out-
side the nest-site does not cause the mother to retrieve it - she
only does so when the kitten cries.

Nest-site shifting

In felids the nest-site is sometimes changed a few days or weeks
after parturition and this may occur several times.   The mother
carries her infants one at a time to a new site, until all have been
retrieved.   Such behaviour has been recorded in the lion (Schaller,
1972) and in the cheetah (Adamson, 1969).   Leyhausen (1979)
believed that shifting of nest-sites may help to protect the young
from discovery by predators.   Corbett (1979), who observed

nest-site shifting in feral domestic cats, gave the one possible explanation for this behaviour as being a response to the accumulation of food remains and faeces at the den. This does not disagree with Leyhausen's idea since presumably the food and faeces could attract predators. Nest-site moving has also been observed in other carnivores including golden jackals (van Lawick-Goodall and van Lawick, 1970) and African hunting dogs (Kühme, 1965).

Nest-site attendance

The frequency and duration of visits to the nest-site varies and in some species, such as small mice, voles and rats, the mother remains with the young for long periods. In contrast, the rabbit mother spends most of her time away from the nest-site and only visits the young once every 24 hours (Zarrow, Denenberg and Anderson, 1965). In his observations of free-ranging domestic cats Corbett (1979) found that the one mother, whose behaviour he studied in detail, averaged three hunting bouts per day. In between hunting the mother stayed with her young and suckled, played and rested with or near them. The feral cat mothers that he watched rested with their kittens for most of the day and night, and hunted at dusk and dawn. In the laboratory, domestic cat mothers also spend long periods of time with their young in the first few weeks, only leaving them for brief periods to feed (personal observations). Indeed it has been reported by Baerends-van Roon and Baerends (1979) that their free-living cat mothers (who lived at the author's home but could wander freely in the surrounding countryside) stayed with their young continuously for the first two days after parturition and did not eat, drink, urinate or defaecate during this time.

2   Patterns of nursing and milk let-down

Nursing positions

To nurse the young the female takes up a body position which
seems to facilitate the infants location of, and attachment to, the
nipples. In many species, including the cat, dog, and rabbit, the
female lies down, but in mice and often in rats, she crouches over
the pups, and in hares the female sits on her haunches. As well as
taking up a nursing position the mother may rouse her young for a
suckling session by licking them as does the cat (Schneirla,
Rosenblatt and Tobach, 1963) or by picking them up and licking them
as does the rat (Rosenblatt and Lehrman, 1963). The cat female can
also help her kittens to find the nipples by making slight shifting
movements of her body.

Nipple preferences

Ewer (1959, 1961) found that in the domestic cat, kittens
develop teat preferences, and hence a teat order, a few days after
birth. More recently it has been established that the young of two
other carnivores, the snow leopard (McVittie, 1978) and the mountain
lion (Pfeifer, 1980) also exhibit teat preferences. Ewer (1959)
believed that teat orders reduced the likelihood of the young
fighting over nipples and thus increased the probability of indi-
vidual survival to weaning age. Pfeifer (1980) agreed with Ewer,
and further suggested that reduced fighting would mean that the
young could be nursed with minimal disturbance to their mother, who,
as the kittens grow older, becomes increasingly intolerant of their
presence. Hence she may allow them to suck for longer (ie until
they are older) than she would if they did fight. Nipple orders
have also been reported for at least one rodent species, the green

Acouchi (Kleiman, 1972).

Sucking behaviour and milk let-down

The behaviour patterns that the young display once they have
attached to a nipple, have been described for a variety of species.
Ewer (1973), in a review of the carnivore literature, established
that in many felids, including the domestic cat, and in some members
of other families, for example the red fox, the badger and the
European otter, the young tread the mother's ventrum with their
forepaws as they suck. In some other species, including the domestic
dog, the infant's snout pushes against the mother's ventrum while its
front paws are positioned on either side of a teat. Ewer suggested
that these behaviour patterns serve the function of stimulating milk
flow and although this seems a plausible explanation there is no
direct evidence as yet. Two studies where the relationship between
sucking behaviour and patterns of milk let-down have been investi-
gated in detail are McVittie's (1978) study of snow leopard cubs and
the study by Drewett, Statham and Wakerley (1974) of rats. Only the
latter however provided direct evidence. McVittie (1978) described
two distinct nursing patterns that occurred after attachment to the
nipples in snow leopard cubs. The first pattern begins with the
cubs showing a general restlessness followed by movements of the jaw
which she called 'jaw-sucking'. Jaw-sucking lasts for some time and
then the second type of behaviour is seen. It is characterised by
a rhythmic back and forth motion of both ears and is called 'ear-
wiggling'. McVittie believed that it is during the ear-wiggling
stage that cubs are consuming milk, for several reasons.

1   Jaw-sucking can last for periods of up to 37 minutes whereas
     ear-wiggling never lasts longer than 52 seconds.

2   Jaw-sucking always lasts for at least 3 minutes when followed by ear-wiggling.

3   Competition for nipples only occurs during the jaw-sucking period.

4   If a nursing session is terminated after jaw-sucking the cubs continue to be restless but when it terminates after an ear-wiggling phase the cubs invariably fall asleep.

If McVittie was correct in thinking that ear-wiggling characterises nutritive sucking and jaw-sucking non-nutritive sucking then jaw-sucking could be providing the stimulus for milk ejection.

Before discussing the results of Drewett *et al* (1974) the workings of the mammary gland and the basic mechanism of milk ejection are discussed briefly.   Although, as Cross (1977) explained, there is considerable variation both in the gross structure of the mammary gland, and in suckling habits, across the mammals, the production and release of milk is much the same for all members of this class.   Milk is produced in the alveoli of the mammary gland.   In most species about 75 per cent of milk is stored in the alveolar lumina and is called 'alveolar milk', the rest, known as 'sinus milk', lies in the collecting ducts, or sinuses, and cisterns.   Young can obtain sinus and cistern milk without the active process of milk ejection occurring, however alveolar milk only becomes available after alveolar contraction.   The alveoli are invested in myoepithelial cells.   It is believed that sucking causes excitation of the neurohypophysis which results in it releasing oxytocin into the bloodstream.   On reaching the mammary capillaries oxytocin evokes contraction of the myoepithelial cells and as the alveoli contract, milk is expelled from the lumina into the collecting ducts.   However, as illustrated below, the way in which

sucking induces the release of oxytocin does not seem to be the same in all species.

In rats, Drewett *et al* (1974) described several patterns of behaviour that pups exhibit when sucking. Through the use of anaesthetised mothers and injections of oxytocin into the bloodstream, it was possible for them to relate the pups activities to the event of milk ejection. At first the pups were quiet on the nipples, then at the time that the oxytocin would be having its effect on the myoepithelium of the alveoli, the pups began to show treading movements - shifting their weight from one foot to another and pushing against the glands; the next phase, which lasted for 5 seconds, was characterised by the pups stretching their bodies rigidly; and finally the pups became quiet again. It was thought that treading was triggered by the contraction of the mammary gland and that stretching occurred when the pups began to consume milk. A number of experiments were run to test these suppositions and it was found that indeed treading was a response to milk ejection and occurred regardless of whether the pups received any milk subsequently. The treading movements of rat pups are similar to those, described earlier, in carnivore species when they are sucking. However, in the latter, treading is thought to be a stimulus to milk ejection rather than a response to it (Ewer, 1973).

The frequency and duration of nursing bouts in different species are reflected in their patterns of attendance at the nest-site, so, as might be expected, the rat and the rabbit contrast sharply in their nursing habits. As mentioned earlier, rabbits only visit their young once a day. When they do so they nurse them for about 3 minutes. Cross (1977) explained that the milk ejection reflex in the rabbit is powerfully developed. About 85 per cent of

the milk yield in a nursing session is alveolar milk which the pups only have access to after they have stimulated the release of oxytocin by vigorous massaging and sucking of the teats. After about 1 minute of such activity the next 2 minutes are spent gulping milk. In the rabbit then, oxytocin is released in a single pulse, apparently in direct response to the pups' behaviour. The situation is quite different in the rat. The mother stays with her young for long periods and nurses them for up to 15 hours each day (Wakerley and Lincoln, 1971). Wakerley and Drewett (1975) explained that throughout nursing oxytocin is released and milk ejection occurs at intervals of 5-10 minutes. It appears that although the pups have to be sucking their mother for milk ejection to occur, the release of oxytocin is spontaneous and is not a specific response to changes in the pups' behaviour. The methods of milk let-down then in the rabbit and rat are both related to their respective nursing patterns and nest attendance habits.

Unfortunately the physiology of milk removal has not been investigated in the cat so how it might function can only be speculated upon. Since the cat is not like the rabbit, who only visits her young once a day, it seems improbable that there would be a single pulse of oxytocin per nursing session. The cat spends long periods with her young in the early weeks and in this respect is similar to the rat. Hence it is possible that, like the latter, there are multiple ejections of milk during a suckling bout. Treading in kittens has been proposed as a stimulus for oxytocin release and milk let-down (Ewer, 1973) and if this is the case, then the cat differs from the rat where oxytocin release occurs independently of such an obvious behavioural stimulus from the pups.

3   Species without nest-sites

So far the cat has only been compared to altricial and semi-altricial species which keep their young at a nest-site.   However in many primate species the infant spends much of its time, in the early weeks after birth, with its mother, either being carried by her or clinging to her.   It is thus afforded constant protection and potentially free access to her nipples.   It is easy to see how the primate mother's tasks differ from those mothers whose offspring live at a nest-site.

Different again, is the caretaking rôle of mothers in precocial species, and some of the features of the mother-infant relationship in these animals are now described for the purposes of comparison with the cat and other semi-altricial and altricial species.

1.2.3 Maternal care in precocial species

1   Protection of the young

To some extent it seems that mothers of precocial young have a less critical rôle in their infants' survival.   Although the pig is an exception, in most ungulates the young do not have the safe harbour of a cryptic nest which their mother has prepared.   Instead they tend to have one of two strategies for self-protection: they either follow their mothers as do young sheep, caribou, wildebeest and chamois, and are called 'followers', or they remain hidden while their mother feeds as in gazelles, most cervids, and many antelopes, and are called 'hiders' (Lent, 1974).   Mothers of hider species usually do not approach their infants in their hiding places but wait at some distance for them to come out.   In follower species the mother and young have more frequent contact with one another. As mentioned above, members of the *Suidae* family build nests for

their young. Piglets need a nest for warmth in their first few days (Walser, 1977) but it probably also serves the function of keeping the large litters, that for example equids, ovids and bovids do not have to cope with, together and camouflaged. Hystricomorph rodents also have large litters of precocial young. Infant guinea pigs begin to follow their mother within a week and later they follow their siblings and other adults (King, 1956). This contact keeping behaviour must be comparable to following in ungulates.

2 Patterns of nursing and milk let-down

Nursing positions

In most ungulates the female nurses her offspring while standing up so that bodies are in reverse parallel and at an acute angle (Lent, 1974) but in some species the mother does lie down, eg the roe deer, and members of the *Tapiridae* and *Hippopotamidae* families. Pigs also nurse their young lying down and piglets have a teat order (McBride, 1963; Fraser, 1973; Hemsworth, Winfield and Mullaney, 1976).

Sucking behaviour and milk let-down

There is considerable variation in patterns of nursing and milk let-down in the ungulates and the pig (which is a monogastric species) and the cow (a ruminant) represent two extremes. Blaxter (1961) reported that in sows the nursing frequency is once every 50-60 minutes throughout the day and that cows under pasture grazing conditions nurse their calves three times daily for 15 minutes each session. When piglets suck they only obtain milk if milk ejection occurs (Cross, 1977) because the ratio of alveolar to sinus milk in this species is very high. A single pulse of oxytocin is released

in response to the whole litter sucking and massaging the teats
(especially the anterior pair) and the milk ejection phase lasts
about 15 seconds.   The piglets then drink all the available milk.
In cows, and even more so in goats, the ratio of alveolar to sinus
milk is low and the milk ejection process is not a prerequisite for
milk removal by the young.   The release of oxytocin does not always
seem to be associated with sucking but when it is released it causes
milk to be transferred from the lumina of the alveoli into the
cistern.   The cistern has a large capacity in the cow and the calf
can withdraw milk from it by the pumping action of its sucking.

   Descriptions of the nursing and milk ejection patterns of the
pig and the cow suggest that the cat is probably similar to neither
and that the best model to compare the cat with is still the rat.

1.3   THE RELATIONSHIP BETWEEN PATTERNS OF MATERNAL CARE AND SOCIAL
ORGANISATION IN MAMMALS AND IN PARTICULAR THE ORDER CARNIVORA

1.3.1 General Introduction

   The basic tasks that a mammalian mother has to fulfil in the
early stages of her infants' lives have been described but so far it
has not been considered that, in some species, the mother is not the
sole caretaker.   While in solitary species a female has to rear the
young on her own, in group living species she may have help from other
group members.   The relationship between the care of the young in a
species and its social organisation, are now discussed.

   Wilson (1975) has summarised what is presently known about the
social systems of the families of living mammals.   He assigned a
grade of sociality to each family, while acknowledging that within
some of them there may be species exhibiting different levels of social
organisation.   In all mammals the basic unit of the society is the

mother and her offspring.   If this is found to be the largest social
grouping of a species then it is considered to be solitary.

The more primitive members of the class Mammalia, including many
of the monotremes, marsupial and insectivore orders, are solitary and
so are many other species which live nocturnally or underground
(Wilson, 1975).   Where the typical social grouping of a species
extends beyond the mother-infant unit, the species is considered to
be social, but as already mentioned, there are various grades of
sociality.   Wilson placed these in the following order (from least
to most complex): unorganised herds or other forms of motion group;
mated pairs; harems, packs, bands and troops; and various com-
binations of some of these.   He pointed out that in general it is
the larger members of each order and those that live above ground
that have the higher grades of social organisation.   Since within
the order Carnivora there is considerable diversity in the social
organisation of species, examples from only this group of mammals
are used to illustrate the relationship between patterns of
offspring caretaking and sociality.

1.3.2 <u>Social organisation and maternal care in the order Carnivora</u>
      <u>excluding the domestic cat</u>

In solitary species the mother alone carries out all the care-
taking duties since her association with her mate endures only for
the period of courtship and mating.   Examples include the weasel,
the otter, brown, black and polar bears, the lynx, the leopard and
the cheetah (Ewer, 1973).   In some carnivore species, eg foxes,
jackals and coyotes, there is a pair bond.   The male stays with
the female when the young are being reared and brings provisions to
them at the den (Kleiman and Eisenberg, 1973).   Hence some of the

parental duties are shared.   MacDonald (1977) has found that in the red fox the male may be associated with a group of females rather than a single mate.   The females of such groups are often mother and daughters, or perhaps sisters, and although only the dominant vixen breeds the others help with rearing her cubs.   In the lion there is an even greater degree of communality in the rearing of young.   It is not uncommon for two or three lionesses to have litters at about the same time and, if they do, for them to become companions who spend a lot of time together and rear their cubs jointly (Schaller, 1972).   They freely suckle each other's young (as indeed will any lactating female in the pride), although they do sometimes favour their own cubs and take them aside or chase other cubs away before nursing.   Caring for the young includes protecting them and a lioness who sees any cub, her own or otherwise, in a potentially dangerous situation, vocalises a warning to it.   In the social canids groups have a number of adults of each sex.   In several species of these pack living animals, members of the group, including the female's mate, help with the rearing of her pups. Kühme (1965) explained that in the African hunting dog females nurse each others' young and even compete to do so.   When the pack goes off to hunt the pups are not left alone, as are lion cubs, but are guarded by several adults.   Females and some of the males take turns at pup-guarding.   After a successful kill the hunters return to the pups and their guards and regurgitate meat for them.   In this species then there is an even greater sharing of parental tasks among group members than in the lion.

1.3.3 Social organisation and maternal care in the domestic cat

Grades of sociality

The domestic cat has traditionally been viewed as a solitary species (Kleiman and Eisenberg, 1973; Wilson, 1975). However a number of recent studies (Laundré, 1977; Dards, 1978; MacDonald and Apps, 1978; Corbett, 1979) have revealed that in certain habitats cats live in social groups whose members include related individuals of several generations and immigrants from neighbouring areas. Fagen (1978) believed that such sociality is a facultative response to changes in the distribution, quantity, quality and reliability of the limiting resources of food and shelter. The domestic cat, having evolved alongside man, who has provided, some-times inadvertently, new and richer habitats for it, has been more flexible in its social organisation than its relative the wild cat (*Felis sylvestris*) which is territorial and solitary (Corbett, 1979). Populations of cats are found around human institutions such as hospitals, dockyards (Dards, 1978), farms (Laundré, 1977; MacDonald and Apps, 1978) and Buddhist temples (Fagen, 1978) to name a few. In most of these places cats are provided with shelter and are regularly fed by humans. More temporary group living has been reported in free-ranging cats in North Uist (Corbett, 1979). Generally speaking it is only in winter when rabbits are scarce and hard to catch that the animals move closer to the crofts, where they survive on scraps of food provided by the inhabitants, and live a more communal existence (Corbett, 1979).

Groups of cats tend to have as their core members several related females, for example sisters and their daughters, and one adult tom who may or may not be related to the females. In large populations such as the one in Portsmouth Dockyard (Dards, 1978)

where 154 individuals were counted, there were a number of such
female groups with between 2 and 9 adult female members in each.
Dards explained that young females born into the groups become group
members whereas young males generally leave after a year or two.
The fate of these emigrants is not always known but some at least
establish a home range and become associated with a female group,
elsewhere. In Laundré's (1977) study group there were three immi-
grant toms and one immigrant female so it is not unknown for females
to leave their natal group.

Social interactions between group members were described in
both Laundré's study (1977) and the study by MacDonald and Apps
(1978). The latter explained that amongst their cats amicable
interactions were far more common than aggressive ones and the only
serious attacks observed were made upon strangers. Although
individuals hunted alone, when they were resting, about half their
time was spent in actual bodily contact with other cats. Laundré
recorded a higher frequency of aggressive interactions between his
animals but these almost all occurred at feeding time when milk was
provided for the 11 cats and they crowded around the single dish.

The feral and free-ranging domestic cats that Corbett (1979)
studied did not live socially except when the latter stayed close to
farms - then groups were comprised of females and one adult tom.

The mother's rôle in rearing the young

In cats which do not live in social groups rearing of the young
is carried out entirely by the mother. Corbett (1979) only once
observed a free-ranging male taking prey to a den but he pointed out
that this food was probably intended for the mother rather than her
young who were not yet eating meat. However, in group living

populations, there is the opportunity for some of the caretaking of the young to be shared, and in domestic cats it seems that other females in the group do give the mother help in looking after her kittens, especially if they have young themselves. A detailed account of such aid giving behaviour is presented by MacDonald and Apps (1978). Two females (sisters) who had litters within 18 days of each other shared the same nest. Both licked and severed the umbilical cords of the kittens in the second litter when they were born and communal nursing was observed with kittens sucking indiscriminately from either mother. The kittens of these females died from cat flu when the younger litter was a week old, but one of the females went on to give help to a third female (her mother) when she had her litter (a single kitten) two weeks later. She not only spent time in the nest grooming the new kitten and its mother but she also brought prey to them which effectively meant the mother did not have to leave her kitten to search for food.

Communal nursing has been observed in the laboratory cats used in this study (personal observation). Although pregnant females are normally placed in individual cages to litter down, they sometimes give birth in their pens (see Chapter 2 for details of housing). On one occasion two females had their litters at the same time and in the same nest box. Since it was not possible to tell which kittens belonged to which cat the mothers were housed in a pen of their own and allowed to rear their litters together (see Plates 1 and 2). Kittens sucked from either female and quite often both mothers would lie together in one nest tray suckling all the kittens. When the kittens were older it was quite common to see just one of the mothers with the young while the other rested alone on a shelf where the kittens could not reach her. Communal rearing has also been

PLATE 1   Communal rearing of the young.   Two mothers
           who reared their young together are seen
           with kittens on-nipple, and still by mother.
           The kittens sucked from either female.

PLATE 2   Communal rearing of the young.   One mother
           stays with the kittens while the other rests
           on the shelf (out of view).   Some of the
           kittens are exploring the room (out of view).
           The mother shown is in the sit position.
           The kittens are still by mother.   Notice the
           litter box bedding of wood shavings.

observed where three mothers littered down at the same time.

To summarise, the care of the young is entirely the job of the mother if she lives alone, but if she is a member of a social group then she may receive help from other females. So far, the relationship between social organisation and rearing of the young has been considered almost entirely from the mother's viewpoint. However, the experiences of the kittens must also be very different, depending on the social environment in which they are reared.

The social environment in which the young are reared

The feral cats that Corbett (1979) studied on the Monach Islands, Scotland, were territorial and solitary. Feral kittens therefore grow up in social groups limited to a mother and litter mates only and in the family that Corbett observed the group broke up when the kittens disappeared at about 7 weeks of age. Unfortunately it was not known whether this is typically the age at which kittens disperse since Corbett felt that his presence may have precipitated the event. Free-ranging cats on North Uist led a less solitary existence (Corbett, 1979). In winter, as already mentioned, they lived around the crofts and farms in numbers of up to 30 cats per dwelling. The rest of the year, when they were independent of human provisioning, they had individual ranges which, unlike those of the feral cats, were overlapping. Females raised some of their litters at crofts but the two families that Corbett observed were born in the field. During their first two months of life the kittens' main source of social contact was their mother. However, she was frequently followed around by a male who often rested near the den so it is possible that the kittens had some interactions with him. When her young were about 8 weeks old the female took them to her croft,

where they too were fed by the inhabitants. Corbett did not report how or when dispersion of the kittens occurred so a comparison with feral cats cannot be made.

In the populations of cats that Laundré (1977), Dards (1978) and MacDonald and Apps (1978) described, adult females tended to live in groups and were often related to one another. MacDonald and Apps observed two females rearing their litters together and, as described earlier, they suckled and groomed each other's young. Although Dards and Laundré did not report communal nursing, the opportunity for it must have existed in the colonies of cats that they studied. A kitten growing up in a society where females raise their young together, or at least near each other, would have social contacts with individuals outside its own family. For example, in the farmyard cats that Laundré studied, Fagen (1978) pointed out that a kitten would have interactions with 'littermates, older full and half siblings, uncles, aunts, cousins, the father and unrelated adult males'. A richer social environment could not be found in the lion pride.

In a society like the one just described, the young do not disperse at weaning as do feral kittens. They remain in the group for some time if they are male and possibly for their whole lives if they are female. Social bonds that are formed during infancy therefore are not broken when the kittens become independent of the female's milk and begin to catch prey for themselves.

1.4 DETAILED STUDIES OF MOTHER-KITTEN INTERACTION

Although general aspects of maternal behaviour in the domestic cat have been discussed and compared to other mammals, the fine details of behavioural interactions between the mother and her kittens

have not yet been described. Several studies have been conducted which do just this (Schneirla, Rosenblatt and Tobach, 1963; Haskins, 1975; Moelk, 1979) and they provide essential background information for the present study.

Schneirla *et al* (1963) identified three developmental stages in the feeding relationship of the female and her young in the 8 weeks after parturition. In the first stage, from birth until the end of the third week, the mother is mainly responsible for initiating feeding sessions. Returning from an excursion outside the nest-site, the mother lies down on her side, arches her body around the kittens, extends her front and rear legs to enclose them, and 'presents' her mammary region to them. The kittens are aroused by thermal and tactile stimuli, the former provided by the close proximity of the mother's body, the latter by her licking and other movements. The kittens make their way towards her ventral surface and, after nuzzling, manage to locate and attach to the nipples. Suckling then commences. Time spent nursing kittens decreases up to the 14th day and then levels off for a while before decreasing again in the 3rd stage.

In the second stage, from about the 20th - 30th days, both mother and kittens initiate feeding. The kittens are now able to walk around and so can actively approach their mother outside the nest-site, when she is resting or eating. The female is accommodating and lies down when the kittens nuzzle her - or, if already lying, shifts her position to expose her mammary region. When the mother initiates a feeding session by presenting to the kittens, they respond quickly and efficiently and are soon attached to the nipples.

In the third stage, which begins around the 30th day, the

mother's rôle in initiating feeding diminishes. In addition she tolerates her kittens on the nipple for shorter periods and actively avoids them where possible. The kittens become opportunistic and approach and nuzzle their mother whenever she is in reach. The behaviour of the female, as well as her presumed lessening supply of milk, contribute to the weaning process during this stage.

The work of Haskins (1975) and Moelk (1979) supports the findings of Schneirla et al (1963) but their approaches were different and each provided more details of certain aspects of the mother-young relationship. Schneirla et al presented information on interactions between mother and kittens and how they change with time. The results from Haskin's study gave information on changes in the mother's behaviour and changes in the kittens' behaviour but quantitative measurements of interactions between the mother and her kittens were not made. The main difference between the two studies was that Schneirla et al were concerned with the dynamics of the relationship between mother and offspring while Haskins' work dealt more with how the mother and kittens spend their time and how this changes during the kittens' development. Moelk's study provided full descriptions of interactions between the mother and her growing kittens and although her data was generally not quantitative, this was compensated for by her attention to detail and her objective interpretation of results.

In all three studies mentioned above individual variation was recorded in some aspects of maternal behaviour but it was not subjected to thorough quantification. Schneirla et al observed that mothers varied across several behavioural measures. They attributed the variability to a number of different factors, although quantitative evidence to support doing so was sometimes lacking.

The factors included parity of mother, litter size, and nervousness of mother.

Parity

Throughout the course of parturition multiparous mothers made fewer gross bodily movements during contraction and emergence, licked their kittens more, and seemed generally to be in a more relaxed state than primiparous mothers.

Litter size

The initial amount of time spent nursing was proportional to the litter size (although it is not clear what the sample of each litter size was). Litter size also affected the females' behaviour between the 30th and 40th days. Observations of mothers with single kittens revealed that they left their kittens less frequently than females with larger litters.

Nervousness

In general, pregnant females were found to use one of the rear corners of their cage as a nest-site but 'nervous, maladjusted' females tended to be more variable in their choice of a place to settle. In addition, wide variation was found between mothers in the time of the first appearance, and frequency in the early days *post partum*, of 'presenting' of the mammary region to the kittens. The possible causes of this variation were not discussed.

In his study Haskins (1975) emphasised how similar mothers were in their behaviour but did draw attention to the variability they showed in their licking rates. However if his Table 3 is examined, it can be seen that there was also considerable variability in

mothers' frequency scores on several behavioural measures including in litter box, lactation position and vocalisation. Variability in the scores of kittens in different litters is also apparent when his Table 4 is examined, eg for the measures suckle or nuzzle, and nuzzle.

Moelk (1979) described marked variability in what she termed 'temperament', amongst kittens and therefore it does not seem unreasonable to expect similar differences to be found in the behaviour of adults.

In summary, although individual variation in maternal behaviour has been observed in cats, quantitative data is lacking on the extent and nature of the differences between individual mothers and their litters.

1.5 THE NATURE OF INDIVIDUAL DIFFERENCES IN MOTHER-INFANT RELATIONS AND METHODS OF DESCRIPTION

One of the challenges in a study of individual differences in maternal (or any other) behaviour is to find an economical way of describing the differences and to avoid making too many inter-individual comparisons. Even in the study of individuality, generalisations are useful. Since no standard method for describing and classifying individual differences in mother-infant relations has been developed, most researchers have devised their own. A selection of the methods of data collection and analysis that have been used are now described along with some of the funda-mental findings of the studies that employed them.

Hinde and Spencer-Booth (1971a) conducted a study aimed at describing the individual differences in mother-infant relations in a captive colony of 31 rhesus monkey mother-infant pairs. Their method of comparing individuals consisted of ranking animals

according to their mean scores on various behavioural measures at
four stages during their development: 4-6 weeks, 7-12 weeks, 13-18
weeks and 19-24 weeks. All the behavioural measures were concerned
with physical contact between the mother and her infant and many of
them indicated who was making or breaking the contact. Examples
include: the time that the infant spent off its mother, the number
of times that the infant was rejected by its mother when it attempted
to make contact, the infant's rôle in maintaining proximity (the per-
centage of approaches made by the infant minus the percentage of
leaves by it). Hinde and Spencer-Booth wanted to find out if the
ranking of individuals in one age period was the same in the next and
so discover if the differences between individuals were stable over
time. To do this they calculated Spearman rank correlation
coefficients between values of various measures at different ages.
Correlations were highly significant in the earlier weeks but less so
when weeks 13-18 were compared with weeks 19-24. However in general
there was overall stability in individual differences. Thus it was
established that the differences between mother-infant pairs at any
one age were not merely a product of random variations or sampling
deficiencies. Since mother-infant pairs differed on a number of
independent variables - sex of infant, parity, and dominance rank of
mother, the authors were able to investigate the contributions of
these factors to the overall individual differences. They duly
found that the variables only accounted for the differences to a
limited extent. Finally they were interested in discovering
whether differences between mothers, infants, or both, were making
the greatest contributions to differences between pairs. Again
correlational methods were used on the individuals' ranked mean
scores. The general finding was that in the early weeks

inter-mother differences accounted for most of the variation but that in the later weeks the infants became an important source of variation.

Hinde and Spencer-Booth's study concentrated on illustrating the quantitative differences between mother-infant relationships. The behavioural measures employed described behavioural acts but not the ways in which they were performed. For example, rejections were scored but there was no distinction made between rough rejections and gentle ones. Hinde and Simpson (1975) however felt that much of the variation in rhesus mother-infant interaction was in fact qualitative in nature, but rather than use subjective measures of maternal behaviour they instead set out to develop means for 'describing, assessing and classifying qualities of relationships' in an objective fashion. One of the ways they did this was to take several measures which were related to one another and that together would refer to a quality, and combine them to create a kind of composite measure. For example, one quality they considered for rhesus monkey mothers was 'maternal warmth'. A variety of maternal measures were thought to contribute to this quality, namely time spent in ventro-ventral contact with the infant, time spent grooming the infant, and time spent with arm around infant (both of these last two while in ventro-ventral contact). By comparing the scores of three mothers on these measures when their infants were between 2 and 10 weeks old it was found that one mother consistently scored highest on all measures while another scored lowest. It was possible therefore to rank all three mothers on maternal warmth.

Hinde and Simpson only used objective methods in their work but other researchers studying the same colony of monkeys (Stevenson-Hinde, Stillwell-Barnes and Zunz, 1980) have since found that

subjective ratings of mothers and infants can contribute considerably to the understanding of individual differences in the interactions of mother-infant pairs.   Mothers and infants (at one year of age) were assessed, using the following method: they were given a score of between 1 and 7 on each of 33 behaviourally defined adjectives, eg aggressive, protective, tense.   Through a principal components analysis of the ratings it was found that 3 main components emerged and these could be characterised by the behavioural traits of confident, excitable and sociable.   Mothers' and infants' scores on the three traits were correlated with certain measures of their social interactions (those between the mother and her infant and those between the infant and other memebrs of the group), eg frequency of close contacts initiated by the mother, the percentage of approaches by the infant to the mother minus the percentage of leaves, and frequency of all contacts initiated by infant to monkeys other than mother while the infant was off mother.   The results are difficult to summarise briefly but some interesting relationships were found between mother and infant ratings and their social behaviour, eg excitable mothers initiated many close contacts with their infants, their daughters were rated as excitable, their infants of both sexes were rated as not confident, and their infants initiated little play or approach with other group members.

Apart from Stevenson-Hinde *et al* (1980), in studies of rhesus monkeys, authors have tended to rank mother-infant pairs on a continuum rather than group them as distinct types.   Altmann (1980) used the opposite approach in her work on free-ranging baboons *(Papio cynocephalus)*.   She split mothers into two groups, according to one aspect of their maternal behaviour, and from then on all her comparisons were made between the two types of mother.   She did,

however, frequently refer to individuals to illustrate her points and this proved to be a very useful way of increasing the reader's understanding. The two types of mother that Altmann described were termed either restrictive or *laissez-faire*. The placement of a female in either group depended on her behaviour towards her infant during its first two months of life. *Laissez-faire* mothers restrained their infants from breaking physical contact far less than did restrictive mothers who tended to prevent their young from going off to explore.

After classifying the mothers, further comparisons were made between the two maternal types and it was found that *laissez-faire* mothers exhibited the following patterns of behaviour when their infants were younger than those of restrictive mothers. (Restrictive mothers showed the same behaviour, only when their infants were older.)

1   Rejecting, ignoring and ceasing to follow their infants.

2   Increasing the distance between themselves and their infants more than decreasing it.

3   Punishing their infants by biting, hitting and pushing them.

Infants of *laissez-faire* mothers reached the various stages leading up to weaning and independence more quickly than infants of restrictive mothers and in addition never experienced the same degree of protection and restriction that the latter did during their first few weeks after birth.

Altmann was interested in the factors which might determine a female's maternal style, and in the effects that maternal style might have on her infant's behaviour, both in the short and long

term.   (Her findings on these topics are discussed in the next two

sections.)   In addition she was concerned with intra- and inter-

generational consistency of maternal style, ie whether females were

consistent in their maternal style with different offspring, and

whether daughters showed the same maternal style as their mothers.

Altmann provided evidence, albeit from a small sample of animals,

for intra-generational consistency.   She also had some rather more

tentative evidence for inter-generational consistency of maternal

style (see page 136, Altmann, 1980).

Finally, it is of interest to compare and contrast some of the

methods used in the non-human primate work discussed above, with

those used in studies of human mother-infant relationships.   In

Ainsworth and Bell's study (1969) of humans, mothers were divided

into types, or groups, which were then subject to further compari-

sons and so in this respect there were similarities with Altmann's

work (1980).   However, in the latter, groups of mothers were dis-

tinguished on the basis of one rather broad aspect of their

relationship with their infants, while in contrast, Ainsworth and

Bell were concerned with more intricate differences between mothers,

and in only one situation - the feeding situation during the

infants' first year.   They identified 9 patterns of mother-infant

interaction during feeding and each mother was considered to show

one of these patterns.   Mothers were assigned one of the 9 patterns

on the basis of how they rated on the following 4 aspects of the

feeding interaction.

1   The timing of feedings

     For example - When did the mother feed her baby, how

     often, and at what intervals?   Did she time the

     feedings in response to the baby's signals?

2   Determination of the amount of food ingested and the
end of feeding.

For example - Was the baby allowed to determine the
amount of food he ingested, and to terminate the
feedings himself?

3   Mother's handling of the baby's preference in kind
of food.

For example - How did the mother handle rejections
of new or disliked foods?

4   Pacing of the rate of the baby's intake.

For example - To what extent did the mother allow
the baby to proceed at his own rate?

Once a particular pattern of feeding had been assigned to each
mother, the next step was to see how these patterns correlated with
other aspects of the mother-infant relationship, namely the baby's
amount and pattern of crying, the mother's attitudes and infant care
practices, and the baby's behaviour in a strange situation
(experimentally induced at one year). Through these correlations
the authors were able to build up a broad and detailed picture of
the individual differences in mother-child relationships.

One interesting difference between human and non-human studies
is that in the former, behavioural measures are sometimes used which
focus on the qualitative aspects of the interactions between the
mother and her infant. Ainsworth (1979) devised measures, for
example, which would describe how tender and careful a mother was in
handling her baby, and how positively or negatively the baby
responded to the mother's return after an absence. As with the other
measures used in the study, she translated these behavioural
categories into frequencies and durations thus. The percentage of

the total 'holding time' in which the mother handled her baby
tenderly and carefully, and the percentage of 'mother-enters-room'
episodes in which the baby greeted her positively. Subjective
assessment was used rather differently here than in the work of
Stevenson-Hinde *et al* (1980) where mothers were rated on the basis
of their general behavioural characteristics and not specifically on
their mothering styles.

1.6 FACTORS WHICH CONTRIBUTE TO INDIVIDUAL DIFFERENCES IN MOTHER-INFANT RELATIONS

1.6.1 General Introduction

In investigating factors which might contribute to the varia-
bility that can be found between mother-infant pairs, one of two
approaches may be taken. The first, used by Hinde and Spencer-Booth
(1971a) and White and Hinde (1975), is to take a group of mothers who
differ on a number of variables, such as parity, social rank, sex of
infant, and try to determine which affect the mother-infant relation-
ship and how they do so. White and Hinde did this by placing
mother-infant pairs in sub-groups which differed on one variable
only, eg primiparous versus multiparous mothers, and comparing their
behaviour. This method does not always provide straightforward
answers, since the effects of different variables tend to interact
with one another and need to be teased apart statistically. The
other method, which has probably produced clearer results, involves
experimental manipulation of the appropriate variables. Groups of
mothers and their young, which are strictly comparable on all but
one parameter, which is varied in a controlled fashion, are examined
for differences in behaviour. For example, Priestnall (1972)
wanted to investigate the effects of litter size on mother-infant

relations in mice, so he set up three groups of multiparous females of the same inbred strain, which had litters of 2, 5 and 8 respectively and looked for differences in their maternal behaviour. In this way he was able to analyse the effects of one variable without the confounding effects of others. Both types of study have contributed to our knowledge of the factors which can influence patterns of mother-infant interaction. Some of these factors are now detailed, along with a selection of the studies which have investigated their effects.

1.6.2 Litter size

Priestnall (1972) found that litter size in mice affects a number of different maternal behaviours. In particular he found that mothers with small litters spend more time in the nest with their young. In rats, small litters also receive more maternal care than large ones (Seitz, 1954). However the relationship between the number of young and the maternal behaviour that a female exhibits is not always an inverse one, for in sheep Ewbank (1967) found that ewes with twins nurse them more frequently than ewes with only one lamb. The effect of litter size on the maternal behaviour of cats were discussed in 1.4.

1.6.3 Sex of infant

White and Hinde (1975) discovered that some aspects of the mother-infant relationship seem to vary according to the sex of the infant in rhesus monkeys. In the early stages, up to week 10, male infants spend more time with their mothers than female infants, but after 30 weeks the opposite trend is found. Jenson, Bobbitt and Gordon (1968) observed the same patterns of behaviour in male infants

of pig-tailed macaques. In baboons however (Altmann,1980) sex of infant does not appear to greatly influence mother-infant relations. No information is available concerning the effect of sex of infants in species where the litter size exceeds one or two.

1.6.4 Parity, age and experience of mother

It is commonly reasoned that multiparous mothers must be more competent than females who are rearing their first infant. Nadler (1975), in his study of captive gorillas, found that most multiparous females showed an improvement in maternal proficiency over their primiparous performance and that on the whole multiparous mothers were more adequate mothers than primiparous females. Jay (1963) found that in langurs, older females who had had many infants were more efficient mothers than very young females but it is not clear whether he knew if these young females were primiparous. A number of studies have failed to reveal significant differences between primiparous and multiparous mothers, eg in rats (Moltz and Robbins, 1965) and rhesus monkeys (Seay, 1966; White and Hinde, 1975). In a way, it is surprising that differences were found in langurs but not in rhesus monkeys because in both of these (and many other primate species) young females are thought to gain some experience in caring for young by observing the mothers in their group and, in the case of langurs, even handling their infants (Hinde, 1974). Most of the females that Nadler (1975) studied had no opportunity for learning from older females when they were young because 80 per cent of them were separated from their mothers soon after birth and were reared with peers or in isolation. Perhaps this explains why he found clear differences between primiparous and multiparous females.

In their study of human mother-child relations Jacobs and Moss

(1976) were concerned with the nature of the social interactions between the mother and infant rather than in rating the competence or efficiency of mothers and they found considerable differences between mothers with their first-born versus their second-born infant. The differences were quantitative rather than qualitative, however, because although the mothers were found to show less social, affectionate and caretaking behaviours with the second child, the patterns of care they exhibited were similar with both children (suggesting that there is consistency in styles of mothering). An interesting finding was that if the second infant was male and/or of the opposite gender to the first, then the change in maternal care was less.

It is difficult to make comparisons between humans and non-human primates because in the latter, when a new infant is born, the mother is generally no longer caring for her previous offspring, whereas in humans the attention that a mother devotes to her young must be divided when a second baby is born and the first one, as in the study by Jacobs and Moss is still very young (under 3 years).

1.6.5 Social rank of mother

In a captive colony of rhesus monkeys low status mothers took more initiative in making ventro-ventral contact with their infants and rejected them less frequently than higher status mothers (White and Hinde, 1975). Somewhat in contrast to these findings, De Vore (1963) observed that in free-ranging baboons (*Papio anubis*) low ranking mothers, perhaps because they were subject to much agression from their dominant counterparts, were more short-tempered and less responsive to their infants. It seems that there is not a simple relationship between rank and maternal behaviour but that it

may vary according to the species and the animals' social and physical environments. Indeed, in another study of free-ranging baboons (*Papio cynocephalus*, a close relative of *P anubis*), Altmann (1980) found that, unlike the baboons in De Vore's study (1963), low ranking mothers were not short-tempered and unresponsive, but were restrictive and kept their infants close to them.

1.6.6 Personality of mother

In studies of non-human primates, personality differences between mothers are sometimes cited as contributing to the variability that is observed in maternal care, eg Jay (1963). Instead of 'personality' the term 'temperament' may be used, eg Altmann (1980, page 134) and in the study by Stevenson-Hinde *et al* (1980) of rhesus monkeys neither term was used - the animals were 'subjectively assessed'. 'Personality' is the term used for purposes of discussion in this thesis and is broadly defined as phenotypic variation in individuals which is reflected in all aspects of their behaviour. The term holds no implication as to whether 'personality' is chiefly determined by genetic or experiential factors.

When attributing individual variation in maternal behaviour to personality differences great care must be taken not to use the style of maternal behaviour itself as evidence for a particular personality type. In the studies whose results are described below it is felt that generally, such circularity in reasoning was avoided. For example, in the study by Stevenson-Hinde *et al* (1980) two sets of data were collected on the mothers in their colony of rhesus monkeys. One set of data consisted of subjective ratings of the mothers on a series of behaviourally defined adjectives - ratings which provided the basis for scoring mothers on 3 measures -

excitable, sociable and confident.   The other data set was collected

on social interactions between mothers and their infants.   The sub-

jective assessment of mothers was not on their maternal behaviour as

such but on their general behaviour in the group.   Hence the two

sets of data were independent and so could be correlated with one

another.

The results from some studies are now presented.   Jay (1963)

found that in langurs a female's personality seemed to affect her

maternal behaviour.   She discovered that it was important in

determining the way in which a mother handled and held her infant -

tense, nervous mothers who were easily irritated often startled

their young by making quick unpredictable movements, unlike females

who were more calm and relaxed.   Females who were considered to be

generally rather irritable were observed also to be more irritable

with their infants at weaning than other females were with their

infants at the same stage.

The results from the study by Stevenson-Hinde *et al* (1980) have

already been discussed in the previous section (1.5).   They demon-

strated how the personality of both mother and infant are related to

patterns of mother-infant interaction.

In baboons, Altmann (1980) found that a female's social rank

was a good predictor of her maternal style but that an even better

predictor was her glance rate, and therefore that maternal style may

be at least partially related to general temperament.   Females with

high glance rates (nervous females) tended to be restrictive mothers.

In most studies of non-primate mammals, personality differences

between individuals, if considered at all, tend to be referred to

briefly and often anecdotally but rarely seriously discussed.   Yet

some workers (Chamove, Eysenck and Harlow, 1972) believe that the

emotionality differences that are found in different strains of rats, and which can be experimentally induced in individual rats (Denenberg, Ottinger and Stephens, 1962), may be considered as personality differences. Furthermore, there is evidence that emotionality differences in mother rats affect their relationship with their infants and hence the emotionality of their offspring (Ottinger, Denenberg and Stephens, 1963).

Personality differences between breeds and between individual cats are well documented in the popular literature (Beadle, 1977) but have not been subjected to scientific investigation.

1.6.7 Nutritional state and milk yield of mother

Maternal diet during lactation has been demonstrated to affect milk yield in sheep (Arnold, Wallace and Maller, 1979). In this study and in a study of cats (Gallo, Werboff and Knox, 1980) it has also been shown that maternal diet can influence the mother-infant relationship. Neither study however revealed whether it was the milk yield or the nutritional state of the mother which had a more direct effect on the relationship, although Arnold *et al* (1979) suggested that milk yield in the ewe is a major determinant of the strength of the ewe-lamb bond. They found that ewes fed a high protein diet during lactation, when compared to ewes fed a low protein diet, began to reject their lambs (when they tried to suck) when the lambs were older, ie began weaning them later. Milk yield (measured in cc/day) was monitored in each of the experimental groups throughout lactation. In the low protein group the yield was lower although it decreased at about the same rate as the high protein group. The decline in milk yield was not paralleled by a decrease in sucking in either group, in fact ewes allowed their lambs to suck until their

milk yield had decreased to a specific low level which was thought might be some sort of threshold level at which rejections begin. The level was the same for both groups and since it was reached sooner in the low protein group, they began to wean their lambs earlier.

In contrast with control cat mothers fed a nutritionally balanced diet, mothers who were fed a nutritionally inadequate diet (protein restricted) during gestation and lactation were found to interact quite differently with their kittens (Gallo *et al* 1980). Mother and kitten behaviour was recorded, during the first 2 weeks after parturition, in a series of separation tests and it was found that the kittens of protein restricted mothers cried more than control group kittens both in the presence and absence of their mother. (Unlike the control group kittens, the experimental group kittens did not show a decrease in vocalisations when their mother was returned to them.) Protein restricted mothers paid little attention to their kittens after reunion whereas control mothers immediately retrieved their kittens and began nursing them. Gallo *et al* concluded that early undernutrition increases emotionality in the developing young and reduces the attentiveness of the mother and that together these behavioural changes disrupt mother-offspring socialisation and maternal attachment formation.

The main effect of a low protein diet on the ewes in the study by Arnold *et al* (1979) was to bring forward the onset of weaning. Although the effect on the mothers in the study by Gallo *et al* (1980) seems to be more severe, it is argued in Chapter 4 of this thesis that some features of their behaviour are similar to those normally associated with weaning in the cat.

1.6.8 <u>Early experience of mother</u>

In most studies, where the individual differences in mother-
infant relations can be described as occurring naturally (ie they
have not been experimentally induced), there is not enough infor-
mation available on the early experiences of the mother to draw con-
clusions about whether their maternal behaviour may be the outcome of
such experiences.   An exception is Altmann's study (1980) of baboons
where some evidence is presented to suggest that a female's maternal
style may be at least partly determined by the maternal style of her
mother.   (Further details are given of these findings in 1.7 where
the effects of individual differences in mother-infant relations on
infant development are discussed.)

In some studies the effects of certain early experiences have
been examined in terms of the later maternal behaviour of female
infants.   Social isolation during infancy has been demonstrated to
lead to the development of abnormal behavioural characteristics in
rhesus monkeys, including inadequate maternal behaviour in females
(Harlow, 1959; Harlow, Harlow, Dodsworth and Arling, 1966).
Similar findings were made by Nadler (1975) in his study of captive
gorillas - female infants who had been separated from their mothers
in the first week of life were abusive and neglectful of their own
first born infants.   These studies do not show that it is depri-
vation of maternal care only that leads to the later inadequate
mothering behaviour of their female infants, since in social
isolation the latter are deprived of more than a mother.   Indeed,
in both the rhesus monkeys and the gorillas, it was found that if
infant females were raised with peers, their later maternal
inadequacy was far less.

There is some evidence to suggest that temporary disruption of

the mother-infant relationship in rats can effect the later maternal
behaviour of female infants. Denenberg (1970) found that if a
female rat is handled in her infancy this experience has effects on
the behaviour of her offspring. He suggested that these effects
were mediated through the maternal behaviour of the female (however
other possibilities cannot be ruled out). It is thought that
handling effects result from the temporary separation of the infant
from its mother.

1.7 THE EFFECTS OF INDIVIDUAL DIFFERENCES IN MOTHER-INFANT RELATIONS ON THE INFANT'S BEHAVIOUR

Many students of individual differences in the mother-infant
relationship have been concerned with the effects of these dif-
ferences on the offspring's behaviour, both during the early stages
of the relationship and later on in its development. As explained
in 1.1, some studies have focused on the effects that the variation
found in 'normal' mother-infant relations can have on infant
behaviour, whilst others have mainly dealt with the effects on the
infant of a disrupted mother-infant relationship (often where the
disruption has been caused by a separation of the mother from her
infant). Only the former type of work is discussed in any detail
in this section. Hinde and Spencer-Booth (1971b) gave a full
account of the effects of temporary separation from the mother on
infant rhesus monkeys. The effects of mother-child separation are
the subject of considerable controversy with Ainsworth (1962) and
Bowlby (1969) for example, taking the view that separation can have
both considerable short, and long term, effects on the child's
social development, and others, including Clarke and Clarke (1976)
arguing the opposite - that separation does not necessarily have

profound effects on the child's later social behaviour.

The effects of naturally occurring individual differences in the mother-infant relationship on infant's behaviour are now considered. As indicated in 1.1, only results from primate studies are available. Both short and long term effects on the infant's behaviour have been investigated, although the former perhaps with more difficulty, since in studying a relationship it is not always possible to say whether the infant's behaviour is the cause or an effect of the differences in that relationship.

Perhaps the most comprehensive study to date, on the short and long term effects on the infant's behaviour of individual differences in the mother-infant relationship in non-human primates, is that of Altmann (1980) on free-ranging baboons. She found that right from the early weeks after birth *laissez-faire* mothers (see 1.5 for the distinction between *laissez-faire* and restrictive mothers) left their infants more than restrictive mothers and, at least partly in consequence, their infants also left them more often. So from the beginning these infants were more independent. In the first 3 months they interacted with other members of the troop more than the young of restrictive mothers and were groomed more often by individuals other than their mother. Altmann described in detail how the dynamics of mother-infant spatial relations change with time and how they vary with the two types of mothering style, but the basic point she made was that at every age infants of restrictive mothers were less advanced in the development of their independence. Altmann thought that in the early months restrictive mothering probably gave an infant a higher chance of survival since it was better protected from falls, disease, kidnapping by other females, and predation. However she believed that at later stages the

infants of *laissez-faire* mothers would fare better in the event of their mother's death. At 1 year old they could probably survive alone, whereas infants who had had restrictive mothering would be likely to die, since they had not achieved the same degree of self-sufficiency. Hence maternal style may differentially affect the survival of offspring. As already stated (1.5), Altmann presented some tentative evidence that daughters adopt the same maternal styles as their mothers, when they in their turn raise young. There is however a problem here in determining the importance of the mother's rank as opposed to her maternal style. Altmann found a clear relationship between the two, with almost all *laissez-faire* mothers ranking above the median. Since daughters tend to rank similarly to their mother, it is difficult to say whether it is the daughter's rank, or the maternal style and/or rank of her mother that is most important in determining her own maternal style. Somewhat similar to Altmann's findings were those of Stevenson-Hinde *et al* (1980) on rhesus monkeys. They demonstrated that the character-istics of infant rhesus monkeys at 1 year old tended to be the same as their mothers. Hence 'confident' mothers had confident infants, 'excitable' mothers had excitable infants who were not confident, and 'sociable' mothers had sociable infants.

A review of the literature on the effects of individual dif-ferences in mother-infant relations on human infant development by Dunn (1976) indicated that most studies do not produce as clear cut results as Altmann's (1980) on baboons. There is considerable debate concerning in particular the long term effects of different types of mothering or mother-infant relationships. As Dunn pointed out, even where short term links can be made between mothering style and patterns of child development, it is not known

whether these effects are immutable or how and to what extent they matter in the longer term.

1.8 SUMMARY

1   In order that the rationale behind the present study should be fully appreciated, two broad areas of research are reviewed in this introductory chapter. The basic features of maternal behaviour in the domestic cat are described in order that any details of individual differences in the mother-kitten relationship, subsequently revealed in this study, should be properly understood. The literature on individual differences in mother-infant relations, which is concerned almost entirely with primate species (at least where naturally occurring individual differences are being considered), is introduced in order that methods of research and findings can later be compared with those in the present study of a carnivore species.

2   Patterns of maternal care in the cat are compared with those of other species and this approach is of particular value when considering nursing behaviour and patterns of milk availability since no direct evidence is available on the species. Of the mammals for which direct evidence has been reported on mechanisms of milk let-down and its relation to sucking, the rat would appear to be the best model for the cat, although there may be some fundamental differences eg treading is thought to be a stimulus to milk ejection in cats but in rats it has been demonstrated to be a response to it. The close relationship between patterns of nest-site attendance and frequency and duration of nursing in semi-altricial and altricial species is illustrated.

3   The social organisation of the domestic cat is shown to be one which is largely determined by the availability, distribution and

quality of the resources, food and shelter.   Where these are localised and in abundance such as in dockyards, hospitals and farms, cats tend to live in groups with a core of several adult females (which in some cases have been known to be related).   Where a more patchy distribution of food and shelter is found, such as that described on the Monach Islands of Scotland, cats tend to be solitary and territorial.   Group living females may receive help with rearing their young and may help others, but the solitary-living female raises her young on her own.   The social experiences of young, reared in each situation, are contrasted.

4   The detail of interactions between the cat and her young from birth to weaning is described.   During this period there are believed to be three major stages in the relationship, characterised by the extent to which the mother or the young are responsible for, or share, the rôle of initiating social interactions, and especially feeding interactions.   At first the mother is solely responsible, then the rôles are shared, and finally the kittens initiate the great majority of interactions.   It is pointed out that, although some individual variation in the mother-kitten relationship has been noted by several authors, reports tend to be anecdotal.

5   Methods of describing individual differences in the mother-infant relationship are discussed, and the use of various subjective and objective, qualitative and quantitative techniques compared. Whilst subjective ratings on individuals have been employed for some years in studies of human mother-infant interaction, it is only relatively recently that such methods have been applied in non-human primate work.

6   Factors affecting the mother-infant relationship have been examined using experimental techniques where differences between

individuals have been induced, and by taking advantage of naturally

occurring individual differences in mother-infant pairs.   In a num-

ber of studies, factors such as parity of mother and sex of infant

have been found to have less profound effects than perhaps were

expected.   In others, factors such as personality, social rank and

nutritional state, have been found to be of considerable importance.

7   The effects of naturally occurring individual differences in

the mother-infant relationship on the infant's later behaviour are

the subject of considerable debate in human studies because even

where proximate effects are revealed it is not known whether these

bear any relation to later developmental stages.   In non-human

primate work there are indications that maternal style and per-

sonality may have both short and long term effects on infant

development.

CHAPTER 2   <u>MATERIALS AND METHODS</u>

2.1 THE CAT COLONY

2.1.1 History of the colony

The cats used in the study were members of the breeding colony housed in the Cat Unit of the University of Edinburgh Centre for Laboratory Animals, Bush Estate, Roslin, Midlothian, Scotland. The cats are of mixed breed; the majority are short-haired and there is a great variety of coat colours (Plates 3 and 4). The colony was established in 1970 and its original members were weaned kittens from the Small Animal Breeding Station (which closed in 1971) on Bush Estate. The Unit is not Specific Pathogen Free (SPF) but the kittens were screened for disease (ectoparasites, endoparasites, feline panleucopenia (infectious enteritis), etc) and the colony is a minimal disease one. After the establishment of the colony only one introduction from an outside source occurred - a ginger tom in 1972 (who was also screened for disease). The colony has been closed since then. Inbreeding is controlled through the breeding practice (see 2.1.2 on new breeding group members).

In 1977 when observations on the colony were begun, there were 7 breeding groups in the Cat Unit. Over the next 3 years the Unit expanded and 4 new breeding groups were established whilst the oldest 2 were retired. The colony now has 106 breeding queens - making up 9 breeding groups. In addition to the breeding stock of adult cats the Unit also houses a large number of young animals (up to several hundred at any one time). Although some of these are kept for breeding, the majority are sold and issued from the Unit at about 6 months of age.

2.1.2 Housing

The cats in the colony can be divided into 4 classes according

PLATE 3   A new breeding group of young male and female
cats, illustrating the diversity of coat
colours in the colony.   From left to right
are a mackerel tabby, a ginger and white, a
blotched tabby (above), a Siamese type (below),
a black and white, a mackerel tabby and
white, and another blotched tabby.

PLATE 4   A new breeding group.   Coat colours not seen
in Plate 3 include ginger (foreground),
tortoiseshell (two cats to the right of the
ginger), tortoiseshell and white (to the
right of the tortoiseshell) and black (two to
the left of the ginger).

to the way in which they are housed.

1   Breeding group members.

2   Pregnant queens and nursing queens, and their kittens.

3   Vaccinated kittens.

4   New breeding group members.

1   <u>Breeding group members</u>

A typical breeding group has 1 tom ($\male$) and 8 to 15 queens ($\female$) (Plate 5). Each group occupies a pen, 7m x 2.4m x 2.4m (Plate 6). The floor has a bitumen finish so that the cats do not slip when running. In the pen there are 3 large aluminium trays which contain wood shavings. The cats generally rest and sleep in one of these and use the other two for urination and defaecation. Along one of the 7m walls is a wooden shelf, 0.5m wide and 1.5m from the floor. The cats rest, sleep and run about on this shelf. The windows and ventilators are situated along the length of the same wall just above the shelf. In the centre of the floor is a wooden frame-like construction for the cats to claw and climb upon (Plate 6). It measures approximately 0.5m x 1.0m x 0.5m. The pen is heated by radiators and pipes. Troughs of water placed just outside the pens maintain the humidity.

Pregnant queens (Plate 7) are taken from their group pens a few days prior to parturition and are placed in individual cages (Plate 8) in one of the maternity rooms.

2   <u>Pregnant queens and nursing queens, and their kittens</u>

Pregnant queens are placed in cages in order that they are not disturbed by other cats during and after parturition. The mother and her young remain in the cage until the mother is removed - usually at 8 weeks. The queen is then returned to her breeding

group.   The kittens remain in the cage until just after 12 weeks.
At 8 weeks and 12 weeks they are vaccinated against feline
infectious enteritis.

The cages in the maternity rooms are arranged in 2 rows, one
above the other, in racks along one of the walls (15m long).   There
are 3 such rooms, housing 60 cages in total.   The cages, which are
made of galvanised steel, are of 2 very similar sizes
(1.12m x 0.50m x 0.38m and 1.06m x 0.55m x 0.46m).

In some of the cages the back and sides are solid, whilst the
front (comprising 2 doors) and floor are grilles (Plate 8).
In others all 4 sides and the floor are grilles (Plate 13).
Privacy is maintained between the latter type of cages by the place-
ment of aluminium sheets between them.   Inside each cage there is a
litter box (nest box) and a sanitary tray.   In the litter box the
mother and her kittens nurse and rest (Plates 20 and 28).   Since the
sanitary tray is changed on a daily basis the mother sometimes uses
it as a place to rest away from her kittens before they can climb
out of the litter box.   Three different designs of litter box are
currently in use in the Cat Unit.   Of these, only the first
type (A) was available at the time of the study.   However it was
quite suitable because its low sides made observation of the mother
and kittens possible.   It is made of aluminium and measures
0.45m x 0.32m x 0.11m (Plate 29).   The type (A) tray is
identical to the sanitary trays.   The second type of litter box (B)
is made of polypropylene and measures 0.43m x 0.29m x 0.14m
(Plate 13).   The third type of litter box (C) was recently
designed and made to specification for the Unit.   It is made of
anodised aluminium and measures 0.38m x 0.36m x 0.11m (Plate 20).
Measurements are all of the inner base.   Both (B) and (C) type

boxes however have front walls which slope up and out from the base, adding 5cm to the overall length. Type (C) litter box seems to be quite successful - its particular advantage is that it allows the queen great freedom of movement which may be especially important when she has a large litter of, say, 6 kittens. Type (B) with its high sides, perhaps affords the family more privacy however. Various materials are used as bedding in the litter box. In the present study, as described in 2.2.3, wood shavings were used (Plate 2). (Wood shavings are also used in all sanitary trays.) Paper sacking (Plate 29) and paper sheeting (Plate 13) are now also in use as bedding material. The food and water dish sits on the floor between the litter box and sanitary tray.

After weaning and vaccination all litters who are within about 3 weeks of age of each other are placed together in pens.

3   Vaccinated kittens

The pens in which the young vaccinated cats are housed are identical to those described for the adult breeding groups. Up to 20 kittens are housed together.

4   New breeding group members (Plate 9)

When a new breeding group is formed kittens are selected from the groups of vaccinated animals. The individuals that make up the new breeding group therefore live together from an early age. Females on average reach puberty at between 7 and 12 months, with an average of 9 months, whilst in males the variation is from 10-14 months, with an average of 12 months (Robinson, 1977). For this reason the tom chosen for a new breeding group is older than the females by at least a few months, where possible. In order to minimise inbreeding the tom and queens originate from different

breeding groups.

2.1.3 Feeding

All the cats are fed and given fresh water twice daily, at 0900 h and 1600 h. The aim, especially where nursing females and their kittens, and weaned kittens are concerned, is that food availability should be *ad lib* (or at least as close an approximation to it as possible), and therefore meal sizes are measured accordingly. The diet for breeding group members, nursing queens and their kittens, contains the following ingredients: 'Scoff-a-lot' (a high protein commercial diet supplied by Dofos, Edinburgh, consisting of liver, heart, tripe, kidneys etc), fish meal, dried milk powder, vegetable oil, cooked flaked maize, and vitamin supplement. They are all mixed together with water. Weaned kittens between 3 and 6 months of age are fed the same diet but with a slightly smaller amount of 'Scoff-a-lot'.

2.1.4 Cleaning

The cages in the maternity rooms are washed between occupants. Trays in cages and pens are changed on a daily basis. The pens which house both young animals and adult breeding groups are regularly swept and washed out.

2.1.5 Health

Once a month the whole colony is given Citrazine worming powder as a preventative measure. Kittens are also dosed at 8, 10 and 12 weeks.

2.1.6 Breeding

In northern latitudes the domestic cat tends to show peaks of conception in late January to March and May to June (Scott, Carvalho da Silva and Lloyd-Jacob, 1957). The gestation period is about 65 days although it varies between 58 and 71 days (Robinson, 1977). Domestic cats are usually anoestrous in October, November and December. However if the natural day length is extended during Autumn and Winter, using artificial illumination, cats also have an oestrus period in November (Scott and Lloyd-Jacob, 1959). In the study colony illumination is maintained at approximately Spring time levels (14 h light/10 h dark). The temperature fluctuates around $65^{\circ}F$ and on warm Spring and Autumn days it may rise to $75^{\circ}F$. In Table 2.1 breeding records of the colony in the years 1976 to 1979 are given. The total number of kittens born each year and the number of breeding queens in the colony each year are stated. The percentage of births that occurred in each month has been calculated for each year. The mean percentage of births in each month has been calculated for the 4 years. The peak birth months tend to be, on average, February, March and June but births do occur throughout the year.

TABLE 2.1   Breeding records of the colony 1976-1979
(Based on data supplied by D Hay)

Year	1976	1977	1978	1979	
Total number of kittens born	385	393	526	754	
Number of breeding queens	51	69	98	112	

Kittens born in	%	%	%	%	Mean %
January	4	7	7	7	6
February	22	16	11	13	16
March	16	13	17	10	14
April	5	10	6	8	7
May	1	7	6	6	5
June	24	13	10	12	15
July	5	8	10	12	9
August	9	7	14	7	9
September	3	1	3	5	3
October	4	11	3	3	5
November	2	7	9	9	7
December	5	0	4	8	4

2.2 OBSERVATIONS ON MOTHER-KITTEN INTERACTION

2.2.1 General Introduction

An important requirement for the study was that a reasonably large number of mothers should be sampled. This was primarily to ensure that if individual differences in mother-kitten relations did exist a wide range of differences would be observed and statistical tests could be applied to the data. Variables which might affect mother and kitten behaviour, such as parity of mother and size of litter, had to be controlled where possible. In order that the data on all mothers and litters be strictly comparable, the sampling method had to be chosen with care. In addition it had to be borne in mind that the sampling method chosen would characterise the type of data collected and hence place limitations on the results and their possible interpretation.

2.2.2 Animals used in the observations

Seventeen families (where mother and litter compose the family) were chosen for the study on the basis of 2 criteria - the mother had to be multiparous, and the litters had to have 2, 3 or 4 kittens. For a number of reasons a range of litter sizes, instead of just one size, was chosen, and no particular sex ratio was specified. The Unit is a commercial enterprise and therefore kittens could not be culled to produce litters of specific size and sex ratio. Fostering was not feasible either, because of the risk of kitten losses from this procedure. Finally, it would have been impractical to cause delays in the study through waiting for litters of one particular composition to be born. There was one major advantage in using a range of litter sizes and sex ratios - if a death occurred in a litter during the course of its study, obser-

vations on that litter could be continued. With litters of only one specified composition the occurrence of kitten death in a litter would have rendered the litter unusable for the study.

Detailed information on the effects of litter size on maternal and kitten behaviour is not available for the cat (1.4). However it was reasoned that, whatever the effects of litter size, the differences between families with 2, 3 or 4 kittens would be less than between families with a single kitten and families with more than 4 kittens. In a short study (conducted on the same colony after the present study had been completed) (Innes, 1980), it was suggested that there may be some differences in behaviour between 'small' (with 1-3 kittens) and 'large' (with 4-6 kittens) families. Differences within each of the two ranges of litter sizes were not examined. The results of Innes (1980) seem to bear out the decision not to choose litters of widely ranging sizes. Nonetheless the effects of litter size are taken into account in the present study (3.6.3 and 3.7.2).

No work has been conducted on the effects of sex ratio, or the occurrence of kitten death on maternal and litter behaviour, and these two variables are also examined in this study (3.6.3 and 3.7.2).

Each family was assigned a unique code number (eg C1, C8, B5). The code numbers are used in the text to refer to each family or its members, eg 'mother B2', 'litter C7'. Details of the litters, including their date of birth, the number born, stillbirths and deaths, and the number and sex of kittens surviving at 6 weeks, are presented in Table 2.2.

Stillbirths

In some cases, eg C5 and A1, when a kitten was stillborn, the mother ate it soon after delivery. C5 ate her stillborn kitten

starting with the hind feet and finishing with the head but in other litters in the colony headless corpses have been found.

Deaths

The kittens which in Table 2.2 are recorded as having died and been eaten, in fact just disappeared, but must have been eaten by their mother.   For neither C8 nor B4 was it known whether the kitten died, or was killed by the mother.   The kitten in C8 disappeared on 3 March 1979.   On the previous day it was found to be in poor condition and apparently suffering from a bladder complaint. It was removed from the cage and hand-fed during that day.   It was replaced in the late afternoon.   It is not improbable that the kitten died because of its poor state of health, however the mother may have contributed to its death.   She was observed to be behaving aggressively towards her kittens on 28 February 1979 - striking at them when they approached her.

The cause of the death of the kitten in litter B5 was unknown but in litters B2 and B4 deaths were thought to be a result of maternal neglect.   The kittens in both litters had problems locating and attaching to the nipples and their mothers were unresponsive to their difficulties.   It is quite feasible that the kittens died from dehydration and/or malnutrition.   These deaths are discussed more fully later.

TABLE 2.2 <u>Families used in the study</u>

Family	Date of birth	Number born	Stillbirths/deaths	Litter composition at 6 weeks	
				♂	♀
C1	8.2.79	3		2	1
C2	8.2.79	4		2	2
C3	3.2.79	3		1	2
C4	8.2.79	4		0	4
C5	9.2.79	4	1 stillborn and eaten (sex unknown)	1	2
C6	14.2.79	4		0	4
C7	1.2.79	4		3	1
C8	1.2.79	4	1 died at 35 days and was eaten (♂)	2	1
B1	5.4.79	3		2	1
B2	13.4.79	6	2 stillborn or died soon after birth (sex unknown) 2 died at 5 days and were partially eaten (sex unknown)	0	2
B3	15.4.79	2		1	1
B4	8.4.79	3	1 died at 1 day and was eaten (sex unknown)	0	2
B5	18.5.79	4	1 died at 3 days(♂)	3	0
B6	9.5.79	4		2	2
B7	11.4.79	4	1 stillborn or died shortly after birth (sex unknown)	3	0
B8	7.4.79	3		2	1
A1	24.5.79	5	1 stillborn and was eaten (sex unknown)	2	2

2.2.3 Housing of animals and observation conditions

The rooms where pregnant and nursing queens are normally housed were unsuitable for the purpose of conducting observations because of the disturbance caused by the daily feeding and cleaning routines.   Instead observations were made in a smaller room 5m x 2.4m x 2.4m which became in effect another maternity room.   It was quieter than the main maternity rooms and cleaning and feeding could be done outside observation hours.   The room was lit by three fluorescent strip lights (2 x 40w and 1 x 65w).   Eight cages were arranged in racks along 3 of the walls and a chair for the observer was situated in the centre of the other wall.   The grille fronts of the cages were painted matt black to facilitate observation of the animals.

Each cage had a type (A) litter box (Plate   29   ) and a sanitary tray, both filled with wood shavings.   The low sides of the litter boxes made observation of the mother and her new born kittens possible.   A maximum of 8 litters could be housed in the room but since births were not synchronised, all 8 cages were not initially occupied by mothers with litters.   Within 2 weeks of the first cage being occupied, however, 8 litters of suitable size had been obtained, either from the main maternity rooms or from the pregnant queens already housed in the observation room.   Each litter was observed for 6 weeks.   This period was chosen because according to Schneirla *et al* (1963), by day 42 the mother-kitten relationship would have advanced well into the 3rd stage and weaning would be taking place (1.4).   (Kittens of various ages between 0 and 6 weeks are shown in Plates 10-16.)   Families were moved from their cages and placed in the other maternity rooms at the end of their 6 week observation period.   New pregnant queens could then be accommodated

PLATE 5   An adult tom (centre) with two queens resting
together on the shelf in their group pen.

PLATE 6   The members of a breeding group in their
pen.   The tom (resting in the crouch
position) and a queen (walking) are seen
on the shelf.   One queen is seen sitting
on the wooden frame construction.   In
the foreground a queen is seen showing
typical oestrous behaviour.
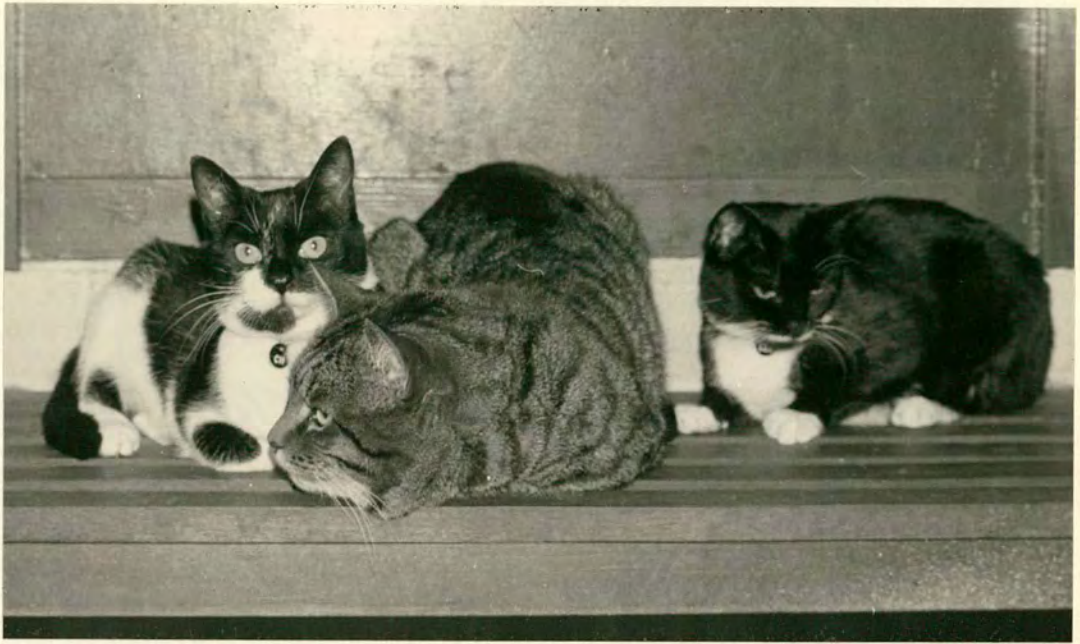
PLATE 9   New breeding group members

PLATE 10   A mother is seen with her 4 day old kittens.
           She is in the on-side-lie position.   Her
           ventrum is poorly exposed due to its
           orientation relative to the floor and due to
           the positioning of her legs.   The kittens
           are still by mother except for the one in
           the foreground who may be active.
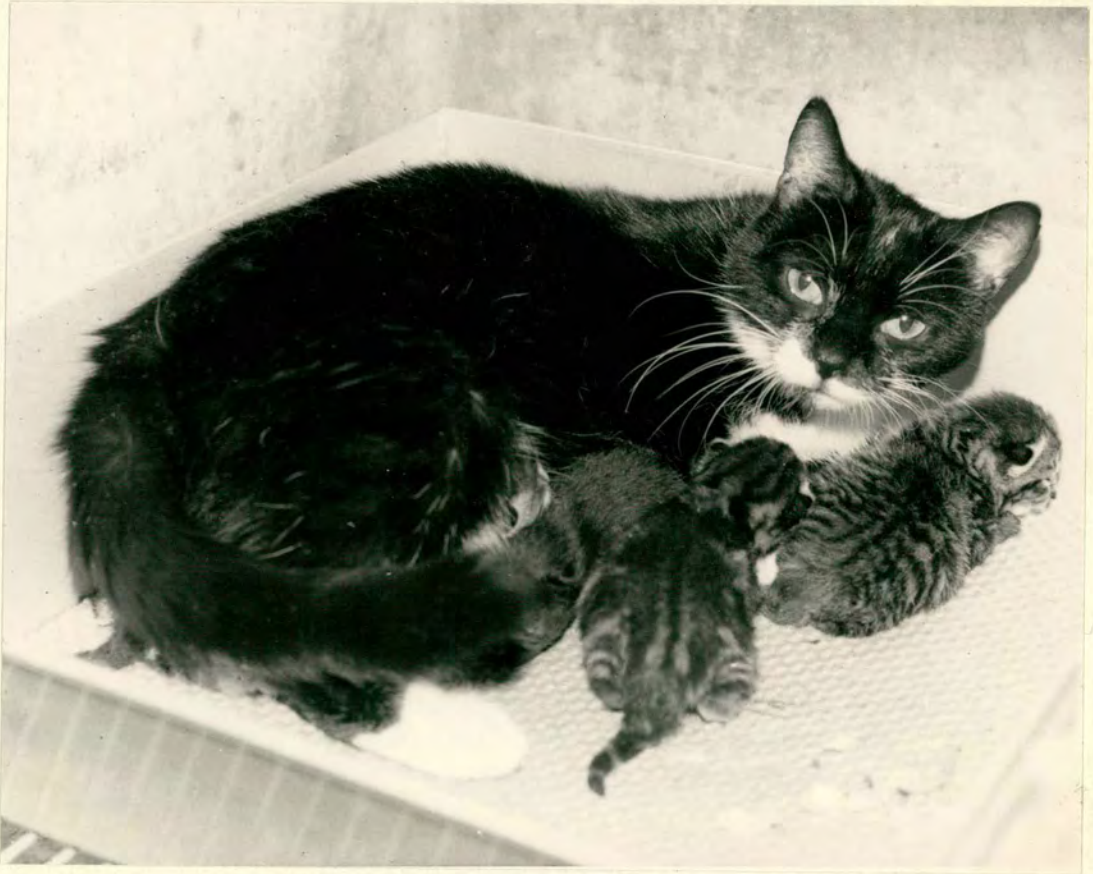
PLATE 11 One week old kittens, huddled

PLATE 12 Two week old kittens, huddled

PLATE 13   Three week old kittens in a Type (B) litter
           box with paper sheeting as bedding.   The
           cage is the type with grille sides and back.

PLATE 14   Four week old kittens.   The kitten on the
           right is showing stand on play, and the one
           on the left, roll on back.

PLATE 15   Five week old kittens.   The kitten at the
           rear left is seen beginning to climb out
           of the Type (B) litter box.

PLATE 16   Six week old kittens active on the floor of
           their cage.

in the observation room.

2.2.4 Sampling method

The sampling method that was employed is termed fixed-interval time point sampling (FITP) (Chow and Rosenblum, 1977) but is also known as scan or instantaneous sampling (Altmann, 1974). In this method, several animals (in the present study, members of a family) are scanned in turn and their behaviour scored. The shorter the time that it takes to scan the animals, the closer the record approximates to a simultaneous, or instantaneous one. The scan is repeated at fixed intervals, in this study - 1 minute 30 seconds.

In the present study it was desirable that comparable behavioural records be collected on all families. However it was not possible to have the 17 families under observation at one time. The births of suitable litters (2.2.2) were not synchronised and in any case the observation room accommodated a maximum of 8 families (2.2.3). As a compromise, however, by scanning each family in turn within the fixed interval, comparable records could be collected on families which occupied the observation room together (2.2.5).

There were a number of other reasons why FITP was particularly suited to the study. Up to 8 families could be observed at the same time each day, and provided that the observation session was sufficiently long (so that a large number of scans of each family could be made) a representative sample of the animals' behaviour could be obtained. If focal litter sampling had been used instead of scan sampling, a more complete behavioural record of each animal's actions and interactions could have been collected. However in a given period of observation time, the same number of

individuals could have been observed only if their observation sessions had been short. In this case the samples would have been unrepresentative unless the rate of change of behaviour was particularly high. This did not appear to be so. It would not have been clear under such circumstances whether differences that were found between individuals were real differences, or artefacts of the sampling method. Long focal sessions would have provided representative samples but would have been uneconomical in the sense of taking more 'observer time'. In addition, focal sampling records could not have been collected on check sheets which had the advantage that there was no need for long decoding or transcription sessions (2.2.8 and 2.2.9).

There were however several disadvantages with FITP. Data on interactive events between the mother and her kittens, such as approaching, leaving, initiating nipple attachment and terminating nipple attachment, could not be reliably obtained. Since these events are of short duration, the records of their occurrences collected using FITP (with the fixed-interval chosen), would have been gross underestimates. Focal litter sampling would have provided details of such interactions. In addition, information on actual frequencies and durations of behavioural events and behavioural states would have been collected. Frequencies and durations can only be estimated if data is collected using FITP (Chow and Rosenblum, 1977). During observation sessions, as described in the next section (2.2.5), the observer had to walk around the room, stopping at each cage to record the behaviour of its occupants. Some of the mothers occasionally reacted to the observer's approach towards, or presence at, their cage (especially during their first few weeks in the observation room). The behaviour they

exhibited could be described as either <u>excited</u> or <u>disturbed</u> (2.2.7 for definitions). (Such behaviour is elicited less readily when the observer is seated in front of a cage for some time.) Both <u>excited</u> and <u>disturbed</u> behaviour were recorded.

2.2.5 <u>Observation sessions</u>

Observation sessions were of $1\frac{1}{4}$ hours duration. (Initially the sessions were of $2\frac{1}{2}$ hours duration but it was decided that sufficient data was collected in half the time. In addition, a wide range of behavioural states and activities were observed with $1\frac{1}{4}$ hours.) Four observation sessions were conducted per week for the first 6 weeks after birth.

Observations were made between 1130 h and 1530 h and so came after the morning feed and before the afternoon one. The females had normally finished their first meal of the day before observations were begun.

The fixed-interval time point method of sampling was used. The fixed-interval was the time it took to walk round the 8 cages, scanning them in turn, and returning to the first cage. Looking into a cage, noting the behaviour of the mother and her kittens, scoring a check sheet (2.2.8), and then moving to the next cage, took about 10 seconds. The round of 8 cages therefore took 1 minute 20 seconds. A further 10 seconds was required to return to the first cage and so in total the fixed-interval was 1 minute 30 seconds. Even if all the cages were not occupied the observer had to wait until 1 minute 30 seconds had elapsed before starting the next round of scans. The process was repeated 50 times and therefore each animal's record contained 50 scores. For each circuit a separate check sheet was scored.

2.2.6 Diary entries

After each observation session comments on the behaviour of individual mothers and their litters were entered into a diary. No particular protocol was followed in writing these entries. In Appendix A edited versions of the diary entries on each family are presented for weeks 1 to 6. In editing, the chief aim was to avoid repetition (which the 4 entries for each week often contained) and to ensure the same terms were always used to describe the same phenomena. Terms used in the diary that are not defined in 2.2.7 are defined and discussed in 3.2 and 3.3.

2.2.7 Behavioural measures

A number of the names given to measures are the same as those used in other studies of cat behaviour (West, 1974; Haskins, 1975; Barrett and Bateson, 1978). In most cases the definitions have been reworded but, unless specifically stated, the meanings remain the same. It is also indicated where measures have been renamed.

1 Maternal measures

Location (scored by Haskins) - There are 3 possible locations in the cage - the 2 boxes and the floor space between them. The litter box was type (A) and therefore identical to the sanitary box. By definition then, whichever of the two boxes was most frequented by the kittens was termed the litter box. When scoring location, animals are recorded as being in the left hand box, the right hand box, or in between the two boxes (as indicated in Figure 2.1 of the check sheet design). After each session the term litter box is affixed to the appropriate box when the scores in each have been totalled. The other 2 locations are then termed - the other box and in between.

Body positions and activities

Stand (scored by Haskins) - The pads of all 4 paws and no other part of the body are on the ground (Plate 8).

Sit (scored by Haskins) - The pads of the front paws are on the ground, the front legs are straight, and the rump is squarely on the ground (Plate 17).

Crouch (scored by Haskins) - The ventrum is in contact with the floor, and all 4 paws are supporting the weight of the body with pads in full contact with the ground (Plate 18).

Lie (scored by Haskins) - The ventral surface is in contact with the ground and is supporting the weight of the body, and the legs are partially extended or tucked underneath the body.

Sit-nurse - The same as sit except that one or more kittens are attached to the nipples (Plate 19).

On-side-lie - One side of the body is in contact with the ground, the ventral surface is partially or fully exposed, and the legs lie out to one side (Plate 20).

Half-sit - The body is in a position intermediate between sit and on-side-lie positions. The front of the body is raised by one or both forelegs and the rear end is resting on the side of the body (Plates 21 and 27).

Note: Half-sit and on-side-lie are sub-divisions of Haskins' lactation position.

Shift (scored by Haskins) - A change in orientation of the body while in sit-nurse, or while in half-sit or on-side-lie when kittens are in contact with the mother. Haskins' shift differs because it was only scored when

the mother was in <u>lactation position</u> (ie half-sit or on-side-lie).

<u>Walk</u> - Locomotion about the cage.

Activities

<u>Eat</u> (scored by Haskins) - The mother is taking food into her mouth, is holding it in her mouth or is seen or heard eating.

<u>Drink</u> (scored by Haskins) - The mother's head is inside the water dish and she is lapping.

<u>Vocalise</u> (scored by Haskins) - The utterance of any sound by the mother.   Haskins did not distinguish different vocalisations but in Appendix B descriptions are given of the vocalisations recorded in this study.

<u>Carry</u> (scored by Haskins) - The mother picks up a kitten in her mouth or attempts to do so.

<u>Lick</u> (scored by Haskins) - Contact between the mother's tongue and the body of a kitten (Plate 22).

<u>Groom</u> (scored by Haskins) - Self-licking or grooming.

<u>Paw</u> - A treading movement of the mother's fore paws on a kitten's body with the claws being extended and con-tracted (Plate 23).

<u>Excited/Disturbed</u>   For speed, excited and disturbed behaviour, which are quite similar, were scored as one category, since the scan sampling technique requires that the scoring of behaviour should be instantaneous. Excited and disturbed behaviour are each shown as responses to external events such as the approach or presence of the observer, or voices outside the room. However excited and disturbed behaviour are also observed

on occasions where there is no apparent stimulus. (It
is quite obvious usually when a mother is reacting to the
observer.) When a mother is excited she tends to roll,
rub her head against the kittens (Plate 24), rub against
the bars, stand up and sit down repeatedly and often
purrs loudly. Excited behaviour is generally shown by
individuals who are very friendly to the observer. Dis-
turbed mothers often stand up (if in half-sit or on-side-
lie), may begin to walk around, and may not settle down
again for some time. They often cry or make brrp-cry
vocalisations (Appendix B). They may also make slight
backing-off movements from the observer.

2 Kitten measures

Location (scored by Haskins) - as for mother.

Body positions and activities

Nuzzle (scored by Haskins) - The kitten is making gross
body movements and is pushing its face against the
mother's ventrum, legs, neck, or tail (Plate 25).

On-nipple (scored by Haskins but termed suckle) - The
kitten has its face against the mother's ventrum and is
not making gross body movements, or it may actually be
seen to be attached to the nipple. Sometimes the fore-
paws are held at either side of the kitten's head,
against the mother's ventrum, and treading (alternate
pressing of either paw against the mammary area) may be
seen (Plates 20 and 26).

Still by mother (scored by Haskins but termed still) -
The kitten is motionless and in contact with the mother
but not on-nipple (Plates 20 and 27).

Still by self - The kitten is motionless and not in contact
with either the mother or another kitten.

Huddle (scored by Haskins) - The kitten is motionless
and in contact with other kittens but not the mother
(Plates 11 and 28).

Active (scored by Haskins but termed move) - The kitten is
moving around, in or out of contact with the mother or
other kittens, and may or may not be playing (Plates 16 and 25).

Eat - As for mother.

Vocalise (scored by Haskins) - The utterance of a cry from
a kitten.   Although grunts were very occasionally heard
in the early weeks, these were not scored.   Haskins
scored all vocal sounds produced by kittens.

Paw and bite (scored by Barrett and Bateson but termed
cat contact) - The kitten paws and/or bites another
kitten.

Roll on back (scored by West but termed belly-up; a sub-
division of Barrett and Bateson's wrestle) - The kitten
is on its back with its paws in the air (Plate 14).

Stand on (scored by West but termed stand-up) - The kitten
stands on or over the body of another kitten and paws,
and/or bites it (Plate 14).

Paw and bite mother - The kitten paws and/or bites the
mother.

Back arch (scored by Barrett and Bateson but termed arch) -
The kitten is stationary or in motion and its spine is
curved upwards, the body is often held in a sideways
orientation.

Crouch (scored by Barrett and Bateson but termed stalk;

similar to West's pounce) - The kitten is stationary or

slowly moving (or briefly running) with its head and body

held in a straight line and close to the ground.

Climb out - The kitten attempts to, or succeeds in,

climbing out of one of the boxes (Plate 15).

Paw and bite object (scored by Barrett and Bateson but

termed object contact) - The kitten paws and/or bites

an object such as wood shavings or the litter box.

> Note: Many of the terms (indicated above) that
> Haskins used in his 1975 study have also been used
> in two subsequent reports of his work (1977 and
> 1979).

2.2.8 Method of scoring behaviour

Quantitative data collection was carried out by recording on

check sheets (Figure 2.1).

1 Maternal behaviour

When scoring the mother a tick was placed in the appropriate

box on the check sheet to indicate her location and body position

(ie stand to walk). If the mother was exhibiting any of the

behavioural categories from eat to excited/disturbed, ticks were

placed in the appropriate boxes. (For vocalise, the type of

vocalisation was recorded - Appendix B.)

2 Kitten behaviour

Kittens were not scored individually but instead the number of

kittens performing each of the behavioural measures from nuzzle to

active were recorded. If the kittens were also involved in other

activities, from eat to paw and bite object, the number of kittens

doing each activity was recorded. For vocalise, the scoring method

was one-zero (Altmann, 1974), with a score of 1 being given when 1 or more kittens were crying.

Check sheets provided a quick and easy method for collecting data. After one relatively simple data reduction step (2.2.9), the data could be transferred directly to computerfiles. There the data could be further manipulated and statistical analyses of the data performed.

FIGURE 2.1 : <u>Check sheet design</u>

Date: Sheet:

Families										
Location	L	In	R							
Mother										
Kittens										
MOTHER										
Stand										
Sit										
Crouch										
Lie										
Sit-nurse										
On-side-lie										
Half-sit										
Shift										
Walk										
Eat										
Drink										
Vocalise										
Carry										
Lick										
Groom										
Paw										
Excited/Disturbed										
KITTENS										
Nuzzle										
On-Nipple										
Still by M										
Still by self										
Huddle										
Active										
Eat										
Vocalise										
Paw and bite										
Roll on back										
Stand on										
Paw and bite M										
Back arch										
Crouch										
Climb out										
Paw and bite object										

Key: L = left hand box, R = right hand box, In = in between

PLATE 17 The mother is seen in the sit position with
          her kittens still by mother.

PLATE 18 This pregnant queen is seen in the crouch
          position
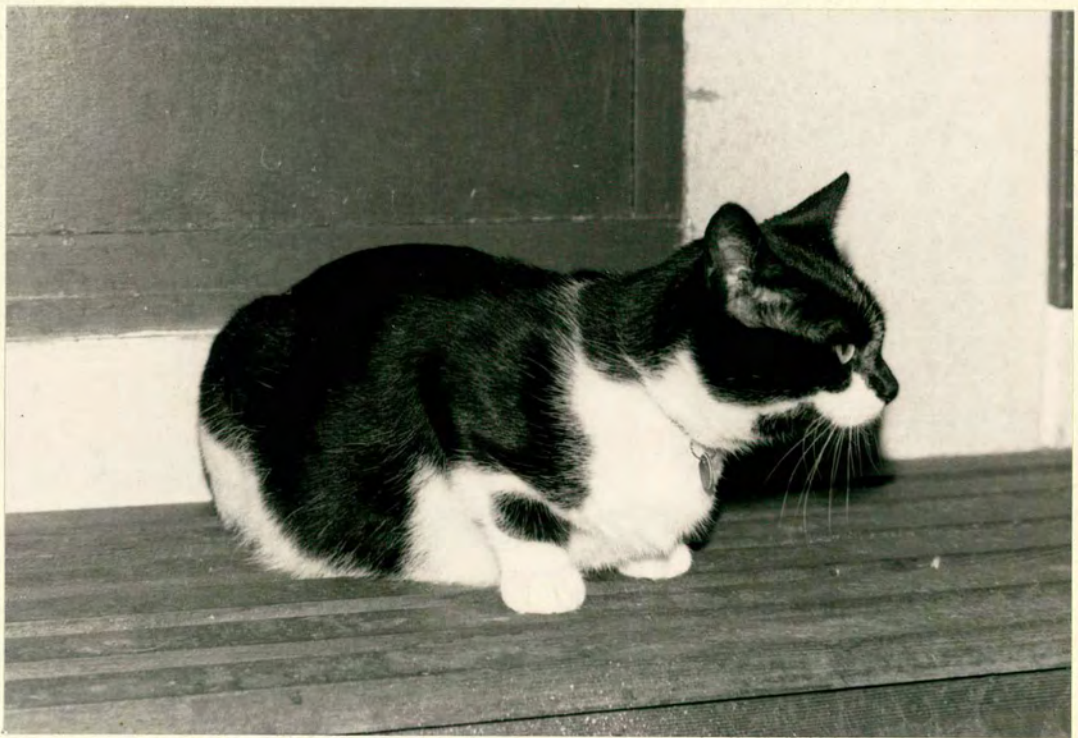
PLATE 19   Sit-nurse.   The mother is sitting with one
          kitten (barely visible between her legs)
          attached to the nipple.   The kitten to the
          left of mother is showing roll on back play.

PLATE 20   A mother in on-side-lie, nursing her kittens
          in a Type (C) litter box.   The kittens are
          all on-nipple except for the individual to the
          far right who is still by mother.   Notice the
          kitten third from the right with fore paw held
          against the mother's ventrum while on nipple.
          In the on-side-lie position of this mother the
          legs are held away from the ventrum to make
          room for the kittens and the orientation of
          the ventrum exposes the nipples fairly well.

PLATE 21   The mother is nursing kittens in the half-sit
           position.   Notice how she supports her rear
           end with the side of her body and her front
           end with the front legs.   As illustrated the
           ventral surface is exposed to the kittens in
           this position.   At least two of the kittens
           are on-nipple.

PLATE 22   The mother is seen standing and licking her
           kittens who are described as being still
           by mother since they are asleep and in
           contact with her forepaws.

PLATE 23 The mother is seen pawing - notice how her
          claws are extended.   She is in the
          on-side-lie position.

PLATE 24 The mother is exhibiting excited behaviour -
          she is rubbing her face against her kittens.
          The family are in a Type (C) litter box.

PLATE 25   The kitten second to the left is seen
            nuzzling.   It is pushing itself towards the
            mother's ventrum with its hind legs.   The
            kitten to its right is on-nipple.   The
            other two kittens are active.   The mother
            is in on-side-lie.   Notice how well her
            ventral orientation exposes the ventrum -
            her kittens have easy access to the nipples.

PLATE 26   Three kittens seen on-nipple.   The mother is
            in on-side-lie.   Both her leg position and
            ventral orientation help to expose the
            nipples so well to the kittens.

PLATE 27   The mother is in half-sit.   Notice that her
          ventrum is well exposed by its orientation.
          The legs also are quite well positioned to
          reveal the nipples.   One kitten is seen
          on-nipple, the rest are still by mother.

PLATE 28   These kittens are huddled.   They are in a
          Type (A) litter box with paper sacking as
          bedding material.

2.2.9 <u>Reduction and treatment of quantitative data</u>

After each session the data collected (50 scores for each animal (2.2.5)) was subjected to the following treatment.

1 Data on mothers

Location: the percentages of scores in which the mother was in each location were calculated. These added up to 100.

Body position: the percentages of scores in which the mother was in each body position <u>stand</u> to <u>walk</u> were calculated. These added up to 100.

Activities: the percentages of scores in which the activities <u>eat</u> to <u>excited/disturbed</u> were recorded were calculated. <u>Each</u> percentage could be between 0 and 100 and so the percentages did not together add up to 100.

2 Data on kittens

Scores on every measure were divided by the number of kittens in the litter to give a mean score for the litter (an average kitten score).

Location: as for mother.

Measures <u>nuzzle</u> to <u>active</u>: as for mother body position.

Measures <u>eat</u> to <u>paw and bite object</u>: as for mother activities.

Although data was collected on all the measures listed above, analyses were not necessarily performed on all the data. In some of the analyses, described in Chapter 3, only a selection of measures are used. Where this is the case it is always stated. Furthermore, in some of the analyses, mean weekly percentage scores are calculated and used instead of session percentage scores, but the type of score used is always clearly stated.

2.2.10 Weighing kittens

The kittens in each litter were weighed, to the nearest 5 grams, using a Pesola 500g balance, when they were 7, 14, 21, 28, 35 and 42 days of age approximately. Each kitten was placed inside a cotton bird bag and the spring balance was attached.

2.2.11 Missing data

Behavioural and weight records on some of the families were incomplete due to illness of the observer. In 3 families there were weeks when all 4 observation sessions were missed (B2, week 3; B4, week 4; B8, week 4). In 5 families some observation sessions were missed from certain weeks but estimates were made of the mean weekly scores from the data on sessions that were recorded (B4, week 3; B7, week 3; B8, week 3; B1, week 4; B7, week 4).

CHAPTER 3   <u>QUALITATIVE AND QUANTITATIVE RESULTS</u>

3.1 GENERAL INTRODUCTION

In this chapter both qualitative and quantitative results are presented. Qualitative data were collected in the form of a diary (2.2.6). In the diary information was gathered on many aspects of the mother-kitten relationship and kitten development, in each family. Quantitative data were collected on specific maternal and kitten behavioural measures (listed and defined in 2.2.7) using the fixed-interval time point sampling technique (2.2.4), and were recorded on check sheets (2.2.8). The findings from each source of information are presented quite separately in this chapter but are fully integrated in Chapter 4. The value of having collected both qualitative and quantitative information is emphasised in 4.4. Each source of data produces its own unique set of results and, in addition, some results which complement and thus support each other. In many cases also qualitative results aid the interpretation of quantitative findings.

3.2 QUALITATIVE RESULTS ON FEEDING INTERACTIONS: DETAILS OF INDIVIDUAL DIFFERENCES IN THE MOTHER-KITTEN RELATIONSHIP

The qualitative data, from which the results presented in 3.2 - 3.5 arise, are presented in edited form in Appendix A (2.2.6) and can be referred to for information on specific families.

3.2.1 Kittens' access to the nipples

When kittens were on-nipple their mothers were usually in one of 3 body positions - on-side-lie, half-sit, or sit (Plates 17, 20, 21). The mother's nipples tended to be exposed when she was in half-sit and on-side-lie. Therefore if she took up either of these positions beside her kittens, they were able to easily locate and attach to her

nipples.   Mothers generally used on-side-lie more than half-sit,
although some mothers showed a greater preference than others for the
former position.   The sit position did not appear to facilitate
nipple attachment to such an extent as half-sit or on-side-lie since
the nipples were less well exposed and accommodation for the kittens
at the ventrum was limited (Plate 17).   However access to the
nipples could be made easier if the mother held her front legs apart
and away from the body so that more space was created under her.
When kittens were attached to the nipples the mother was said to be
in sit-nurse (Plate 19).

   In half-sit or on-side-lie positions it was observed that the
ventral surface could be exposed to varying extents.   Two factors
affected the exposure of the ventrum - the positioning of the front
and rear legs and the orientation of the ventral surface, ie its
position relative to the floor.   When the ventral surface was maxi-
mally exposed the front and rear legs were outstretched so that they
did not hinder the kittens' access to the nipples, and the female
was resting with her ventrum facing out to the side (Plates 26, 27,
29, 30).   Mothers who showed high exposure of the ventral surface
included C2, C4, C7, B5, B6 and B7.   Unlike these females, some
mothers did not always make access to their nipples easy, either due
to the position of their legs, the orientation of their bodies, or
both (Plate 10), eg C1, week 1;   C3, weeks 1-3;   B2, weeks 1-2;   B4,
week 1.   As a consequence, the kittens of these mothers had problems
in locating the nipples.   Only female C1 responded to her kittens'
difficulties - she shifted her body so that the kittens were better
placed in relation to her ventrum.   (Some mothers showed quite a lot
of shifting even if their kittens did not have problems and this
seemed to ensure that the kittens always located the nipples

quickly - eg B7.)   The other mothers were unresponsive to their

kittens' efforts to gain the nipples and often the kittens became

exhausted and gave up trying to do so.   By week 3 however, the kit-

tens in most families had overcome their prior difficulties.

Unfortunately the diary does not make it clear why this was.

Nevertheless, it seems likely that the kittens found it easier to

gain the nipples for two principal reasons:

1   they were physically stronger and so could push their

way in to the nipples more forcefully

2   learning had improved their skills at locating the

nipples (Rosenblatt, 1972).

It was also the case that some mothers began taking up positions in

which the ventral surface was better exposed.

An even more fundamental feature of the mother's behaviour,

which affected her kittens' success in locating and attaching to the

nipples (especially in weeks 1 and 2), was her body position, rela-

tive to the kittens, when in half-sit or on-side-lie.   This depended

on the manner in which she took up the positions.   For the kittens

to be able to make their way with ease to the nipples the mother had

to position herself so that the young would lie along her ventral

surface.   She could achieve this by orientating herself appropriately

while standing (or sitting) and then easing herself into position and

pushing her kittens forward slightly so that she did not lie on them.

Some mothers were very careful and took up position beside their kit-

tens so gracefully that the kittens were hardly disturbed at all, eg

C2, weeks 1 and 2.   Most mothers were competent at orientating and

positioning themselves but some occasionally trapped a kitten behind

them (Plate 31), eg C1, weeks 1 and 2; B4, weeks 1 and 2.   C1

responded quickly to her kittens' attempts to escape from being

PLATE 29 The mother is in on-side-lie and there are
          one or two kittens on-nipple.   This mother
          has orientated her ventrum so that both
          lines of nipples are maximally exposed.
          Her legs are away from the ventrum so that
          they do not hinder the kittens' access to
          the nipples.   The family are in a Type (A)
          litter box with paper sacking as bedding
          material.

PLATE 30 This mother is in on-side-lie in which the
          nipples are well exposed by her ventral
          orientation and leg position.
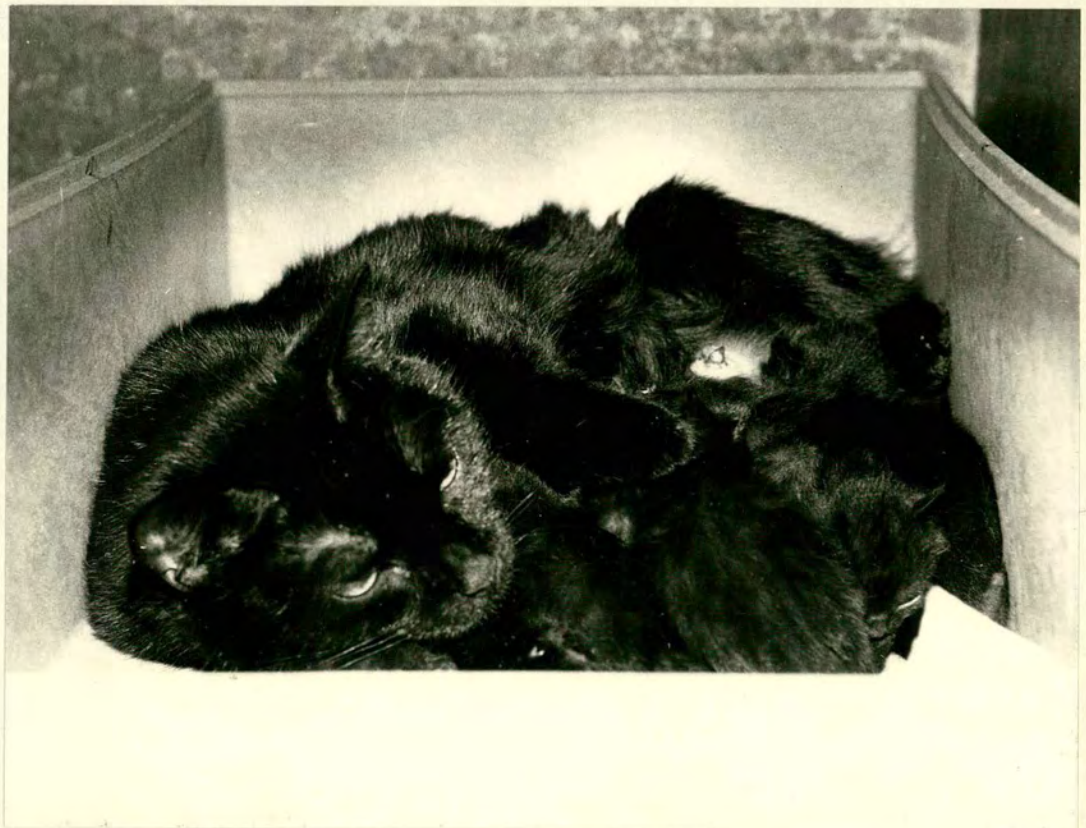
PLATE 31 This mother is seen in on-side-lie.   Her
          ventral orientation exposes the nipples
          quite well but the positioning of her legs
          does not give the kittens much room at the
          ventrum.   Notice that two kittens are trapped
          behind the mother.

trapped and shifted her body so as to free them, or carried them round to her ventral side in her mouth. B4 was not responsive in week 1 but in week 2 she helped a kitten to her ventral surface. There were also some mothers whose kittens spent quite long periods under or behind them and who did not help their kittens to get free, eg C3, week 1; B2, week 1. After the first few weeks, kittens were far less frequently seen trapped under or behind their mother's bodies, apparently because they were larger and stronger and could easily escape.

The length of time that a female stayed in either half-sit or on-side-lie without interruption was also found to affect kittens' on-nipple behaviour. Each time the mother took up one of these positions the kittens had to search for and find the nipples before they could attach to them, so if the mother disrupted sucking by sitting or standing up, and then initiated it again by resuming half-sit or on-side-lie, the kittens had to relocate the nipples so that they could reattach to them. If the mother disrupted her kittens repeatedly, then the result was that they used much of the time that they could have been on the nipple, actually searching for the nipples (ie nuzzling). Mothers C5, weeks 1-3; B3, weeks 1 and 2; and A1, weeks 1 and 2, frequently broke up bouts of on-nipple by standing up, rolling over on their backs, or leaving. B3 kittens became exhausted, apparently as a result of their mother's behaviour, by constantly having to relocate the nipples. Most of the other mothers allowed their kittens to remain attached to the nipples without any interruptions in the early weeks, and stayed in half-sit or on-side-lie even after the kittens had fallen asleep and come off the nipples. Some mothers spent exceptionally long periods of time beside their kittens in half-sit or on-side-lie (usually the latter),

even in later weeks, eg B4, weeks 1-5;   B5, weeks 1-6.

3.2.2 Initiation of feeding interactions

Feeding interactions began in a number of different ways, depending on who initiated the interaction, what position the mother was in prior to the interaction, and what position she was in when the kittens attached to the nipples.   The interactions are divided below, first into those in which the mother was in half-sit or on-side-lie when the kittens first attached to the nipples (or at least soon after) = Type 1, and secondly those in which she was sitting = Type 2.   Further sub-divisions are then made.

Type 1

Initiated by mother: (a) The mother took up half-sit or on-side-lie beside her kittens without their prompting.   The kittens either began to nuzzle and then attach to the nipples immediately or, if they were asleep, some time later, when they had awakened.   The mother herself sometimes wakened the kittens by licking and/or pawing them.

Initiated by kitten(s):   (b) The kittens approached their mother when she was in half-sit/on-side-lie, nuzzled her and then made nipple attachment.

(c) The kittens nuzzled and perhaps made nipple attachment when their mother was sitting beside them and she immediately took up half-sit/on-side-lie.

(d) The kittens approached their mother, who was in a body position other than half-sit/on-side-lie, and began nuzzling and perhaps attached to the nipples and she took up half-sit/on-side-lie.

Type 2

Initiated by kitten(s): (a) The kittens nuzzled and attached to the nipples when their mother was sitting beside them and she remained sitting.

(b) The kittens approached their mother, who was sitting, nuzzled and attached to the nipples, and she remained sitting.

(c) The kittens approached their mother, who was in a body position other than sit, and began nuzzling and perhaps attached to the nipples and she got into the sit position.

In all feeding interactions observed in the first 3 weeks the mother was initially beside her kittens in the litter box. (The kittens did not begin to make their first unsteady walking steps until about $2\frac{1}{2}$ weeks of age (Plate 13) and could not usually climb out of the litter box until the 4th week.) These interactions were 1(a), 1(c) and 2(a). In 1(a) the mother makes herself positively available to the kittens for feeding. In 1(c) she responds to their behaviour and takes up a position that appears to make nipple attachment easier for the kittens. In 2(a) the mother is not being so accommodating and the kittens have to persevere with attempting to make nipple attachment while their mother is sitting. Some families used 1(a) interactions almost exclusively, eg C1, C6, C8, B4 and B6. Others mostly used 1(a) interactions but were occasionally observed in 1(c) interactions (especially from week 2 onwards), eg B5 and B8. Finally there were some families in which 2(a) interactions were quite often observed, eg C3, weeks 1 and 2; C2, week 2. Over the course of the 3 weeks there was a general tendency for 1(c) and 2(a) interactions to become more common. From week 4, the interactions in which kittens made approaches to their mothers became more common and so did Type 2 interactions,

where mothers did not get into half-sit or on-side-lie for their
kittens, but remained sitting.   However there was considerable indi-
vidual variation between families in the interactions they tended to
use.   For example, at week 6, some mothers were still making them-
selves positively available for their kittens to attach to the
nipples by getting into half-sit or on-side-lie beside them (ie 1(a)
interactions).   These were females C1, C4, C7, B4, B5, B6 and B7.
Other mothers were less accommodating but nevertheless generally
responded to their kittens nuzzling by taking up half-sit or on-side-
lie, eg C2, B1, B3 and A1.   From week 4, mother C3 allowed her kit-
tens to attach to the nipples whenever she was sitting but she did
not get into half-sit or on-side-lie for them.   The other mothers
were, to varying extents, rather less receptive to their kittens'
attempts to make nipple attachment during the last 3 weeks.   They
discouraged their kittens from doing so in a number of different
ways.

1 By standing up when the kittens were on-nipple, and thus
dislodging them from the nipples, eg C5, weeks 4 and 6.

2 By leaving when the kittens had only been on-nipple for a very
short period, eg B8, week 5.

3 By taking up positions such as crouch and lie, in which the
nipples were hidden, eg B8, week 5;   and remaining in that
position even when the kittens nuzzled, eg C5, week 6.

4 By walking around a lot and not responding to the kittens who
followed them crying.   Such kittens were clearly attempting to
make nipple contact because they nuzzled whenever their mother
stopped to rest, eg C6, week 6;   C8, weeks 4 and 5;   B2, weeks
4-6.

5 By generally avoiding their kittens, eg C8, weeks 4-6;

B2, week 5;   B8, weeks 5 and 6.

6 By responding to their kittens' approaches with aggression
such as vocalisations (yowl and growl) and striking the kittens,
eg C8, weeks 4 and 5.

3.3 QUALITATIVE RESULTS ON BEHAVIOUR NOT DIRECTLY RELATED TO FEEDING. DETAILS OF INDIVIDUAL DIFFERENCES IN THE MOTHER-KITTEN RELATIONSHIP

3.3.1 Mother's attentiveness

Attentiveness included not only spending a lot of time with the
kittens but also actively paying attention to them by looking at them.
Attentive mothers were also those who returned quickly to their kit-
tens after an absence.   Most mothers became less attentive over the
first few weeks but in this early stage of the mother-kitten relation-
ship, mothers did differ in how attentive they were.   Mothers who
were especially attentive included C8, weeks 1 and 2, B7, weeks 1 and
2.   Those who were considered inattentive were C3, week 1;   B2,
weeks 1 and 2;   B3, weeks 1 and 2;   B4, week 1 (this last did stay
with her kittens but paid them no attention).   The other mothers
were either very attentive or moderately so.

Inattentive behaviour may have been related to other aspects of
the mother's behaviour such as whether she reacted to external
events, or whether she was disturbed or excited.   These behavioural
characteristics are discussed below in 3.3.6.

3.3.2 Licking of kittens (Plate 22)

Mothers were observed to differ considerably in terms of how
much they licked their kittens and quantitative data was collected on
this measure, so that mothers could be compared.   One observation of
interest however was that licking often occurred in conjunction with

the mother eating.   The following events were often witnessed: the mother went to the food dish, took a mouthful of food and carried it back to the litter box where she stood over the kittens and began eating, usually dropping some of the food on the kittens' bodies. In the process of picking up the food she licked the kittens and then, having eaten the food, she licked them for a while before returning to the food dish.   This chain of events was usually repeated several times.   After eating had terminated, licking kittens and self grooming often occurred together.   It was interesting to note that some mothers seemed to spend more time grooming themselves, than licking their kittens.

3.3.3 Pawing of kittens (Plate 23)

Pawing was seen most commonly when the kittens were on-nipple and the mother was in on-side-lie or half-sit.   However some mothers were observed pawing when they were sitting, and their kittens were asleep beside them, eg C4, week 1.

As mentioned in 3.2.2, this pawing sometimes woke the kittens who then began nuzzling.   Pawing seemed to reflect a state of excitement perhaps exemplified by C4 who was a rather excitable mother (3.3.6).   Mothers differed in their pawing behaviour with some pawing a great deal, others doing so only occasionally, and yet others almost never.

3.3.4 Vocalising (Appendix B)

Mothers differed considerably in how vocal they were and in which vocalisations they tended to use.   Quantitative data was collected on vocalisations, however a few points are worth mentioning here.   The brrp vocalisation was used most frequently when the

mother was at a distance from her kittens, eg when she was returning
to them after an absence from the litter box, or when she was
watching them explore and play around the cage. Mothers were most
often heard purring when the kittens were on the nipple. However
some mothers purred almost continuously (eg B7) and therefore did so
in many other situations. There were some mothers who were almost
never heard to purr, eg B4 and Al. Only one mother, B2, cried to
any great extent. She did so when she was pacing restlessly around
her cage.

3.3.5 Mother's tolerance of her kittens outside the feeding context

A mother's tolerance of her kittens was assessed mainly through
(a) her reaction to her kittens making playful approaches to her and
through (b) her behaviour when the kittens were actively moving
around the cage and playing, but not interacting with her. Mothers
tended to behave in one of the following ways.

1   Mothers sat and watched their kittens when they played and
were tolerant of the kittens when they pawed and climbed on
them, eg C2, week 5; C3, weeks 5 and 6; C7, weeks 5 and 6;
B1, week 6; B3, week 5. Some of the mothers made brrp vocal-
isations to their kittens (C3, B1 and B3), and C7 licked her
kittens when they pawed her.

2   Mothers actively moved around when their kittens were
playing, eg C4, week 6; B4, week 6; B6, week 6; B7, weeks
4-6; Al, week 6. Some of these mothers purred and made brrp
vocalisations to their kittens (B4, B6 and B7). B6 also
rolled on her back playfully.

3   Mothers ignored and avoided their kittens when they were
playing, eg C6, week 6; B5, week 6; B8, week 5. C6 sometimes

moved away when her kittens pawed her.

4   Mothers showed aggression when their kittens played, eg C8,
week 5.   This mother yowled (aggressive vocalisation) at her
kittens.

Mothers who fell into either 1 or 2 categories were termed tolerant,
3 and 4 intolerant.

3.3.6 Mother's personality

In the diary, and in the summaries of diary entries presented in
Appendix A , a number of terms were used to describe the general
behaviour of mothers.   Definitions of these are given below.

Quiet   The mother is not highly active, but is rather peace-
ful.   When she does move around she does so quietly.

Excited   As 2.2.7.

Disturbed   As 2.2.7.

Reactive   The mother shows a change in behaviour in
response to the approach or presence of the observer,
or other external events, such as loud noises.   She
may either show excited or disturbed behaviour as des-
cribed in 2.2.7.

3.4. CLASSIFICATION OF MATERNAL TRAITS AND MOTHER-KITTEN RELATIONSHIPS USING QUALITATIVE DATA

Mothers have been shown to vary on a number of behavioural
characteristics, but to illustrate their individuality by comparing
each mother, on each behavioural characteristic, is a laborious task.
It was therefore attempted to classify mothers on the basis of
several selected behavioural characteristics and then to see how the

classes compared on other characteristics. The method is now des-
cribed.

3.4.1 Quality of care

In the first two weeks *post partum* certain mothers, C3, B2 and
B4, were recorded as showing poor exposure of the ventral surface in
half-sit and on-side-lie positions; they trapped their kittens
behind or underneath them when in these two positions due to their
inappropriate orientation when taking up the positions; and they
were inattentive. It was decided that mothers who showed these
traits would be defined as exhibiting low quality care. When the
same mothers were assessed on one other important maternal charac-
teristic, reactivity, all mothers were rated as reactive. In
addition, the kittens in all of these families (C3, B2 and B4) were
reported as having some difficulties in locating and attaching to the
nipples. Furthermore, it is interesting that B2 and B4 were 2 of
the 3 litters in which kitten death(s) occurred in the first 3 weeks
(not including deaths that may have been still births - Table 2.2).

Some mothers were considered to show a maternal trait which was
termed high quality care - C2, C7, B5, B6 and B7. Each of these
mothers exposed their ventrum very well in half-sit and on-side-lie
positions; orientated themselves appropriately when taking up the
positions; and were rated as highly attentive. Only one mother,
B7, was sometimes reactive, but she always settled down very quickly
beside her kittens again, in a position where they could easily
relocate the nipples. So, in contrast to low quality care mothers,
high quality care mothers were generally unreactive. (One anomaly
is the death of a kitten of one of the high quality care mothers,
B5, at 3 days. The cause of death was unknown, but it seemed

unlikely that it was the result of the mother's behaviour.)

Mothers who were not classified above as exhibiting either low or high quality care could not be said to fall into one simple category. C1, C4, C5, B1, B3, B8 and A1 could be considered to have exhibited intermediate quality care. They showed some of the characteristics of both low and high quality care mothers and, in addition, had intermediate ratings on certain other characteristics. The 6 mothers however did not necessarily exhibit the same combination of characteristics as one another. They were a rather heterogeneous group and could perhaps have been further sub-divided.

Mother C6 could have been rated as a high quality care mother in week 3 but, before that, she exhibited some low quality care characteristics. No information was collected on the ventral exposure of C8 but her other characteristics would have placed her in the high quality care group. Neither C6 nor C8 could be properly classified.

In Table 3.1 a summary is given of the classification of mothers on the basis of the quality of the care they gave their kittens in weeks 1-3.

3.4.2 Tolerance of kittens

The other classification scheme devised, was based on the relationship (in weeks 4-6) between a mother's behaviour during feeding interactions (3.2.2), and her reactions to her kittens' playful activities (3.3.5). Mothers who usually allowed their kittens to attach to the nipples in half-sit and on-side-lie positions in weeks 4, 5 and 6 (either at the kittens' initiative or their own) and who were tolerant of their kittens when they were active and playing, were considered to be tolerant of their kittens in general.

These mothers were C2, C4, C7, B1, B3, B4, B6 and B7. Mothers classified as being intolerant of their kittens, in the 4-6 week period, were C6, C8 and B8. These mothers tended to take up half-sit and on-side-lie positions (for their kittens to make nipple attachments), less readily and less frequently, than the tolerant mothers above; and when they did so it was almost always at the kittens' initiative. The mothers were also intolerant of their kittens' play.

Six of the 17 mothers could not be placed in either of the above groups of tolerant or intolerant mothers. These were C1, C3, C5, B2, B5 and A1. Two of these mothers - C3 and B5, could however be considered as having exhibited intermediate tolerance. C3 tolerated her kittens' play, but was rarely seen in half-sit or on-side-lie with kittens on-nipple; most nursing took place when the mother was sitting. B5, on the other hand, was still taking up half-sit and on-side-lie for her kittens in week 6, but was intolerant of her kittens' play. At week 6, mother C1 was still initiating feeding interactions with her kittens, by taking up half-sit or on-side-lie beside them, without their prior prompting. However, since no information was collected in the diary on her reaction to her kittens' play, mother C1 could not be classified. The kittens of families C5 and B2 played rather little and no notes were made in the diaries of their mothers' reaction to play when it did occur. It was therefore not possible to classify these 2 mothers. (If the mothers could have been classified on the basis of their feeding interactions alone, both C5 and B2 would have been placed in the intolerant group.) No diary record was available for family A1 in week 6, but up until week 5 mother A1 would have been classified as tolerant.

A summary of the classification of mothers in weeks 1-3, and in weeks 4-6, is presented in Table 3.1.

TABLE 3.1   Classification of mothers on the basis of the quality of
             their relationships with their kittens

Weeks 1-3:	Low quality care	Intermediate	High quality care	Unclassified
	C3	C1	C2	C6
	B2	C4	C7	C8
	B4	C5	B5	
		B1	B6	
		B3	B7	
		B8		
		A1		

Weeks 4-6:	Intolerant of kittens	Intermediate	Tolerant of kittens	Unclassified
	C6	C3	C2	C1
	C8	B5	C4	C5
	B8		C7	B2
			B1	A1
			B3	
			B4	
			B6	
			B7	

In week 1-3 mothers were classified as showing either
low, intermediate or high quality care towards their
kittens.   If they could not be placed in one of these
groups then they were termed 'unclassified'.   Likewise,
in weeks 4-6, the mothers were classified as being
intolerant, intermediate, or tolerant, of their kittens.
Again, some mothers were unclassified.   See 3.4.1 and
3.4.2 for explanations of the above terms.

3.5 SUMMARY OF QUALITATIVE RESULTS

Mothers can be compared on a number of behavioural character-
istics which relate to their interactions with their offspring.
These are

1   The exposure of the mother's ventral surface in half-sit
and on-side-lie positions.

2   The responsiveness of the mothers whose kittens have diffi-
culties in locating and attaching to the nipples.

3   The way in which mothers orientate themselves in relation
to their kittens when taking up half-sit and on-side-lie
positions.

4   The responsiveness of the mothers whose kittens become
trapped behind or underneath them.

5   The length of time that the mothers remain in half-sit or
one-side-lie without interruption.

6   The nature of the feeding interactions. In particular,
whether the mother or the kittens initiate interactions;
whether the mother always allows her kittens to attach to the
nipples; in what position the mother usually nurses her
kittens; if the mother discourages or prevents her kittens
from attaching to the nipples, how she does so.

7   The mother's attentiveness.

8   The mother's tolerance of her kittens' playful activities.

9   The mother's personality.

Mothers are classified on the basis of how they are subjectively
rated on the above behavioural characteristics. In weeks 1-3, most
mothers can be described as exhibiting either low, intermediate or
high quality care. In weeks 4-6 most mothers are classified as
intolerant, intermediate, or tolerant of their kittens. With each

classification scheme there are some mothers who do not fall into any category.

3.6 QUANTITATIVE RESULTS ON FEEDING INTERACTIONS

3.6.1 General Introduction

After the first few observation sessions of the study, in which 100 scans per session were made of each family, the number of scans was reduced to 50 per session (2.2.4 and 2.2.5).   In order to make scores from the early sessions comparable to those in subsequent sessions, the total number of scores for each behavioural measure recorded in one session was transformed into a percentage (henceforth called 'percentage score') of the total number of scans in the session.   The method is described in 2.2.9, but a few examples are given here to clarify the procedure.

If a mother received a total of 23 scores (out of a possible 50, where 50 scans had been made) for on-side-lie, then she would have a percentage score of 46, or a score of 46%, on on-side-lie.

If after 50 scans a litter of 3 kittens had a score of 30 for still by mother, then this score would first be divided by 3 to give an average kitten score, or mean score for the litter, of 10.   The litter would therefore have a percentage score of 20, or a score of 20%, on still by mother.

In some of the analyses performed in 3.6 - 3.8, the data used consist of mothers' and litters' percentage scores for each of 4 weekly sessions for 6 weeks.   In other analyses the data set consists of mean weekly percentage scores (for each of the 6 weeks) which have been calculated for each mother and each litter.   The form of data used in an analysis is always stated.

For the majority of the statistical analyses performed in

3.6 - 3.8 the Statistical Package for the Social Sciences was employed (Nie *et al* 1975).

3.6.2 Evidence for individual differences in maternal and litter behaviour related to feeding

1 Maternal behaviour

In order to ascertain whether mothers differed significantly, and consistently from one another, in terms of their percentage scores on behavioural measures related to feeding, analysis of variance was performed on each of the following maternal behaviour measures: sit, sit-nurse, half-sit, on-side-lie, half-sit + on-side-lie, crouch, lie, crouch + lie, and shift. Half-sit + on-side-lie, and crouch + lie are composite measures used in many of the analyses in the forthcoming sections of this chapter. Half-sit and on-side-lie were made into a combined measure because in relation to feeding they both seem to serve the same function - that of allowing kittens access to the nipples (3.2.1). Similarly, crouch and lie both appear to serve the function of making access to the nipples impossible, and so they too were combined to give one measure.

The data used in the analysis of each behavioural measure con-sisted of each mother's percentage score on the measure in each ses-sion (3.6.1). Two-way analysis of variance with replicates (the 4 percentage scores each week) was employed to take into account both the effects of differences between mothers, and changes with time in weeks.

Analyses of variance were performed on untransformed data and results are presented in Table 3.2. However see Appendix E where tests for normality are run on the data and the results of these tests discussed.

For all measures, except half-sit, both mother, and week main effects are significant. This means that, over the 6 week period, there is significant variation between mothers in their percentage scores on each measure, and that, for mothers in general, their percentage scores on each measure show significant changes across the 6 weeks. (Half-sit scores do not change significantly across the 6 weeks but there is significant variation between mothers on this measure.) The interaction effects between mothers and weeks are also of importance. If the interaction effects were greater than the main effects themselves (indicated by F ratio values of each), then this would indicate that the differences between mothers are not consistent, due to different mothers showing different patterns of

TABLE 3.2 Two-way analysis of variance on maternal behavioural measures related to feeding

	Source of Variance		
	Main Effects		Interaction Effect
Measure	Mothers	Weeks	Mothers x Weeks
Sit	8.91***	19.24***	1.32
Sit-nurse	17.73***	5.64***	2.97***
Half-sit	14.97***	1.03	1.55**
On-side-lie	6.54***	46.01***	1.55**
Half-sit + on-side-lie	9.57***	33.05***	1.80**
Crouch	8.21***	6.61***	2.29***
Lie	6.41***	10.99***	1.79***
Crouch + lie	8.65***	15.98***	2.01***
Shift	3.90***	25.16***	2.08***

F ratios are given with significance levels indicated as follows: ** $p < 0.01$, *** $p < 0.001$

Degrees of freedom are, mothers: 16, 288;

weeks: 5, 288;

mothers x weeks: 77, 288

change across the 6 weeks. However, although the interaction effects

are significant, their F ratio values (for each measure) are con-

siderably smaller than those of the main effects (Table 3.2).

This indicates that although some mothers do change in relation to

one another, there is overall consistency in the differences between

mothers, in terms of their percentage scores on each measure over

the 6 weeks.

In Appendix C graphs showing mean weekly scores (for all

mothers) for each of the measures (except half-sit) are presented to

illustrate the changes that occurred over the 6 weeks. See Figure C(1)

for measures half-sit + on-side-lie, and on-side-lie. See Figure C(2)

for measures sit, sit-nurse, and shift. See Figure C(3) for

measures crouch, lie, and crouch + lie. (Half-sit weekly means are

not plotted but these can be derived by subtracting on-side-lie means

from half-sit + on-side-lie means.) The graphs themselves are self-

explanatory but the trends that various behavioural measures show

over the 6 weeks are discussed and compared with findings from other

studies in Appendix C.   The same applies to the other

graphs presented in Appendix C.

2   Litter behaviour

In order to ascertain whether litters differed significantly

and consistently from one another in their percentage scores on

behavioural measures related to feeding, analysis of variance was

performed on the following measures: nuzzle, on-nipple, on-nipple in

sit, on-nipple in half-sit + on-side-lie. On-nipple in sit and on-

nipple in half-sit + on-side-lie are derived measures. They had to

be derived since on-nipple was scored regardless of the mother's body

position. The derivation procedure is described in Appendix D.

The analyses of variance were performed on untransformed litter

data.   The data on each measure consisted of each litter's percen-
tage score on the measure for each session.   As for the maternal
behaviour analyses, two-way analysis of variance (with replicates)
was used, to take into account both the effects of differences
between litters and differences between weeks.   Results of the
analyses are presented in Table 3.3.   (but see also Appendix E).

For all the measures both litter and week main effects are sig-
nificant.   Therefore, over the 6 week period, there is significant
variation between litters in their percentage scores on each
measure, and for all litters in general their percentage scores on
each measure show significant changes across the 6 weeks.   Since
even where interaction effects are significant, their F ratio values
are smaller than those of the main effects, the differences between
litters can be considered as generally consistent over the 6 weeks
(for all measures).   In other words each litter tends to show the
same patterns of change in its percentage scores on each measure
across the weeks.   (Although where the interaction effects are sig-
nificant some litters are changing in relation to one another over
the 6 weeks.)   In Appendix C   Figure C(7) graphs showing mean weekly
scores (for all litters) of each of the measures are presented to
illustrate their changes across the 6 weeks.   See also Appendix F for
correlations between weeks of selected maternal and litter measures.

TABLE 3.3 <u>Two-way analysis of variance on litter behaviour</u>
<u>measures related to feeding</u>

Measure	Source of Variation		Interaction Effect
	Main Effects		
	Litters	Weeks	Litters x Weeks
Nuzzle	3.83***	37.10***	1.33
On-nipple	4.49***	34.85***	1.60**
On-nipple in sit	6.96***	4.62***	2.02***
On-nipple in half-sit + on-side-lie	4.47***	42.75***	1.53**

F ratios are given with significance levels indicated
as follows: ** p < 0.01, *** p < 0.001

Degrees of freedom are litters: 16, 288
weeks: 5, 288
litters x weeks: 77, 288

3.6.3 The effects of litter size, sex ratio and kitten death in the litter on maternal and litter behaviour related to feeding

Since, as shown in Table 2.2, families differed in litter size, sex ratio in the litter and in whether or not there had been kitten death(s) in the litter, the contributions of these variables to the individual variation in mothers and litters were investigated. It was decided that only the deaths that occurred within the period of observation of a family (ie between the first observation in week 1 and the last in week 6) would be included in the analysis. It was thought likely that such deaths would have more direct effect on the behaviour observed, than deaths or still births that occurred prior to the start of observations on the family. Therefore, only families C8, B2 and B4 were classified as having kitten deaths for the purposes of the analyses (Table 2.2). Regression analyses were performed to examine the relationships between litter size, sex ratio, and kitten death, and maternal and litter behaviour related to feeding. Regression analysis was used, rather than simply a one-way analysis of variance, to examine the effects of kitten death. Regression analysis reveals (through the sign of the regression coefficient), whether significant associations between kitten death and particular behavioural measures are positive associations or negative ones.

The regression analyses were run on untransformed data (as in 3.6.2). However see Appendix E for tests for normality of the data.

1   Maternal behaviour

The behaviour measures are listed with the results of the analyses in Tables 3.4 - 3.6. The SPSS regression analysis programme (Nie *et al* 1975) calculates F ratios and these can be used to

test the significance of the regressions. The regression coefficient gives the slope of the regression line and its sign indicates whether relationships are positive or negative. The coefficient of determination, r^2, indicates the proportion of the variance in each measure accounted for by litter size, sex ratio and kitten death.

Litter size

There is a significant positive association between litter size and shift but significant negative associations between litter size and lie, and crouch + lie; the latter is almost entirely due to the association between litter size and lie.

Sex ratio

Three measures, half-sit, lie, and crouch + lie are associated with higher proportions of males in litters (again the association of crouch + lie is mainly due to lie). On-side-lie is associated with there being a higher proportion of female kittens in litters.

Death

There are negative associations between death and the measures sit, and half-sit, but positive associations with the measures crouch + lie, and shift.

These findings are discussed more fully in 4.2.2 (as are subsequent results (in this chapter) on the effects of litter size, sex ratio and kitten death). However it should be said that even where associations are significant, the variable (whether it be litter size, sex ratio, or death) accounts for only a very small proportion of the variance in the measures (as indicated by r^2 values). The effects of the variables are therefore minimal.

Where two or more variables are significantly associated with the same behavioural measure it may be the case that only one of the variables is in fact associated with the measure and that the

TABLE 3.4   <u>Regression analysis of the relationship between litter</u>
<u>size and maternal behaviour measures related to feeding</u>

Measure	F ratio	Regression coefficient (b)	Coefficient of determination (r^2)
Sit	2.77		
Sit-nurse	0.68		
Half-sit	0.02		
On-side-lie	0.14		
Half-sit + on-side-lie	0.20		
Crouch	0.88		
Lie	5.25*	− 0.018	0.013
Crouch + lie	6.59*	− 0.025	0.014
Shift	5.33*	0.003	0.014

F ratio values are given with significance levels
indicated as follows: * $p < 0.05$

Degrees of freedom: 1, 385

F ratio values are presented for all measures, but only
where these are significant are regression coefficients
(b) and coefficients of determination (r^2) given. (b)
indicates whether there is a positive or negative
association between litter size and the behaviour
measure in question. (r^2) indicates the proportion of
variance in the measure that is accounted for by the
variable litter size.

TABLE 3.5   Regression analysis of the relationship between sex ratio
             and maternal behaviour measures related to feeding

Measure	F ratio	Regression coefficient (b)	Coefficient of determination (r^2)
Sit	3.79		
Sit-nurse	0.80		
Half-sit	11.76**	0.065	0.030
On-side-lie	9.94**	- 0.124	0.025
Half-sit + on-side-lie	1.93		
Crouch	0.17		
Lie	6.24*	0.048	0.016
Crouch + lie	4.98*	0.051	0.010
Shift	1.75		

F ratio values are given with significance levels
  indicated as follows: * $p < 0.05$, ** $p < 0.01$
Degrees of freedom: 1, 385
F ratio values are presented for all measures, but only
  where these are significant are regression coefficients
  (b) and coefficients of determination (r^2) given.   If
  (b) is positive this indicates that the measure is
  associated with a greater proportion of males in the
  litter; if it is negative the association is with a
  greater proportion of females. (r^2) indicates the pro-
  portion of variance in the measure that is accounted
  for by the variable sex ratio.

TABLE 3.6 <u>Regression analysis of the relationship between kitten death and maternal behaviour measures related to feeding</u>

Measure	F ratio	Regression coefficient (b)	Coefficient of determination (r^2)
Sit	4.98*	− 0.037	0.013
Sit-nurse	0.47		
Half-sit	6.14*	− 0.040	0.015
On-side-lie	2.33		
Half-sit + on-side-lie	0.13		
Crouch	0.22		
Lie	0.08		
Crouch + lie	6.48*	0.049	0.014
Shift	5.25*	0.006	0.013

F ratio values are given with significance levels indicated as follows: * $p < 0.05$

Degrees of freedom: 1, 385

F ratio values are presented for all measures, but only where these are significant are regression coefficients (b) and coefficients of determination (r^2) given. (b) indicates whether there is a positive or negative association between kitten death and the behaviour measure in question. (r^2) indicates the proportion of the variance in the measure that is accounted for by the variable kitten death.

associations of the other variables are the result of inter-correlations between the variables themselves. Such results would therefore normally have to be treated with some caution. However since it was demonstrated that for no behavioural measure did any of the variables account for a very large proportion of the variance in that measure, none of the variables have been implicated as having a great effect on the behaviour of mothers or kittens in any instance.

2   Litter behaviour

Regression analyses were also performed on litter behaviour measures related to feeding. (These were the same measures as those on which two-way analysis of variance was performed in 3.6.2.) The results of the analyses, including F ratios, regression coefficients (b), and coefficients of determination (r^2), are given in Tables 3.7 - 3.9. The only significant association is that between on-nipple, and a higher proportion of female kittens in litters (indicated by the negative sign of (b)). However as with the maternal measures, the r^2 value is low, demonstrating that sex ratio does not account for a very large proportion of the variance in on-nipple scores.

TABLE 3.7   <u>Regression analysis of the relationship between litter</u>
             <u>size and litter behaviour measures related to feeding</u>

Measure	F ratio	Regression coefficient (b)	Coefficient of determination (r^2)
Nuzzle	< 0.01		
On-nipple	2.59		
On-nipple in sit	0.50		
On-nipple in half-sit + on-side-lie	2.06		

Degrees of freedom: 1, 385

Since the above F ratios are not significant the
regression coefficients (b) and coefficients of
determination (r^2) are not presented

TABLE 3.8   <u>Regression analysis of the relationship between sex ratio</u>
<u>and litter behaviour measures related to feeding</u>

<u>Measure</u>	<u>F ratio</u>	<u>Regression coefficient (b)</u>	<u>Coefficient of determination (r^2)</u>
Nuzzle	2.15		
On-nipple	4.19*	– 0.044	0.011
On-nipple in sit	3.48		
On-nipple in half-sit + on-side-lie	2.38		

* Indicates that the F ratio significance level is $p < 0.05$

Degrees of freedom: 1, 385

Regression coefficients (b) and coefficients of determination (r^2) are only presented for significant F ratios.   The negative sign of (b), for on-nipple, indicates that higher scores on this measure are associated with a higher proportion of females in litters.

TABLE 3.9   <u>Regression analysis of the relationship between kitten</u>
<u>death and litter behaviour measures related to feeding</u>

Measure	F ratio	Regression coefficient (b)	Coefficient of determination (r^2)
Nuzzle	2.12		
On-nipple	1.63		
On-nipple in sit	0.56		
On-nipple in half-sit + on-side-lie	0.79		

Degrees of freedom: 1, 385

Since the above F ratios are not significant the
regression coefficients (b) and coefficients of
determination (r^2) are not presented.

3.6.4 <u>Details of individual differences in the mother-kitten relationship related to feeding</u>

Mothers have been shown to differ from one another on a variety of behavioural measures related to feeding (as have kittens from different litters - 3.6.2), and the factors litter size, sex ratio and kitten death have been demonstrated to account for only a small proportion of the variance in mothers' and litters' behaviour where they account for any at all (3.6.3).   The nature of the individual differences in mothers and in litters is now examined and the relationship between maternal differences and litter differences investigated. This section is divided into 3 parts on the basis of which measure of maternal behaviour is mainly under consideration.

1   <u>Half-sit + on-side-lie</u>

In order to illustrate the differences in individual mothers' half-sit + on-side-lie behaviour, and their litters' on-nipple in half-sit + on-side-lie behaviour (Appendix D for the derivation of the latter measure), and to investigate the relationship between the two, each litter's mean weekly percentage score was plotted against its mother's mean weekly percentage score (3.6.1 explains how these scores are calculated) for each week (Figure 3.1).   Regression analysis was performed on each week's data and the results are presented in Table 3.10 where regression coefficients (b), t values and their significance levels, and coefficients of determination (r^2) are given.   (The SPSS regression programme was not used for these regression analyses, and the programme used generated t values not F ratio values as in the regressions in 3.6.3.   Therefore t values were used to test the significance of the regression relationships.) Regression lines were calculated and are drawn in the graphs in Figure 3.1.

FIGURE 3.1   In the 6 graphs shown litters' mean weekly
              percentage scores for on-nipple in half-sit
              + on-side-lie for each week (Y axis) are
              plotted against their mothers' mean weekly
              scores on half-sit + on-side-lie.   From
              regression analyses performed on the data
              (Table 3.10) regression lines were calculated
              and these are drawn.
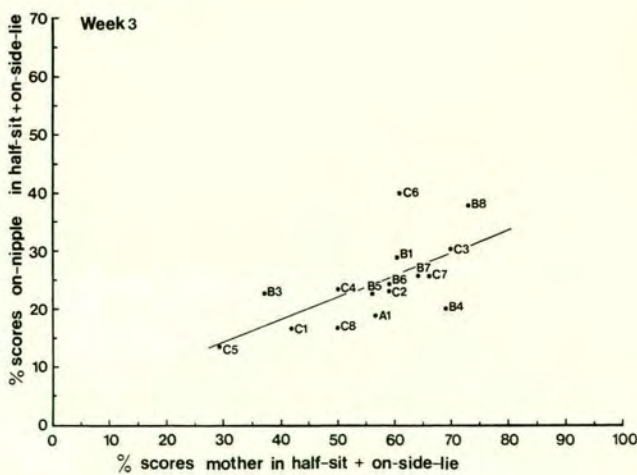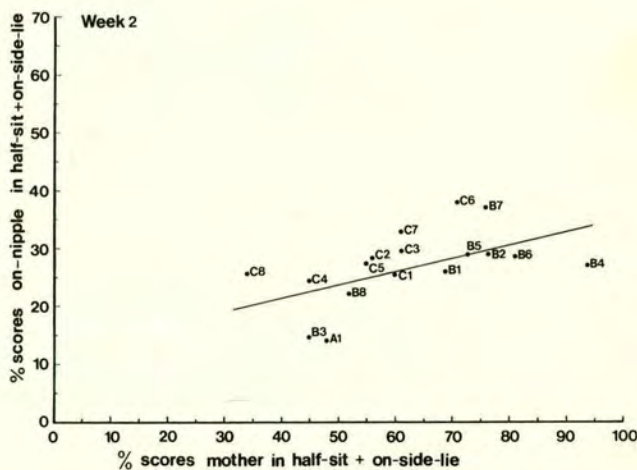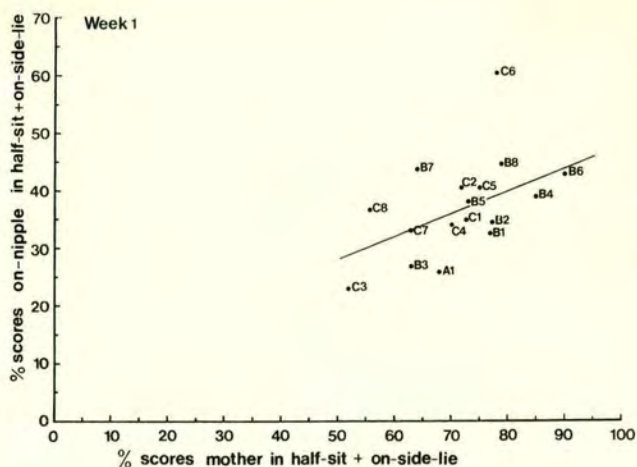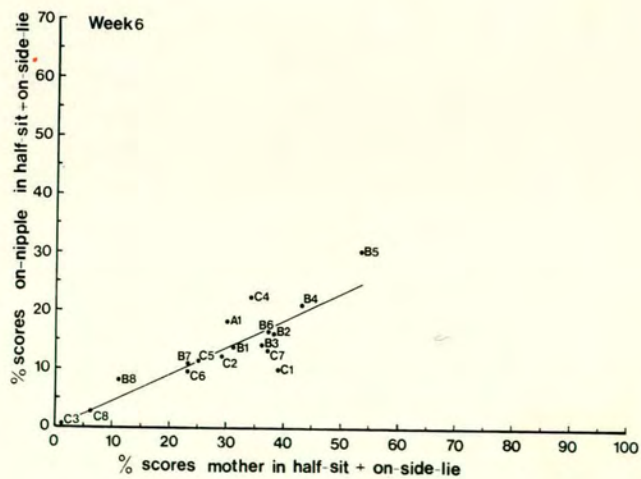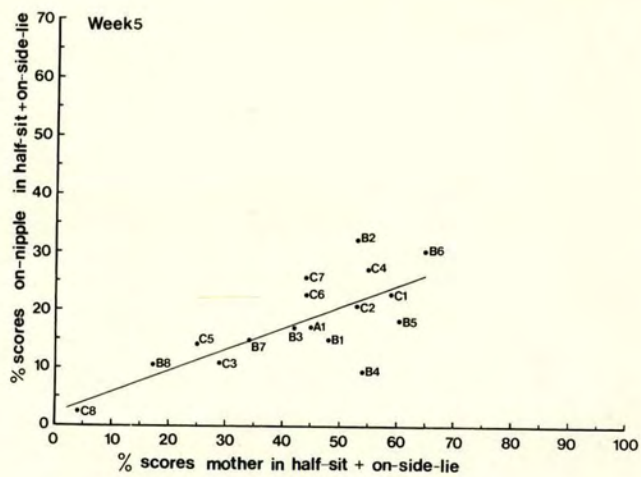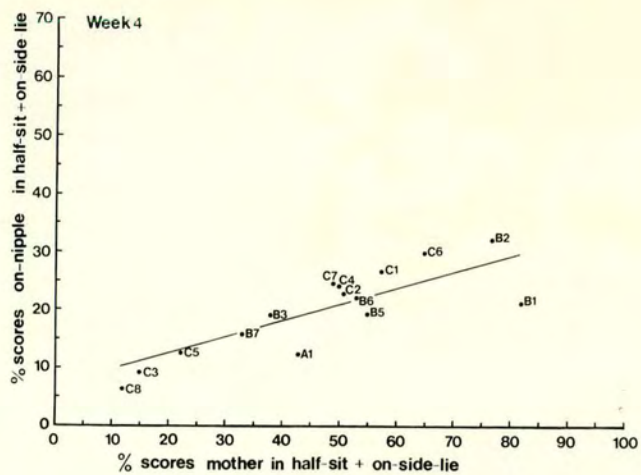
TABLE 3.10   Results of regression analyses in which litters' mean
weekly percentage scores on on-nipple in half-sit
+ on-side-lie, were regressed against their mothers'
mean weekly percentage scores on half-sit + on-side-lie
each week

Week	t	Regression coefficient (b)	Coefficient of determination (r^2)	Degrees of freedom
1	2.289*	0.448	0.259	15
2	2.386*	0.223	0.276	15
3	3.197**	0.385	0.423	14
4	5.728***	0.307	0.716	13
5	4.129***	0.350	0.531	15
6	6.814***	0.465	0.757	15

t values are given with significance levels indicated as
follows * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.   The sig-
nificance of the t values indicates the significance of
the relationship between mothers' behaviour and their lit-
ters' behaviour each week.   (b) indicates whether the
relationship is positive or negative.   (r^2) values indicate
the proportion of variance in litters' scores accounted for
by the variance in mothers' scores.

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t is significant throughout the 6 week period and the regression coefficient always has a positive sign, indicating that there is a significant positive relationship between mothers' behaviour and their litters' behaviour each week. (In Appendix D the relevance of on-nipple in half-sit + on-side-lie being a derived measure is discussed in relation to the regression analyses findings.) Therefore mothers with highest mean weekly percentage scores on half-sit + on-side-lie have litters with highest mean weekly percentage scores on on-nipple in half-sit + on-side-lie, and vice versa.

r^2 is a measure of the proportion of the variance in Y values (litters' scores) that are accounted for by the variance in X values (mothers' scores). r^2 values show an increase up to week 4 (after which they remain high), suggesting that the strength of the relationship between mothers' scores and litters' scores is becoming greater up to this time. In Table 3.11 the variance in mothers' mean weekly percentage scores, litters' mean weekly percentage scores, and the variance around the regression lines (drawn in Figure 3.1) are presented for each week.

The increase in r^2 that occurred between weeks 1 and 4 may have merely been a result of the increase in the mothers' variance in these weeks (and the relative stability in the variance of litters' scores). As such the increase in r^2 may not indicate any real strengthening in the relationship between maternal and kitten behaviour. In week 6 however r^2 has its highest value of all the weeks and the variance in mothers' scores has decreased again. This indicates that the increase in r^2 over the weeks is a reflection of the fact that litters' scores are becoming more closely determined by their mothers' scores. In week 6 for example a litter's score can be predicted more easily from its mother's score

TABLE 3.11   Variance in mothers' mean weekly percentage scores in
half-sit + on-side-lie, litters' mean weekly percentage
scores in on-nipple in half-sit + on-side-lie, and the
variance around the regression lines shown in Figure 3.1

Week	Variance in mothers' scores	Variance in litters' scores	Variance around regression lines
1	97.4	75.4	226.2
2	239.7	43.3	40.3
3	149.5	52.6	55.1
4	423.8	55.6	8.3
5	272.4	62.7	17.2
6	180.3	51.6	5.4

than in week 1.

The regression analyses demonstrate that regardless of the magnitude of a mother's score on half-sit + on-side-lie, her litter's score on on-nipple in half-sit + on-side-lie is in approximately the same proportion to her score, as all other litters' scores are to their mothers' scores. It might have been expected that litters whose mothers had low scores on half-sit + on-side-lie would have spent a greater proportion of those scores on the nipple (since as shown below this would have been theoretically possible), in order to compensate for what appears to be a lack of opportunities to attach to the nipples. However this was not the case. Possible reasons are discussed in 4.1.2, Part 2.

The proportion that on-nipple in half-sit + on-side-lie was of half-sit + on-side-lie was calculated for each litter each week. The mean proportions (for all litters) each week are presented in Table 3.12. It can be seen that for most weeks litters (ie the average kitten in each litter) were on the nipple for less than half of their mothers' scores on half-sit + on-side-lie.

TABLE 3.12   The proportion that on-nipple in half-sit + on-side-lie
was of half-sit + on-side-lie expressed as a mean for
all litters each week

Week	Mean	Standard Deviation	Sample Size (N)
1	0.52	0.11	17
2	0.44	0.12	17
3	0.44	0.10	16
4	0.45	0.09	15
5	0.44	0.12	17
6	0.44	0.16	17

The above means show the proportion of mothers' half-sit
+ on-side-lie scores that their litters (ie the average
kitten in that litter) were on the nipple (ie in on-nipple
in half-sit + on-side-lie), in each week.   For example,
in week 1, litters tended to be on the nipple for 52 per
cent of their mothers' scores in half-sit + on-side-lie.

2   Sit-nurse

It has been demonstrated that litters, whose mothers have low percentage scores on half-sit + on-side-lie, have low percentage scores on on-nipple in half-sit + on-side-lie.   It was of interest to discover whether the above mothers showed any differences in their sit-nurse behaviour.   This might be expected since the kittens of these mothers may attempt to compensate for their low scores on on-nipple in half-sit + on-side-lie, by attaching to the nipples more when their mother is sitting.   The question might be posed therefore – Do mothers who have low percentage scores on half-sit + on-side-lie have high percentage scores on sit-nurse (and vice versa)?   To discover this, sit-nurse scores could have been plotted against half-sit + on-side-lie scores.   However it was decided not to do this, for the following reason.   Sit-nurse comes about through kittens attaching to the nipples when their mother is sitting; if she rarely sits then opportunities for the kittens to attach to the nipples in this position are few.   Therefore, to take into account how much sitting a mother exhibits, her sit-nurse behaviour is expressed as a proportion (in this case a percentage) of the total amount of sitting (ie sit + sit-nurse) that she shows.   Hence the derived $\frac{\text{sit-nurse}}{\text{sit + sit-nurse}}$ percentage provides a measure of the amount of sit-nurse that does occur, given the possible occasions in which it could occur.

Mean weekly percentage scores of sit-nurse as a percentage of sit + sit-nurse, were calculated for each mother each week.   These scores were regressed against each mother's mean weekly percentage scores of half-sit + on-side-lie.   The results of the analyses are presented in Table 3.13.

TABLE 3.13   <u>Results of regression analyses in which mothers' mean</u>
<u>weekly percentage scores on the percentage of sit + sit-</u>
<u>nurse that is sit-nurse, were regressed against their</u>
<u>mean weekly percentage scores on half-sit + on-side-lie,</u>
<u>each week</u>

Week	t	Regression coefficient (b)	Coefficient of determination (r^2)	Degrees of freedom
1	0.865			15
2	0.305			15
3	1.154			14
4	2.236*	− 0.621	0.278	13
5	3.051**	− 0.798	0.383	15
6	2.496*	− 0.627	0.294	15

t values are given with significance levels indicated as
follows: * $p < 0.05$, ** $p < 0.01$. The significance of the
t values indicate the significance of the relationship
between the two maternal measures. (b) and (r^2) values are
only given when t is significant. (b) indicates whether
the relationship is positive or negative. (r^2) values indi-
cate the proportion of variance in Y values (of the percent-
age of sit + sit-nurse that is sit-nurse) that are accounted
for by the variance in X values (of half-sit + on-side-lie)

In weeks 1-3 there is no significant relationship between the two measures, but in weeks 4-6 there is a significant negative relationship. This indicates that in these later weeks mothers with a low score on half-sit + on-side-lie show a high percentage of sit + sit-nurse that is sit-nurse.

Therefore for a high proportion of their total sit score (ie sit + sit-nurse), these mothers have at least one kitten attached to the nipple. In contrast, in weeks 4-6, mothers who have high scores on half-sit + on-side-lie spend relatively little of their total sit score in sit-nurse. The significant regression relationships of weeks 4-6 are illustrated in Figure 3.2. Regression lines were calculated and are drawn in these graphs. The variances around these regression lines are presented in Table 3.14. In this Table also the variances in mothers' mean weekly percentage scores, on the percentage of sit + sit-nurse that is sit-nurse, are presented. Variances in mothers' mean weekly percentage scores on half-sit + on-side-lie are given in Table 3.11.

FIGURE 3.2   In the 3 graphs shown, mothers' mean weekly
            percentage scores on the percentage of sit +
            sit-nurse that is sit-nurse (Y axis) are
            plotted against their mean weekly percentage
            scores on half-sit + on-side-lie (X axis),
            for weeks 4, 5 and 6 respectively.   From
            regression analyses performed on the data
            (Table 3.13) regression lines were calculated
            and these are drawn.
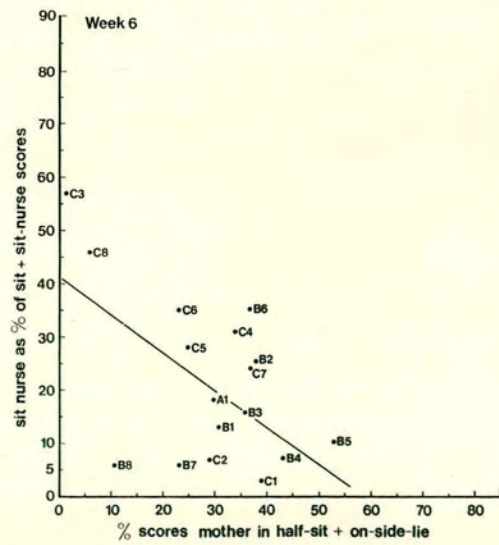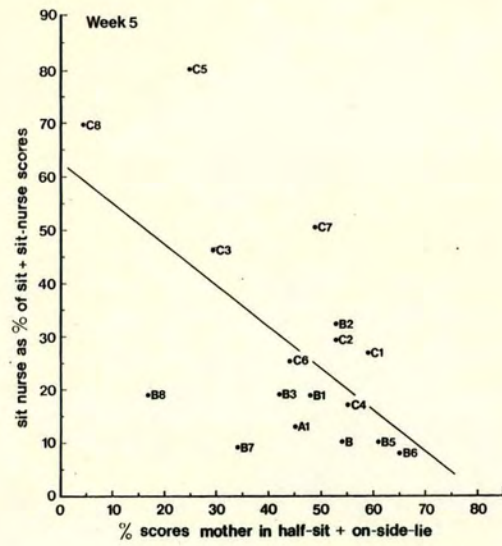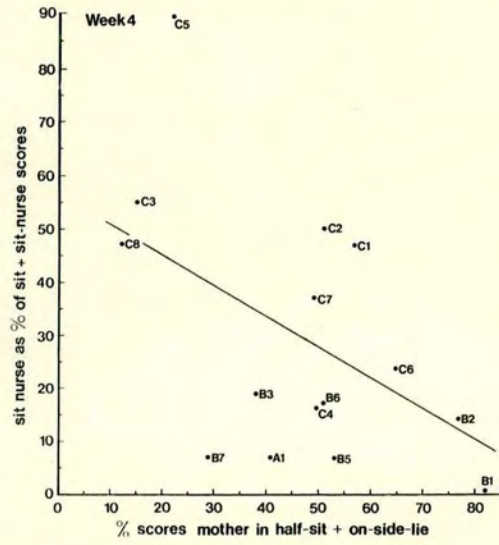
TABLE 3.14   Variances in mothers' mean weekly percentage scores on
the percentage of sit + sit-nurse that is sit-nurse, and
the variance around the regression lines in Figure 3.2

Week	Variance in mothers' scores	Variance around regression lines
1	327.2	
2	445.2	
3	318.9	
4	588.1	224.0
5	453.3	163.0
6	240.3	73.0

The regression lines referred to above were calculated
when mothers' mean weekly percentage scores on the per-
centage of sit + sit-nurse that is sit-nurse, were
regressed against their scores on half-sit + on-side-lie
for each week.   Variances around the lines are only given
where the regression relationships are significant, ie in
weeks 4, 5 and 6 (Table 3.13)

3   Crouch + lie

Finally the relationship between mothers' mean weekly scores on half-sit + on-side-lie and their scores on crouch + lie is investigated.   As explained in 3.6.2, the nipples are covered, and not accessible to the kittens, in the crouch and lie positions.   In the first 3 weeks, most mothers have low scores on crouch + lie, but in later weeks they show a considerable range of scores.   The means of all mothers' mean weekly percentage scores on crouch + lie are presented for each week in Appendix C   Figure C(3) .   Variances in mothers' mean weekly percentage scores on crouch + lie each week are presented in Table 3.15.   (Table 3.11 for variances in mothers' mean weekly percentage scores on half-sit + on-side-lie.)

Mothers' mean weekly percentage scores on crouch + lie were regressed against their half-sit + on-side-lie scores, and the results of these analyses are presented in Table 3.16.

In weeks 1-3 there is no relationship between the two maternal measures.   This reflects the fact that mothers were rather similar in their scores on crouch + lie in these weeks but showed wide differences in their half-sit + on-side-lie scores (Tables 3.11 and 3.15).   In weeks 4-6 however, there is a significant negative relationship between crouch + lie, and half-sit + on-side-lie. This demonstrates that the mothers who used crouch and lie positions most in these weeks tended to be the mothers who used half-sit + on-side-lie, least.   Such a finding seems logical, since if mothers use crouch and lie positions to limit their kittens access to the nipples then it is unlikely that they would also extensively use body positions in which the nipples are well exposed, ie half-sit + on-side-lie.

TABLE 3.15   <u>Variances in mothers' mean weekly percentage scores in</u>
<u>crouch + lie, and the variance around the regression</u>
<u>lines shown in Figure 3.3</u>

Week	Variance in crouch + lie scores	Variance around regression lines
1	4.8	
2	19.4	
3	15.2	
4	116.6	36.7
5	192.9	72.0
6	234.0	45.7

The regression lines referred to above were calculated
when mothers' mean weekly percentage scores on crouch +
lie, were regressed against their scores on half-sit +
on-side-lie for each week.   Variances around the lines
are only given where the regression relationships are
significant, ie in weeks 4, 5 and 6 (Table 3.16)

TABLE 3.16   Results of regression analyses in which mothers' mean
weekly percentage scores on crouch + lie, were regressed
against their mean weekly percentage scores on half-sit
+ on-side-lie, each week

Week	t	Regression coefficient (b)	Coefficient of determination (r^2)	Degrees of freedom
1	1.915			15
2	0.464			15
3	1.894			14
4	2.983*	− 0.335	0.406	13
5	2.992*	− 0.507	0.362	15
6	4.245**	− 0.844	0.546	15

t values are given with significance levels indicated as
follows: * $p < 0.05$, ** $p < 0.01$.   The significance of
the t values indicate the significance of the relation-
ship between the two maternal measures.   (b) and (r^2)
values are only presented when t is significant.   (b)
indicates whether the relationship is positive or
negative.   (r^2) values indicate the proportion of
variance in crouch + lie scores accounted for by the
variance in half-sit + on-side-lie scores.

Graphs of the regressions of weeks 4, 5 and 6 are presented in Figure 3.3. Regression lines were calculated and these are drawn. The variance around the regression lines in weeks 4-6 are presented in Table 3.15.

FIGURE 3.3   In the 3 graphs shown, mothers' mean weekly

percentage scores on crouch + lie (Y axis),

are plotted against their mean weekly per-

centage scores on half-sit + on-side-lie,

for weeks 4, 5 and 6 respectively.   From

regression analyses performed on the data

(Table 3.16) regression lines were calculated

and these are drawn.
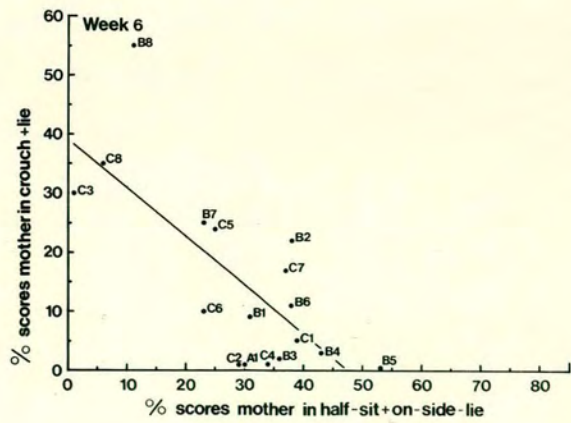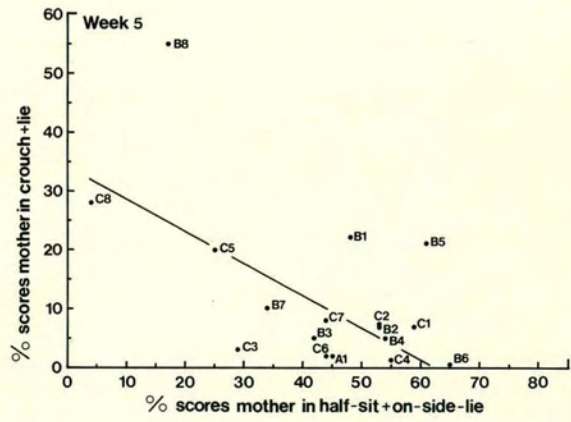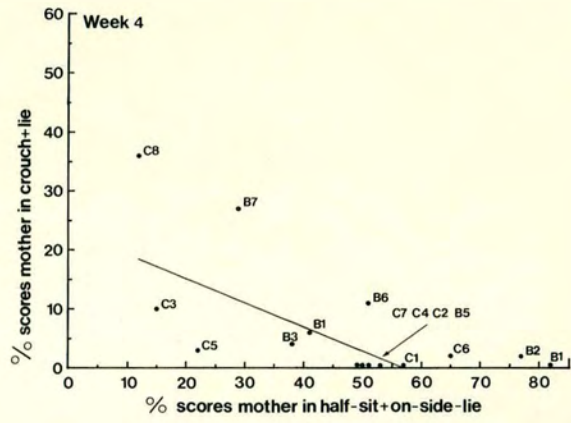
3.6.5 <u>The relationship between weight gain between 7 and 21 days,
and measures of the mother-kitten feeding relationship</u>

It was of interest to know if there was a relationship between
kitten weight gain and various measures of maternal and kitten
behaviour related to feeding. Adequate weight and behavioural data
were available for only 10 litters and the analyses therefore had to
be performed on this rather small sample. Kittens were not weighed
before they were 1 week of age, therefore weight gain from birth
could not be assessed. From the 4th week kittens began taking solid
food and so weight gain could not be related to measures of the
mother-kitten relationship after the 3rd week. It was therefore
decided to investigate the relationship between weight gain and
measures of feeding behaviour in the 10 litters, in the 2nd and 3rd
weeks after parturition. For each week the litters are divided into
two equal sized groups. The 5 litters who, each week, show the
greatest mean kitten weight gains are placed in Group A, and the 5
litters who show lowest weight gains are placed in Group B (Table 3.17).
The two groups have the same membership each week, and each week
Group A litters gain significantly more weight than Group B litters:
week 2, t = 7.60, df = 8, p < 0.001; week 3, t = 5.05, df = 8,
p < 0.01. Litter sizes are given in Table 3.17. There is found to
be no significant difference between the two groups in terms of the
litter sizes of their members: t = - 0.89, df = 8, NS.

If, instead of by weight gain, litters were divided on the basis
of their mean kitten weights at day 7, they would fall into the same
two groups. The mean kitten weights of each litter are given in
Table 3.17. Group A litters are significantly heavier than Group B
litters, t = 3.57, df = 8, p < 0.01.

The mean weekly percentage scores on on-nipple for the litters

TABLE 3.17   Mean kitten weight for each litter at day 7, and the
              mean kitten weight gain for each litter in weeks 2 and 3

	Litter	Litter size	Mean kitten weight at day 7 (g)	Mean kitten weight gain (g) Week 2	Week 3
Group A					
	C1	3	207	82	45
	B3	2	205	70	93
	B5	3	213	92	72
	B6	4	203	77	83
	A1	4	218	69	76
Group B					
	C2	4	182	28	25
	C3	3	173	37	35
	C4	4	139	48	32
	C5	3	195	37	27
	C6	4	178	29	38

Litter size is given for each litter.   Litters
are divided into 2 groups of 5 litters each.
Group A includes the 5 litters who gain most
weight each week and Group B, the litters that
gain least weight.   The 2 groups have the same
members each week.

in each group in weeks 2 and 3 are given in Table 3.18.   In both
weeks Group B have significantly higher on-nipple scores than
Group A: week 2, t = - 2.49, df = 8, p < 0.05;   week 3, t = - 3.20,
df = 8, p < 0.01.   However when each group is compared on on-nipple
in sit, and on-nipple in half-sit + on-side-lie mean weekly percentage
scores (Table 3.18) there are found to be no differences between the
groups in either week, on either measure.   (On-nipple in sit: week
2, t = - 2.01, df = 8, NS;   week 3, t = - 1.60, df = 8, NS.   On-
nipple in half-sit + on-side-lie: week 2, t = - 1.80, df = 8, NS;
week 3, t = - 1.17, df = 8, NS.)

Comparing mothers in the two groups on their mean weekly per-
centage score on sit-nurse and half-sit + on-side-lie (Table 3.19)
reveals no differences between Group A and Group B: sit nurse -
week 2, t = - 1.37, df = 8, NS;   week 3, t = - 1.53, df = 8, NS;
half-sit + on-side-lie - week 2, t = 0.05, df = 8, NS;   week 3,
t = - 0.44, df = 8, NS.

To summarise, it has been demonstrated that Group A litters
weigh more at day 7, gain more weight in weeks 2 and 3, and have
lower on-nipple scores in weeks 2 and 3, than Group B.   However there
are no differences in the on-nipple in sit or on-nipple in half-sit +
on-side-lie scores of the two groups and neither do mothers who dif-
ferences in sit-nurse or half-sit + on-side-lie.

In Appendix G, further statistical analyses performed on kitten
weight data are reported.   Mean kitten weight gains for all 6 weeks
are examined.   Where data is missing, weight gains are estimated.

TABLE 3.18   Litters' mean weekly percentage scores on on-nipple, on-nipple in sit, and on-nipple in half-sit + on-side-lie

| | Week 2 | | | Week 3 | | |
Litter	On-nipple	On-nipple in sit	On-nipple in half-sit + on-side-lie	On-nipple	On-nipple in sit	On-nipple in half-sit + on-side-lie
Group A						
C1	28.0	2.5	25.5	20.0	3.5	16.5
B3	17.0	2.6	14.4	27.0	4.3	22.7
B5	29.0	0.0	29.0	26.0	3.3	22.7
B6	30.0	1.4	28.6	24.0	0.0	24.0
A1	14.0	0.0	14.0	20.0	1.0	19.0
Group B						
C2	36.0	7.6	28.4	28.0	4.7	23.3
C3	35.0	5.3	29.7	36.0	4.9	31.1
C4	26.0	1.6	24.4	28.0	4.3	23.7
C5	32.0	4.5	27.5	34.0	20.3	13.7
C6	39.0	1.0	38.0	44.0	4.0	40.0

(Group A litters have greater mean kitten weight gains in weeks 2 and 3 than Group B litters)

TABLE 3.19   Mothers' mean weekly percentage scores on sit-nurse, and half-sit + on-side-lie

		Week 2		Week 3	
	Mother	Sit-nurse	Half-sit + on-side-lie	Sit-nurse	Half-sit + on-side-lie
Group A					
	C1	6	60	9	42
	B3	8	45	7	37
	B5	2	73	8	56
	B6	4	81	1	59
	A1	1	47	3	57
Group B					
	C2	15	56	12	59
	C3	11	61	11	70
	C4	3	61	9	50
	C5	9	55	43	29
	C6	2	71	6	61

(Litters of Group A mothers have greater mean kitten weight gains in weeks 2 and 3 than those of Group B mothers)

3.7 QUANTITATIVE RESULTS ON MATERNAL AND KITTEN BEHAVIOUR NOT
DIRECTLY RELATED TO FEEDING

3.7.1 <u>Evidence for individual differences in maternal and litter
behaviour</u>

1   <u>Maternal behaviour</u>

In order to asertain whether mothers differed significantly, and
consistently, from one another, in terms of their percentage scores
on behavioural measures not directly related to feeding, analysis of
variance was performed on each of the following maternal measures:
in litter box, stand, walk, vocalisations - brrp, brrp-cry, cry, and
purr (Appendix B), eat, drink, lick, groom, paw, and excited/dis-
turbed.   These measures, and the maternal measures in 3.6.2, which
were also subjected to analysis of variance, make up the majority of
the maternal measures listed in 2.2.7.   (Analysis of variance was
not performed on the data on the few remaining measures.   It was
sufficient to know whether mothers differed in their scores in the
litter box, and so their scores in the other 2 locations (2.2.7) were
not subjected to analysis of variance.   Carry, and the vocalisations -
hiss, growl, and those termed 'various' (Appendix B) were scored so
infrequently, for all mothers, that there was little point in sub-
jecting the data to any analysis.)

Two-way analysis of variance, with replicates, was used to take
into account both the effects of differences between mothers, and
changes with time in weeks, as in 3.6.2.[*]   Results of the analyses
are presented in Table 3.20.   For all measures, both mother, and
week main effects, are significant.   Over the 6 weeks therefore,
there is significant variation between mothers in their percentage
scores on each measure, and for mothers in general, their percentage
scores on each measure show significant changes across the 6 weeks.

* see Appendix E

TABLE 3.20   Two-way analysis of variance on maternal behaviour
measures not related to feeding

	Source of Variation		
	Main Effects		Interaction Effect
Measure	Mothers	Weeks	Mothers x weeks
In litter box	4.87***	34.30***	2.17***
Stand	9.98***	15.02***	1.43*
Walk	6.25***	2.50*	1.94***
Eat	10.94***	21.19***	1.61**
Drink	5.55***	6.36***	0.82
Brrp	14.74***	19.67***	2.36***
Brrp-cry	14.43***	17.59***	2.58***
Cry	58.44***	6.92***	4.86***
Purr	50.67***	7.85***	6.09***
Lick	5.19***	7.62***	1.61**
Groom	7.18***	4.79***	1.65**
Paw	18.50***	19.05***	3.61***
Excited/ Disturbed	16.11***	14.68***	2.73***

F ratios are given with significance levels indicated
as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Degrees of freedom are, mothers: 16, 288
weeks: 5, 288
mothers x weeks: 77, 288

Interaction effects, although significant, are less than the main effects (compare f ratios). This indicates that although some mothers do change in relation to one another, there is overall consistency in the differences between mothers, in terms of their percentage scores on measures, over the weeks.

In Appendix C graphs showing mean weekly scores (for all mothers) for the measures in Table 3.20 are presented to illustrate the changes that occur over the 6 weeks. See Figure C(1)for the measure in litter box; Figure C(4)for stand, eat, drink and walk measures; Figure C(5)for brrp, brrp-cry, and purr measures; and Figure C(6)for lick, groom, paw, and excited/disturbed measures. (Cry means are not plotted - see Appendix C .)

2   Litter behaviour

In order to ascertain whether litters differed significantly, and consistently from one another in terms of their percentage scores on behavioural measures not directly related to feeding, analysis of variance was performed on the following measures: in litter box, still by mother, still by self, huddle, active, play, eat, and vocalise. The measures - paw and bite, roll on back, stand on, paw and bite mother, back arch, crouch, and paw and bite object (all described in 2.2.7) were combined to give the composite measure, play, since the scores on each were rather few each session.

Two-way analysis of variance, with replicates, was used to take into account both the effects of differences between litters, and differences between weeks[*]. For some of the measures - in litter box, active, play, and eat, only percentage scores in weeks 4-6 were used in the analyses; prior to the 4th week kittens were rarely seen out of the litter box, and the other measures were scored

* see Appendix E

infrequently or not at all.   Results of the analyses are presented
in Table 3.21.

Significant differences between litters, and significant dif-
ferences between weeks are found for the following measures - still
by mother, still by self, huddle, and vocalise.   In each case f
ratio values were higher for the main effects of mothers and weeks,
than for the interaction effect of mothers x weeks, although the
latter were significant.   This indicates that the differences
between litters were, in general, consistent across weeks, although
some litters did change in relation to one another, in terms of
their percentage scores on measures, across the weeks.

The following measures - in litter box, active, play, and eat,
showed no significant differences between litters, but they all
showed significant differences between weeks.

In Appendix C , graphs showing mean weekly scores (for all lit-
ters) for each of the measures are presented to illustrate their
changes across the 6 weeks.   See Figure C(1) for the measure in litter
box;   Figure C(7) for the measure still by mother;   Figure C(8) for
active, huddle, and play measures;   and Figure C(9) for still by self,
eat, and vocalise measures.

TABLE 3.21   Two-way analysis of variance on litter behaviour
             measures not directly related to feeding

		Source of variation	
Measure	Main Effects		Interaction Effect
	Litters	Weeks	Litters x Weeks
In litter box (weeks 4-6)	1.34	28.31***	1.38
Still by mother (weeks 1-6)	3.24***	10.27***	1.62
Still by self (weeks 1-6)	4.24***	24.87***	1.91***
Huddle (weeks 1-6)	3.57***	7.89***	1.76***
Active (weeks 4-6)	1.08	13.07***	0.83
Play (weeks 4-6)	1.46	15.32***	0.61
Eat (weeks 4-6)	1.17	26.35***	1.05
Vocalise (weeks 1-6)	2.63***	8.12***	1.43*

F ratios are given with significance levels indicated
as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Degrees of freedom are, litters: 16, 288
                         weeks: 5, 288
                         mothers x weeks: 77, 288

3.7.2 <u>The effects of litter size, sex ratio and kitten death in the</u>
<u>litter on maternal and litter behaviour not directly related</u>
<u>to feeding</u>

Since as shown in Table 2.2, families differed in litter size,
sex ratio in the litter, and in whether or not there had been kitten
death(s) in the litter, the contributions of these variables to the
individual differences in mothers and litters were investigated. As
explained in 3.6.3, only families C8, B2 and B4, were classified as
having kitten deaths for the purposes of the analyses. Regression
analyses were used to examine the relationships between litter size,
sex ratio, and kitten death, and maternal and kitten behaviour not
directly related to feeding. (In 3.6.3, it is explained why
regression analysis, rather than simply a one-way analysis of
variance was used to examine the effects of kitten death.)

The regression analyses were run on untransformed data. However
see Appendix E for tests for normality of the data.

1   <u>Maternal behaviour</u>

The behavioural measures upon which regression analyses were
performed are listed with the results of each analysis in
Tables 3.22-3.24.   (Three measures - brrp-cry, cry, and drink were
not included in the analysis because it was considered that the
results would be difficult to interpret and also of little interest.)

<u>Litter size</u>

Litter size was positively associated with stand, eat, lick and
paw.

<u>Sex ratio</u>

A higher proportion of males in litters was associated with
purr.

Kitten death

The occurrence of death in a litter was negatively associated with brrp, purr, and paw.

These findings are discussed in 4.2.2. However it should be noted that, although the above associations were significant, the r^2 value in each case was small indicating that the variables - litter size, sex ratio, and kitten death - only accounted for relatively small proportions of the variance in the mothers' scores on the measures. As explained in 3.6.3, interactions between the variables themselves may result in associations between certain variables and maternal measures being implicated where none exist.

2   Litter behaviour

Regression analyses were also performed on litter measures not directly related to feeding, in order to investigate the effects of litter size, sex ratio and kitten death. Only measures for which there have been shown to be significant differences between litters were tested (Table 3.21). These measures are listed with results of each analysis in Table 3.25.

Litter size

Litter size is negatively associated with still by self.

Sex ratio

A higher proportion of males in litters is positively associated with huddle.

Kitten death

None of the measures have a significant relationship with the occurrence of kitten death.

TABLE 3.22 <u>Regression analysis of the relationship between litter</u>
<u>size and maternal behaviour measures not directly</u>
<u>related to feeding</u>

Measure	f ratio	Regression coefficient (b)	Coefficient of determination (r^2)
In litter box	< 0.01		
Stand	44.36***	0.038	0.103
Walk	0.06		
Eat	17.71***	0.018	0.044
Brrp	3.03		
Purr	0.13		
Lick	21.13***	0.023	0.052
Groom	2.53		
Paw	21.48***	0.025	0.053
Excited/ disturbed	0.25		

f ratio values are given with significance levels
indicated as follows: *** $p < 0.001$
Degrees of freedom: 1, 385
f ratio values are presented for all measures, but only
where these are significant are regression coefficients
(b) and coefficients of determination (r^2) given. (b)
indicates whether there is a positive or negative
association between litter size and the behaviour measure
in question. (r^2) indicates the proportion of variance
in the measure that is accounted for by the variable
litter size.

TABLE 3.23   <u>Regression analysis of the relationship between sex ratio</u>
<u>and maternal behaviour measures not directly related to</u>
<u>feeding</u>

Measure	f ratio	Regression coefficient (b)	Coefficient of determination (r^2)
In litter box	3.41		
Stand	0.06		
Walk	0.64		
Eat	< 0.01		
Brrp	0.68		
Purr	26.40***	0.005	0.074
Lick	0.16		
Groom	0.03		
Paw	0.02		
Excited/ disturbed	0.04		

f ratio values are given with significance levels
indicated as follows: *** $p < 0.001$
Degrees of freedom: 1, 385
f ratio values are presented for all measures, but only
where these are significant are regression coefficients
(b) and coefficients of determination (r^2) given.   If
(b) is positive this indicates that the measure is
associated with a greater proportion of males in the
litter;   if it is negative the association is with a
greater proportion of females.   (r^2) indicates the pro-
portion of variance in the measure that is accounted for
by the variable sex ratio.

TABLE 3.24   <u>Regression analysis of the relationship between kitten</u>
             <u>death and maternal behaviour measures not directly</u>
             <u>related to feeding</u>

<u>Measure</u>	<u>f ratio</u>	<u>Regression coefficient (b)</u>	<u>Coefficient of determination (r^2)</u>
In litter box	0.31		
Stand	1.72		
Walk	0.02		
Eat	0.22		
Brrp	9.75***	− 0.031	0.029
Purr	15.27***	− 0.097	0.044
Lick	3.60		
Groom	1.36		
Paw	5.21*	− 0.025	0.013
Excited/ disturbed	0.84		

f ratio values are given with significance levels
indicated as follows: * $p < 0.05$, *** $p < 0.001$
Degrees of freedom: 1, 385
f ratio values are presented for all measures, but only
where these are significant are regression coefficients
(b) and coefficients of determination (r^2) given.   (b)
indicates whether there is a positive or negative
association between kitten death and the behaviour
measure in question.   (r^2) indicates the proportion of
the variance in the measure that is accounted for by
kitten death.

Although there are significant associations between litter size, and sex ratio, and some of the litter behavioural measures, r^2 values are low in each case. This indicates that relatively little of the variance in litters' scores on the measures is accounted for by the variables, litter size and sex ratio. These results are discussed further in 4.2.2.

TABLE 3.25 Regression analyses of the relationships between litter size, sex ratio and kitten death, and litter behaviour measures not directly related to feeding

Variable	Measure	f ratio	Regression coefficient (b)	Coefficient of determination (r^2)
Litter size				
	Still by mother	2.06		
	Still by self	6.99***	− 0.009	0.178
	Huddle	0.09		
	Vocalise	0.24		
Sex ratio				
	Still by mother	0.12		
	Still by self	0.18		
	Huddle	5.45*	0.057	0.013
	Vocalise	0.13		
Kitten death				
	Still by mother	1.04		
	Still by self	0.23		
	Huddle	0.18		
	Vocalise	2.23		

f ratio values are given with significance levels indicated as follows: * $p < 0.05$, *** $p < 0.01$

degrees of freedom: 1, 385

f ratios are presented for all measures, but only where these are significant are regression coefficients (b), and coefficients of determination (r^2) given.   (b) indicates whether the relationship between the variable and the behavioural measure is positive or negative.   For sex ratio a positive (b) therefore indicates that the measure is associated with a greater proportion of males in the litter.

(r^2) indicates the proportion of the variance in a measure that is accounted for by litter size, sex ratio or kitten death.

3.7.3 Details of individual differences in the mother-kitten relationship not directly related to feeding

Mothers have been shown to exhibit significant individual differences for all the behavioural measures that were tested in 3.7.1. However although litters were found to show individual differences in their scores on still by mother, still by self, huddle, and vocalize, they were found not to differ on their scores on active, play, or eat.

For kittens to be scored as still by mother, the mother had to be in contact with the kittens but she could be in any of the following body positions - stand, sit, crouch, lie, half-sit or on-side-lie. For kittens to be scored as still by self, or huddle, the mother had to be out of contact with them and could be in any body position. The relationship between still by mother, still by self and huddle and the mothers' body position was not of particular interest and was not investigated further.

The relationship between mothers' behaviour and the kittens' behaviour: active, play, eat and drink could not be further investigated since litters showed no individual variation on these measures.

3.8 CLASSIFICATION OF MATERNAL TRAITS, MOTHERS AND MOTHER-KITTEN FEEDING RELATIONSHIPS

1   Maternal traits

Mothers have been shown to differ on a large number of behavioural measures. However, comparing each mother on each measure is a laborious way of illustrating the differences between mothers. It is possible that certain behavioural measures are related to one another, such that for example, high scores on one

are always accompanied by high scores on certain others and low scores on yet others. Related behavioural measures could be considered as single behavioural traits, and differences between mothers could be therefore thoughtof in terms of the extent to which they manifested different traits. In order to investigate which maternal behaviour categories are related to one another principal components analysis was employed using SPSS (Nie *et al* 1975).

Principal components analysis and other forms of factor analysis have been used quite extensively in behavioural studies in recent years - as statistical procedures for revealing relationships between behavioural elements or behavioural traits (Chamove, Eysenck and Harlow, 1972; Smith, 1973; Huntingford, 1976; Stevenson-Hinde and Zunz, 1978; Ainsworth, 1979; Stevenson-Hinde *et al* 1980). For a thorough explanation of the factor analysis technique see Child (1970) and for a description of its application to behavioural data see Huntingford (1976).

Basically, in the analysis, the original variables in the data are transformed into a set of factors or principal components that are orthogonal (unrelated). The first component is a linear combination of variables which account for more of the total variance in the data than any other linear combination of variables. Successive components that are extracted account for decreasing proportions of the remaining variance. In order to facilitate the best fit of the data such that each variable tends to be more exclusively associated with one, rather than 2 or more factors, the rotation of factor axes may be employed (Child, 1970) - Varimax rotation was used in this analysis (Nie *et al* 1975). The basic outcome of factor or principal components analysis is that relationships between variables (in this analysis, behavioural measures) are

revealed by their loadings on (ie associations with) the same factors. Factor loadings may be positive or negative. The signs have no intrinsic meaning, but if, on the same factor some variables are loaded positively and others are loaded negatively, the factor is said to be 'bipolar' (Child, 1970). Such a factor embodies contrasting groups of variables, which bear a negative relationship to one another.

The data used in the analysis consisted of mothers' percentage scores on a selection of maternal measures (listed in Table 3.26). Not all the maternal measures on which data were collected (2.2.7) could be used because one of the limitations imposed by this statistical method (Child, 1970) effectively meant that the number of measures could not exceed (or at least greatly exceed) the number of mothers. In general, measures which were shown to be of interest in the qualitative results were selected, and measures for which results would be very difficult to interpret were not selected (eg the vocalisations not listed in Table 3.26).

Each week's data were analysed separately. If instead, one analysis was performed on all the weeks' data, any changes that may occur (over the weeks) in associations between particular measures, would be masked.

In each week's analysis, 3 factors were extracted. More factors could be extracted (with the general limitation (Child, 1970) that the latent roots (eigenvalues) of factors should exceed 1.00). However the task of giving behaviourally meaningful interpretations to a large number of factors (which account for rather small proportions of the total variance in the data) would be virtually impossible.

Significant positive and negative loadings of 0.3 and over

TABLE 3.26   <u>Maternal behaviour measures analysed by factor</u>

   <u>analysis</u>

In litter box	Crouch	Walk	Lick
In between	Lie	Eat	Groom
In other box	Sit-nurse	Drink	Paw
Stand	Half-sit	Brrp	Excited/disturbed
Sit	on-side-lie	Purr	

TABLE 3.27   Results of factor analysis of maternal behaviour measures

	Factor 1		Factor 2		Factor 3	
Week 1	In other box	+ 0.88	Eat	+ 0.78	Sit	+ 0.70
	Walk	+ 0.74	Groom	+ 0.66	Crouch	+ 0.53
	Stand	+ 0.60	In between	+ 0.63	Half-sit	+ 0.43
	Excited/	+ 0.41	Drink	+ 0.51		
	disturbed		Purr	+ 0.50		
	Paw	+ 0.33	Lick	+ 0.36		
	In litter box	− 0.88			On-side-lie	− 0.84
Week 2	Eat	+ 0.84	In other box	+ 0.91	Sit nurse	+ 0.59
	Stand	+ 0.81	Walk	+ 0.78	Half-sit	+ 0.39
	In between	+ 0.63			Lie	+ 0.39
	Sit	+ 0.60			Lick	+ 0.31
	Groom	+ 0.60				
	Drink	+ 0.57				
	Excited/	+ 0.53				
	distrubed				On-side-lie	− 0.64
	Brrp	+ 0.38	In litter box	− 0.80	Paw	− 0.58
Week 3	Eat	+ 0.85	Walk	+ 0.81	Brrp	+ 0.73
	In between	+ 0.80	Paw	+ 0.67	Sit-nurse	+ 0.71
	Stand	+ 0.74	Half-sit	+ 0.66	Excited/	+ 0.63
	Groom	+ 0.73	Purr	+ 0.54	disturbed	
	Sit	+ 0.51	In other box	+ 0.50		
	Drink	+ 0.51				
	In litter box	− 0.71			On-side-lie	− 0.64
Week 4	In litter box	+ 0.93	Purr	+ 0.77	Eat	+ 0.75
			Half-sit	+ 0.71	Stand	+ 0.65
			Paw	+ 0.69	Groom	+ 0.63
			Excited/	+ 0.62	Lick	+ 0.60
			disturbed		Sit	+ 0.49
			Walk	+ 0.62		
			In between	+ 0.45		
			Drink	+ 0.36		
			Lie	+ 0.33		
	In other box	− 0.95				
	Crouch	− 0.87	Sit-nurse	− 0.33	On-side-lie	− 0.48
Week 5	Purr	+ 0.90	In other box	+ 0.73	Eat	+ 0.76
	Paw	+ 0.82	Lie	+ 0.65	Stand	+ 0.73
	Half-sit	+ 0.79	In between	+ 0.56	Groom	+ 0.73
	Excited/	+ 0.66	Crouch	+ 0.34	Lick	+ 0.52
	disturbed				Sit	+ 0.48
	Walk	+ 0.53	In litter box	− 0.93		
			On-side-lie	− 0.58		
			Brrp	− 0.32		
Week 6	Stand	+ 0.80	Purr	+ 0.87	In litter box	+ 0.90
	Groom	+ 0.74	Walk	+ 0.80	On-side-lie	+ 0.58
	Eat	+ 0.73	Paw	+ 0.71	Brrp	+ 0.39
	Lick	+ 0.65	Half-sit	+ 0.69		
	Sit	+ 0.53	Excited/	+ 0.65	In between	− 0.86
	Drink	+ 0.44	disturbed		Lie	− 0.62
					In other box	− 0.31

Factor analysis was performed on mothers' percentage scores on each of the measures listed in Table 3.26.   Each week's data were analysed separately. Only significant positive and negative loadings of 0.3 and over are presented.

(Child, 1970), on each factor, for each week, are presented in Table 3.27.

The results indicate many associations between different behavioural measures but, selected for particular attention, are those associations that occur in more than one week. It is note-worthy that although certain groupings of measures were found to be stable across several weeks, they were not always associated with the same factor each week. Slight changes from week to week in the variance accounted for by different groups of measures would lead to the association of different groups with different factors in different weeks.

Eat and groom have positive loadings on the same factor as one another in weeks 1-6 (although it is different factors some weeks). In some of the weeks certain other behavioural measures are also associated with eat and groom, namely stand and sit in weeks 2-6, drink, weeks 1-3, and 6, and lick, weeks 1 and 4-6.

Purr, paw, half-sit and walk are all positively loaded on the same factor in weeks 3-6 and in weeks 4-6, excited-disturbed was also associated with them.

In weeks 1 and 2, half-sit was positively associated with the same factor on which on-side-lie had negative loading, and in weeks 2 and 3, sit-nurse was positively associated with the same factor on which on-side-lie had a negative loading.

In week 4, in litter box was positively associated with the same factor on which in other box and crouch were negatively associated.

In weeks 5 and 6, in litter box, on-side-lie and brrp all had positive loadings on the same factor on which in other box, in between and lie had negative loadings. Crouch was also negatively

loaded on the factor in week 5.

The significance of the above groupings of behaviours are discussed in the light of other results, both qualitative and quantitative, in section 4.4.2.

Although litters were demonstrated to differ significantly on a number of measures using analysis of variance (3.6.2 and 3.7.1), principal components analysis was not performed on the data on these measures, the chief reason being that it seemed unlikely that the analysis would reveal any information concerning the relationships between the measures (nuzzle, on-nipple, on-nipple in half-sit + on-side-lie, still by mother, still by self, huddle, and vocalise) that was not already obvious. For example, it was expected that nuzzle would be positively associated with on-nipple, and that still by mother would have a negative relationship with huddle.

2   Mothers

Factor analysis was used also to discover whether mothers fell into stable groupings (which were associated with different factors) across the 6 week period. The data set was the same as that used in the previous section. However in this analysis mothers, and not behavioural measures, were the variables. Each week's data was analysed separately and 3 factors were extracted in each analysis, as before.

It was found that just one factor explained most of the variation between mothers, each week (Table 3.28). However the associations of individual mothers with factor 1 were not consistent from week to week, eg the mothers that loaded highest and lowest on the factor were not the same in each week (Table 3.29). That is, grouping of mothers were not stable. (The fact that in weeks 3 and

TABLE 3.28   <u>Results of factor analysis on mothers.   The percentage</u>

<u>of the total variance between mothers that is accounted</u>

<u>for by each factor, each week</u>

Week	Factor 1	Factor 2	Factor 3	Total
1	89.8	2.7	1.6	94.1
2	87.3	3.3	2.4	93.0
3	84.7	3.1	2.9	90.7
4	71.6	7.6	6.3	85.5
5	68.6	6.9	5.4	80.9
6	65.3	8.1	4.9	78.3

The total column each week represents the percentage
of the variance between mothers, accounted for by
factors 1, 2 and 3

TABLE 3.29   Results of factor analysis on mothers.   The 5 highest
loading and lowest loading mothers on factor 1, each
week

	Week					
Mothers	1	2	3	4	5	6
High loading	B4	B7	C3	C4	B2	C6
	B8	B5	C6	C1	C7	C4
	C4	B4	A1	C2	C4	C5
	C1	C2	B8	C3	C5	B5
	B6	B1	B4	C6	C1	C2
Low loading	C5	C5	B1	B5	C8	B7
	B7	C4	C5	A1	B3	C7
	C8	A1	C1	B3	B7	B2
	B3	B3	B6	B6	B6	B6
	B2	B8	B3	C8	B8	B8

Mothers in each group (high and low loading) are listed in
order of decreasing loadings.   For example, in week 1, B4
loads highest, and B2 lowest, on factor 1.   In week 3, B2
and B7 were omitted from the analysis, and in week 4, B1,
B4 and B8.   This is due to missing data on these mothers.

4, some mothers were not included in the analysis, does not detract from the general impression of inconsistency in individual mothers' loadings in different weeks.)

It is possible that the inconsistencies in mothers' loadings were due to the fact that whatever maternal trait factor 1 embodied, mothers all tended to vary in their scores on that trait from week to week. It was not clear what particular combination of behavioural measures constituted the maternal trait represented by factor 1, especially as it did not appear to be one of the stable groupings of measures revealed in the previous analysis. In summary, the above factor analysis did not reveal stable groupings of mothers, and the results are therefore not discussed further.

3   Mother-kitten feeding relationships

Individual differences in the feeding relationship have been demonstrated on a weekly basis, using regression analyses in 3.6.4. The aim of this section is to attempt to classify families on the basis of their feeding relationships over the entire 6 week period.

The results from the two-way analyses of variance on the measures, half-sit + on-side-lie, on-nipple, on-nipple in half-sit + on-side-lie, and on-nipple in sit (see Appendix D for the derivation procedure for these last 2 measures) indicate that, for each of these measures, there were significant mother (or litter), and week, main effects and significant interaction effects (Tables 3.2 and 3.3). The f ratio values of the interaction effects were lower than those of the main effects, which means that in general the differences between mothers and between litters could be thought of as consistent over the 6 weeks. However, the fact that the interaction effects were significant does indicate that there was some

variation between mothers and between litters in the patterns of
change they showed in their scores across the 6 week period.   The
aim in this section is to classify families, without the aid of
statistical techniques, on the basis of their patterns of change in
scores in half-sit + on-side-lie, on-nipple, on-nipple in half-sit
and on-nipple in sit.   This is done by plotting the 24 session per-
centage scores (4 sessions per week for 6 weeks) for each of these
measures (except on-nipple in sit) for each family (Figure 3.4).
By using visual means only, families are grouped on the basis of
their similarities and differences in behaviour (see below).   On-
nipple in sit percentage scores are represented in the graphs by the
space between the on-nipple (slashed lines) and on-nipple in half-
sit + on-side-lie (dotted lines) scores.   The solid lines represent
mothers' half-sit + on-side-lie percentage scores.

In Figure 3.4 each family is presented as a member of one of
Group 1 to Group 5.   (These groups are described below.)   In clas-
sifying families, there was less concern for the precise scores that
mothers or litters had on any particular day;   more attention was
paid to the changes in scores, eg were they steady changes, sharp
changes, or were scores highly fluctuating?

Due to missing data (2.2.11) families B1, B2, B4, B7 and B8 had
incomplete records and so were not included in the analysis.   The
other 12 families were divided into 5 groups and the characteristics
of each group are described below.   It should be noted that 4 of
the families, C1, C2, C4 and B5, had scores between days 42 and 44.
However for ease of description it was decided to consider the
scores on these days as 6th week scores;   the analysis only relies
on rather crude differences between mothers and litters in any case,
ie they are not being compared on a day to day basis.

Group 1:   C6, B6 and Al

Mothers in this group show a fairly steady decrease in their
half-sit + on-side-lie scores (although there are day to day fluc-
tuations).   Unfortunately Al's record stops at day 39 (the 4th ses-
sion of the 6th week was on this day) and so it cannot be seen
whether the mother's scores continue to decrease as did mothers C6
and B6;   however their patterns of change are otherwise similar.
The litters' scores on on-nipple tend to show the same general
decreases across the weeks as their mothers' scores, and except for
C6, almost all on-nipple is in half-sit + on-side-lie (indicated by
there being very little space between the slashed and dotted lines,
see above).   C6 mother shows the steepest decrease in scores on
half-sit + on-side-lie in weeks 4, 5 and 6 and it is in these weeks
that her litter shows some on-nipple in sit.

Group 2:   C2, C4 and B5

After an initial drop in half-sit + on-side-lie scores (the
size of the drop differing between mothers) mothers' scores on this
measure remain approximately steady (although with day to day fluc-
tuations) until the 6th week when C2 and C4 show decreases.   The
litters' on-nipple scores show the same general patterns of change
as their mothers' half-sit + on-side-lie scores.   C2 and C4 litters
show some on-nipple in sit during the 6 weeks;   B5 kittens show very
little.

Group 3:   C3, C5 and C8

Mothers in this group show sharp decreases in half-sit + on-side-
lie between the 1st and 4th weeks.   When the scores are becoming
very low, litters' scores on on-nipple in sit show large increases
(indicated by the space between the slashed and dotted lines) so
that even although on-nipple in half-sit + on-side-lie scores

FIGURE 3.4   The graphs shown illustrate changes across
             the 6 weeks in mothers and litters
             percentage scores on the measures half-sit
             + on-side-lie (solid line), on-nipple
             (slashed line), on-nipple in half-sit +
             on-side-lie (dotted line).   On-nipple in
             sit is depicted by the space between the
             slashed and dotted lines.   On the X axis
             are days and on the Y axis, percentage
             scores.   The 12 families are arranged in
             Groups 1-5 as explained in 3.8 (Part 3).
             Group 1 includes C6, B6 and A1
             Group 2 includes C2, C4 and B5
             Group 3 includes C3, C5 and C8
             Group 4 includes C1 and C7
             Group 5 includes B3
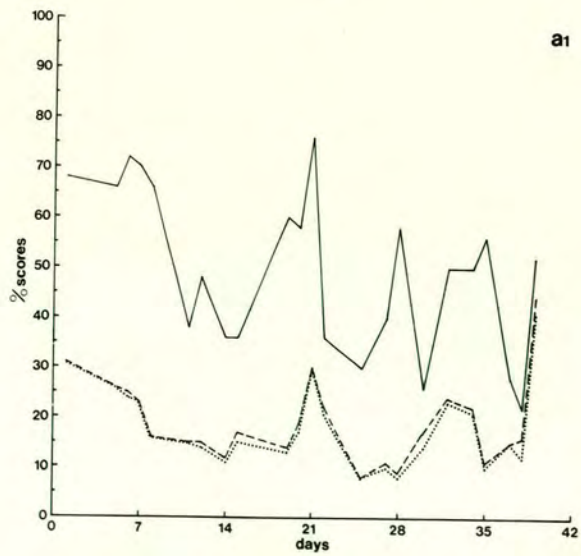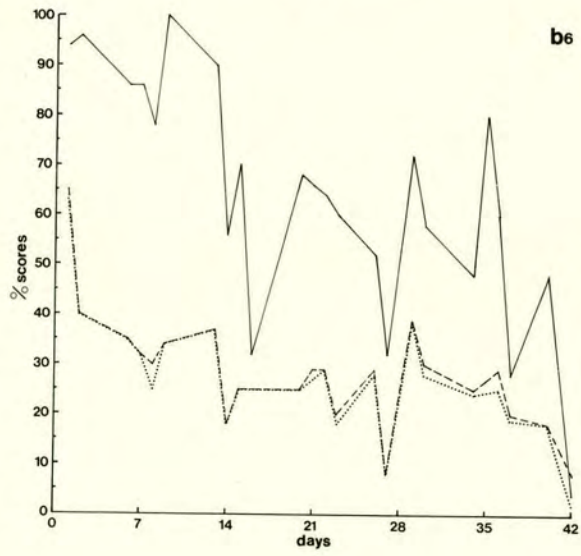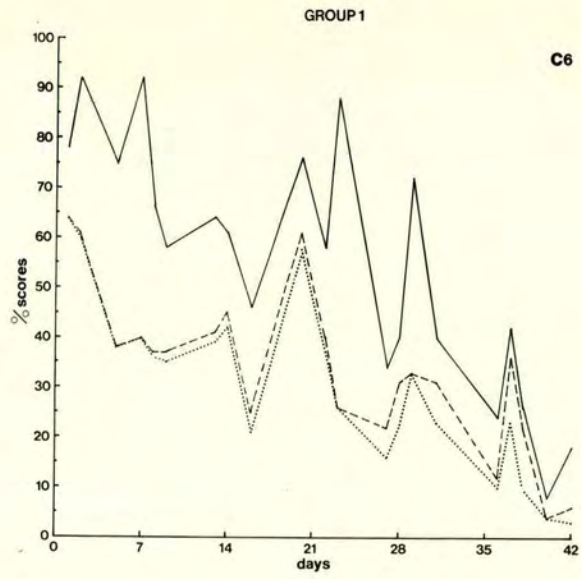
GROUP 1
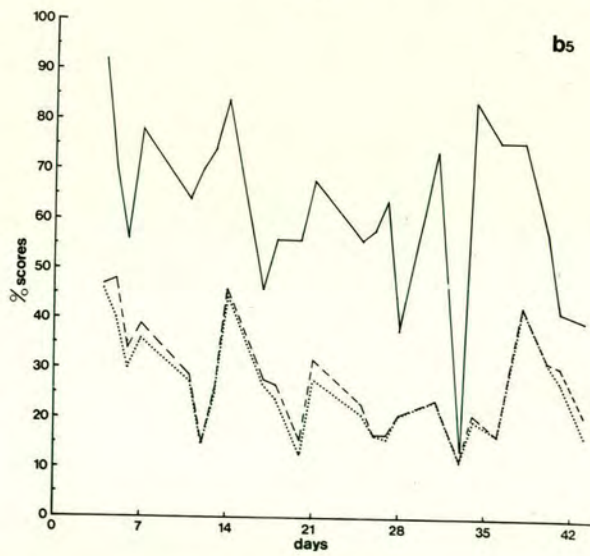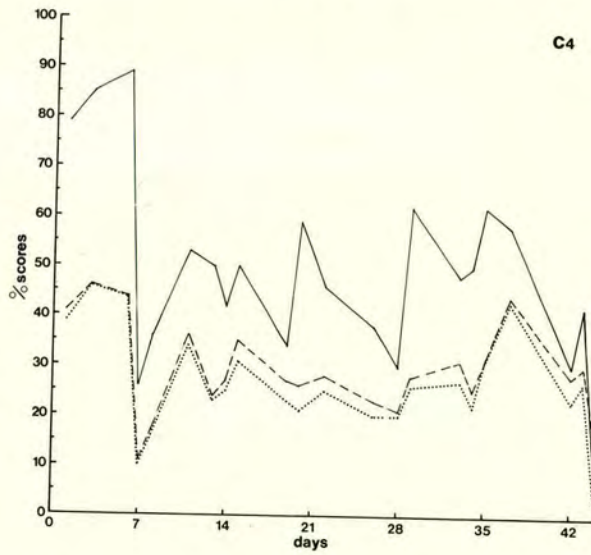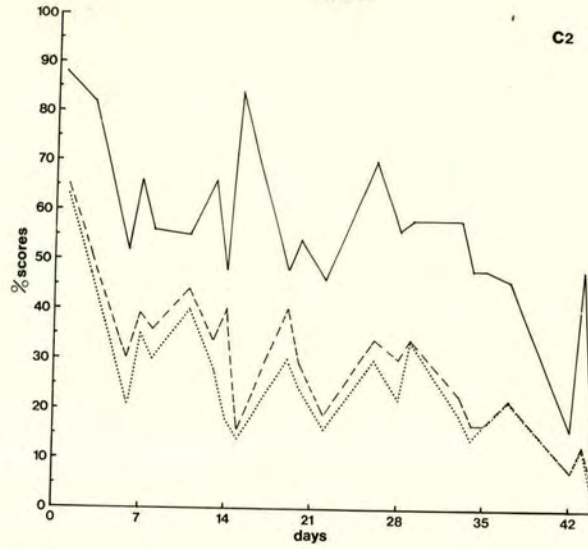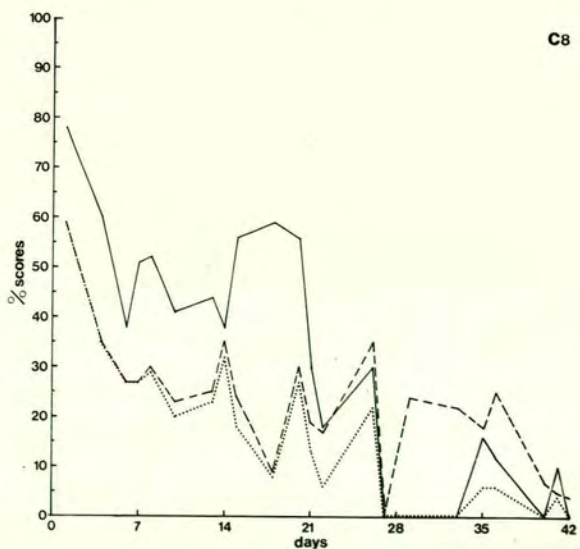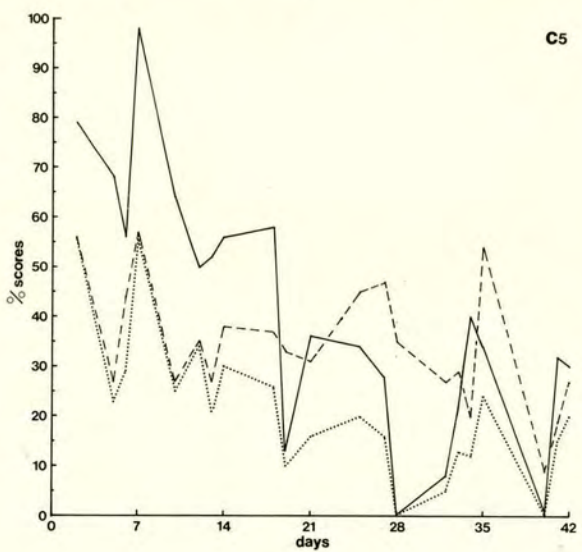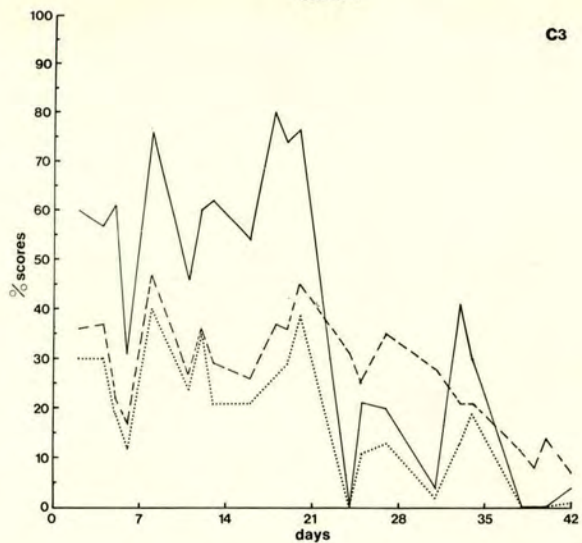
GROUP 2

GROUP 3

GROUP 4
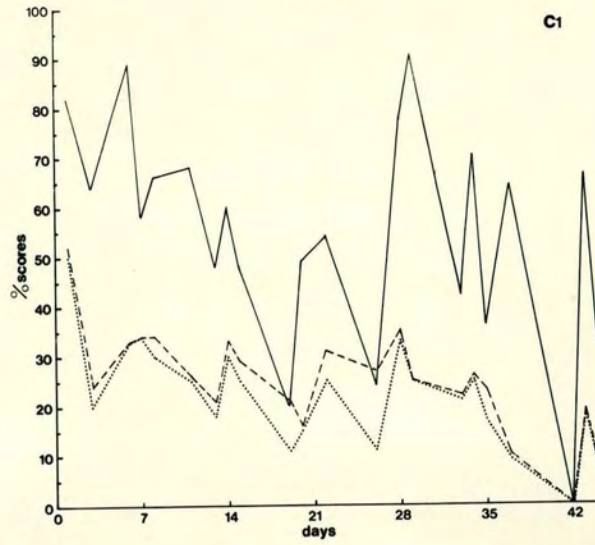
C1
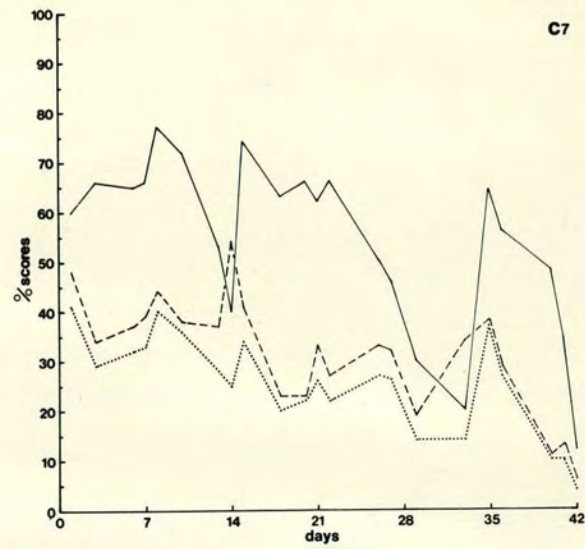
C7

GROUP 5
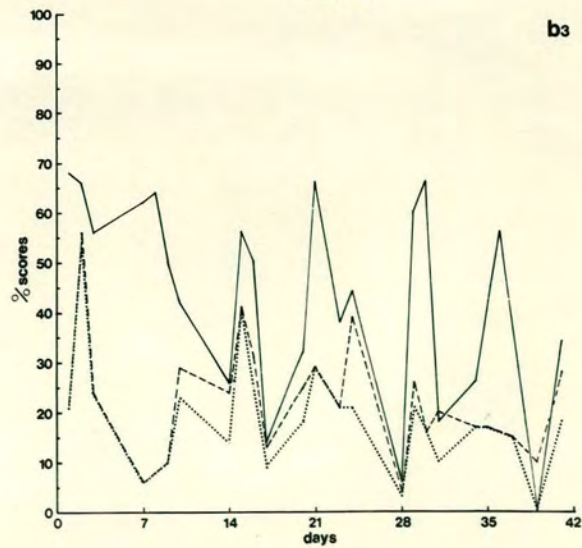
b3

decrease quite dramatically, on-nipple scores generally remain fairly steady before decreasing slowly in the 6th week.

Group 4:   C1, C7

The members of this group are perhaps not as similar to one another as members of other groups.   Both C1 and C7 show a large decrease in half-sit + on-side-lie prior to the 6th week (with lowest scores between days 19 and 26 in C1, and 29 and 33 in C7). After the decrease they both show a large increase in half-sit + on-side-lie.   Litters' on-nipple in sit scores show an increase at the time that their mothers' half-sit + on-side-lie scores decrease, but after the latter increases again, on-nipple in sit decreases and almost all on-nipple thereafter is on-nipple in half-sit + on-side-lie.

Group 5:   B3

There is only one member of this group.   B3 mother shows highly fluctuating scores on half-sit + on-side-lie and her litter's on-nipple scores show similar fluctuations.

The significance of the above groupings of mother-kitten relationships are discussed in the next chapter, and comparisons are made with the groupings of mothers which arose from the classification scheme described in 3.4.

3.9   SUMMARY OF QUANTITATIVE RESULTS

1   Mothers exhibit significant individual differences in behavioural measures related to feeding, and the differences between mothers are in general consistent across the 6 weeks.   All measures, except half-sit, show significant changes over the weeks.

2   Litters exhibit significant individual differences in behavioural measures related to feeding and the differences are, in

general, consistent across the 6 weeks.   All the measures show significant changes across weeks.

3   Litter size, sex ratio and kitten death have significant but minimal effects on some of the maternal measures related to feeding.

4   Sex ratio in the litter has a significant but minimal effect on litter on-nipple behaviour.   Other litter behaviour measures related to feeding are not affected by litter size, sex ratio, or kitten death in the litter.

5   There is a significant positive relationship between mothers' mean weekly percentage scores on half-sit + on-side-lie, and their litters' scores on on-nipple in half-sit + on-side-lie, each week.

6   There is a significant negative relationship between mothers' mean weekly percentage scores on half-sit + on-side-lie, and their scores on the percentage of sit + sit-nurse that is sit-nurse, in weeks 4-6.

7 · There is a significant negative relationship between mothers' mean weekly percentage scores on half-sit + on-side-lie and their scores on crouch + lie, in weeks 4-6.

8   In weeks 2 and 3, there is a significant negative relationship between the mean kitten weight gain in a litter and the percentage score on on-nipple.

9   Mothers exhibit significant individual differences in a number of behavioural measures not related to feeding, and these differences tend to be consistent across the 6 weeks.   All the measures show significant changes over the weeks.

10   Litters exhibit significant, and generally consistent individual differences in a number of behavioural measures not

directly related to feeding (still by mother, still by self, huddle and vocalise) but not in others (active, play, and eat). All measures show significant changes with time in weeks.

11   Litter size, sex ratio and kitten death have minimal but significant effects on some maternal and litter measures not directly related to feeding.

12   Relationships between certain maternal behaviour measures are revealed by principal components analysis. Related measures may be considered as, together, making up maternal traits.

13   Mother-kitten feeding relationships are classified on the basis of similarities and differences in patterns of change over the 6 weeks in the measures - half-sit + on-side-lie, on-nipple, on-nipple in half-sit + on-side-lie, and on-nipple in sit.

In the next chapter the above results are discussed in relation to one another, and in relation to the qualitative results presented in 3.1 - 3.4.

CHAPTER 4   DISCUSSION OF QUALITATIVE AND QUANTITATIVE RESULTS

4.1 THE DESCRIPTION AND CLASSIFICATION OF INDIVIDUAL DIFFERENCES
     IN MOTHER-KITTEN RELATIONSHIPS

4.1.1 General Introduction

In this section, results from the analyses of both qualitative
and quantitative data presented in Chapter 3 are summarised and dis-
cussed in relation to one another.   The aim is to give an overall
understanding of the types of individual differences that exist in
mother-kitten relationships.   Findings from other studies,
especially on the domestic cat, are referred to where relevant.

Individual differences in the mother-kitten relationship are
examined in 2 periods: weeks 1-3, and weeks 4-6.   The early period
is characterised by the kittens' nutritional dependence on their
mother, and the latter period, by the attempts of at least some
mothers, to wean their kittens from this dependence.   The two
periods are discussed in turn, but of course, often with reference
to one another.

4.1.2 Weeks 1-3

1   Qualitative differences in mother-kitten relationships

Quality of care   During the first 2-3 weeks mothers are found
to differ in what is termed the quality of care that they give their
kittens.   The quality of a mother's care is considered to be depen-
dent on the following: her attentiveness, the exposure of her ven-
tral surface in half-sit + on-side-lie, and the care she takes when
getting into these positions (3.4).   On the basis of subjective
assessments on these three aspects of maternal behaviour, mothers are
classified as exhibiting either low, intermediate or high quality
care in weeks 1-3 (Table 3.1).   Low quality care mothers are
reactive whereas high quality care mothers tend to be unreactive to

external events; and as a general rule the higher the quality of the care, the easier it seems to be for kittens to locate and attach to the nipples in the early weeks.

Qualities of maternal care have been described in some primate species, eg rhesus monkeys (Hinde and Simpson, 1975) and humans (Ainsworth and Bell, 1969; Ainsworth, 1979). Most are not strictly comparable with those described for cats (3.2 and 3.3). However, 'maternal warmth' in rhesus monkeys (Hinde and Simpson, 1975) is perhaps not unlike maternal attentiveness in cats. Similarly, the differences in responsiveness and sensitivity that Ainsworth and Bell (1969) described for human mothers during feeding interactions, could possibly be compared with cat maternal behaviour in the same context. For example, during feeding interactions, mothers who orientate themselves inappropriately relative to the kittens, when taking up half-sit or on-side-lie positions, could be considered as insensitive to their kittens; and mothers who do not react appropriately when their kittens cannot locate the nipples (usually as a result of the mother's positioning), could be said to be unresponsive. Further, Ainsworth's (1979) category of 'tender, careful holding' of the infant, seems comparable to the quality of taking care when getting into half-sit or on-side-lie positions beside the kittens, in the mother cat. It should be emphasised however that although the qualities described in the above 3 species may be analogous, the precise behavioural components that comprise the qualities, tend to be rather different in each species.

Types of feeding interaction Although in weeks 1-3 almost all families exhibit 1(a) type feeding interactions (which are initiated by the mother) more commonly than any other type (3.2.2), there are individual differences between families, in the extent to which two

other types of interaction are observed - 1(c) and 2(a).   (The

latter are both 'kitten-initiated' feeding interactions.)   However,

these individual differences appear to bear no straightforward

relationship to the quality of care that the mothers show.   There

are examples of high, intermediate and low quality care mothers, who

each use 1(a) interactions almost exclusively - B6, C1 and B1; and

2(a) interactions are observed in both C3 and C2 families who have

low and high quality care mothers respectively.

2   Quantitative differences in mother-kitten relationships

Mothers' half-sit + on-side-lie behaviour   Mothers show sig-

nificant individual differences in their half-sit + on-side-lie per-

centage scores, across the 6 week period (3.6.2, Table 3.2) and

there is an increase in the variance in mothers' percentage scores

between weeks 1 and 4 (Table 3.11).   The percentage scores of all

mothers decrease during this period, but some more dramatically than

others (Figure 3.4).   Since the interaction effect of mothers x

weeks is less than either of the main effects (Table 3.2), the

general tendency is for mothers who have lower scores in the early

weeks to have lower scores in later weeks.   However, because the

interaction effect is significant, this general rule cannot be said

to hold for every mother.

Patterns of sucking behaviour   In the first 3 weeks (and in

weeks 4-6) there is a significant positive relationship between

mothers' mean weekly percentage scores on half-sit + on-side-lie and

their litters' scores on on-nipple in half sit + on-side-lie

(Table 3.10).   Hence, regardless of the actual magnitude of

mothers' scores, their litters are on the nipple for approximately

the same percentage of those scores (about 45 per cent of them -

Table 3.12), and it is roughly the same percentage each week. Why should this be so? One possibility is that on-nipple behaviour in the cat has a particular pattern, such that for example it tends to have specific frequencies and durations and tends to precede and be preceded by certain other specific patterns of behaviour. Patterning of this kind has been described for on-nipple behaviour in other species, eg the snow leopard (McVittie, 1978) and the rat (Drewett *et al* 1974). Patterns of sucking behaviour in the cat have not been subjected to the same levels of analysis as these two species. However by comparisons with them, it may be possible to gain some insight into on-nipple behaviour in the cat, and answer the questions posed above.

The snow leopard is probably the closest relative of the cat about whom information is available on patterns of non-nutritive and nutritive sucking in a natural situation (McVitie, 1978). In this species it is thought that after the cubs have attached to the nipples they go through a phase of non-nutritive sucking (which may stimulate milk let-down), followed by a phase of nutritive sucking (1.2.2, Part 2). The cubs then usually fall asleep. In the domestic cat, kittens almost always follow a period of on-nipple by a period of sleep. At first they may still be attached to the nipples, but then they lie beside their mother after either moving, or falling, off the nipples. While they are on the nipple it may be that, like snow leopard cubs, there is a phase of non-nutritive sucking, while the kittens tread (Ewer, 1973), followed by a phase of milk drinking.

It is unlikely that the cat has a large store of sinus milk that the kittens can tap off as they wish. Indeed it has been argued that the cat is probably quite similar to the rat, with milk

only becoming available to the young, in quantity, after active ejection of milk from the alveoli (1.2.2).   Milk ejection occurs periodically in the rat and so milk is only available at intervals. If periodic milk supply is also characteristic of the cat then this may explain why kittens are not seen on the nipple during all of their mothers' half-sit + on-side-lie scores;   the kittens perhaps do not remain attached to the nipples between milk ejections (or after several milk ejections have occurred).   If they are satiated from the previous milk ejection then the kittens may fall asleep, and come off the nipple either actively or passively as described above.   If they are not satiated they may come off the nipple any-way when milk has not been forthcoming for some time.

It seems feasible that the patterning of on-nipple behaviour in the cat could be a possible explanation of why all litters spend approximately the same proportion of their mothers' half-sit + on-side-lie scores, on the nipple.   If a mother has a high score on these nursing positions, then presumably the on-nipple followed by off-nipple pattern is simply repeated more often.   It is interesting that in each week the mean percentage (for all litters) of half-sit + on-side-lie scores in which kittens were on the nipple, should be almost the same.   This is perhaps further evidence for a specific patterning of on-nipple behaviour.   It is clear that more research is needed into on-nipple behaviour in the domestic cat.   In par-ticular it would be desirable to measure durations and frequencies of on-nipple behaviour, and to try to describe more precisely, the non-nutritive and nutritive phases of sucking.   Obviously, if such observations could be made in conjunction with physiological experiments of the type Drewett *et al* (1974) performed on rats, then information could also be gained on the relationship between

on-nipple behaviour and patterns of milk let-down.

The significance of sit-nurse behaviour   In weeks 1-3 there is no relationship between mothers' mean weekly percentage scores on half-sit + on-side-lie and their scores on the percentage of sit + sit-nurse that is sit-nurse.   As explained in 4.1.3, a significant negative relationship is found in weeks 4-6; it is postulated that this results from kittens, whose mothers have decreased in their half-sit + on-side-lie scores, attempting to compensate for their mothers' behaviour by attaching to the nipples more often when their mother is sitting.

In weeks 1-3 it would seem that kittens whose mothers have the lower scores on half-sit + on-side-lie either cannot, or do not, try to do this.   One explanation is that if their mother is not sitting next to them in the litter box then they cannot climb out of the box and initiate a feeding interaction elsewhere in the cage.   On the other hand, it may be that young kittens whose mothers have low scores on half-sit + on-side-lie, receive plenty of milk in any case and do not need to also attach to the nipple when their mother is sitting.   Certainly the analysis 3.6.5 shows that there is no relationship between mothers' half-sit + on-side-lie scores and their kittens weight gain (which is an indicator of how much milk they are receiving - Gallo *et al* 1980).

3   The interaction of qualitative and quantitative differences in mother-kitten relationships

No statistical tests were performed to examine the relationship between the quality of care a mother exhibits and the quantity of care she exhibits (measured in terms of her percentage score on half-sit + on-side-lie).   However in weeks 1 and 2 there is

quantitative data on all 4 mothers who show low quality care and it can be seen, in Figure 3.1, that these mothers represent a considerable range of both high and low scores on half-sit + on-side-lie. It therefore appears that there is not a strict relationship between the quality, and the quantity, of care a mother shows, as defined here.

In week 1 it seems that both qualitative differences and quantitative differences in maternal behaviour affect (and are no doubt affected by) kittens on-nipple in half-sit + on-side-lie behaviour. Low quality care mothers tend to have kittens who have difficulties in locating and attaching to the nipples, whereas such problems appear not to be encountered by the kittens of high quality care mothers (3.4); it has been shown that there is a significant positive relationship between mothers' half-sit + on-side-lie behaviour and their kittens on-nipple behaviour in these body positions.

It would appear that as the weeks proceed, qualitative differences between mothers may play a decreasing rôle in accounting for the individual differences (ie variance) in their litters' percentage on-nipple in half-sit + on-side-lie scores. Quantitative differences in mothers' half-sit + on-side-lie scores, however, account for an increasingly greater proportion of the variance in litters' scores between weeks 1 and 4. This is indicated by the increase in coefficient of determination value (r^2) across these weeks (Table 3.10). It is likely that it is in week 1, and progressively less so in weeks 2 and 3, that the quality of care that kittens receive from their mother is most critical. Due to their relatively poorly developed motor abilities and lack of physical strength, the kittens cannot easily overcome the problems with which

low quality care presents them in the early weeks. High quality care, on the other hand, enables kittens to locate the nipples quickly and apparently with less energy expenditure.

Towards week 4 mothers become more variable in their half-sit + on-side-lie scores, whereas after an initial decrease, between weeks 1 and 2, the variance in litters' scores remains stable over the entire 6 weeks. If litter behaviour was not influenced by qualitative differences in maternal care, it is postulated that this finding would not have been made. Litters would have shown a lower variance in their on-nipple in half-sit + on-side-lie scores in weeks 1 and 2 and an increase in the variance in their scores paralleling the increase in variance in mothers' scores on half-sit + on-side-lie.

4.1.3   Weeks 4-6

1   Qualitative differences in mother-kitten relationships

Types of feeding interaction   In general in weeks 4-6, an increasing proportion of feeding interactions are initiated by kittens, however families do differ considerably. In some, mothers are still playing at least an equal rôle in initiating nursing sessions as late as week 6; in others the kittens are responsible for initiating most feeding interactions by week 4 (3.2.2).

Mothers differ in how receptive they are to their kittens' attempts to make nipple contact. Again there is a general tendency for mothers to become less receptive across the 4th, 5th and 6th weeks. Nevertheless there are mothers who readily take up half-sit or on-side-lie when their kittens nuzzle them in week 6; and at the other extreme, mothers who, at week 4, frequently avoid the kittens so that they cannot even attempt to initiate a feeding interaction.

Quite a variety of ways are used to limit kittens' on-nipple behaviour, including avoidance, leaving the kittens shortly after they attach to the nipples, taking up positions such as crouch or lie in which the nipples are concealed, and showing aggression (3.2.2). Schneirla *et al* (1963) also described some of these patterns of behaviour. Interactions between mother and kittens in which the kittens attempt to make nipple contact, and the mother tries to prevent them may be considered as manifestations of weaning conflict - an example of parent-offspring conflict (Trivers, 1974). Weaning conflict has been reported in many mammalian species. In baboons, for example, Altmann (1980) described mothers getting up and walking away from their infants when they attempt to make nipple contact, or shifting their position slightly so that the nipples are inaccessible. On some occasions mothers were aggressive towards their infants.

In the present study, it was found that there are some mothers who fall between the two extremes of those mothers who allow their kittens almost unlimited access to the nipples, and those who attempt to prevent or at least control their kittens' access to the nipples. These mothers often nurse their kittens in the sit position (ie sit-nurse) and do not take up half-sit or on-side-lie positions when the kittens nuzzle.

Tolerance of play   In weeks 4-6, when kittens become increasingly active and playful, mothers differ in their tolerance of such behaviour, as described in 3.3.5. In general, mothers who are tolerant of play are also tolerant in feeding interactions, and mothers who are intolerant of play are intolerant in feeding interactions, although, as illustrated in Table 3.1, some mothers are tolerant in one context but not the other. Schneirla *et al* (1963)

have also indicated the existence of a relationship between mothers'
behaviour in the feeding situation and their reactions to kittens'
play. Indeed, intolerance of play may be considered another mani-
festation of parent-offspring conflict (Trivers, 1974).

2   Quantitative differences in mother-kitten relationships

The influence of the mothers' body posture on the occurrence of
on-nipple in sit   As explained in 4.1.2, the variance in mothers'
mean weekly percentage scores on half-sit + on-side-lie increases
over weeks 1-4, but in weeks 5 and 6 the variance decreases
(Table 3.11).   For example, at week 4 there are some mothers whose
scores on half-sit + on-side-lie are already very low whereas others
continue to have high scores.   In weeks 5 and 6 however, these lat-
ter mothers also show lower scores on half-sit + on-side-lie, and so
the individual variation between mothers is less.   (Figures 3.1 and
3.4 illustrate these results.)

It was found that in weeks 4, 5 and 6, there is a significant
negative relationship between mothers' mean weekly percentage
scores on half-sit + on-side-lie, and their scores on the percentage
of sit + sit-nurse that is sit-nurse.   As discussed in the previous
section, this finding may be due to the fact that, by week 4, kit-
tens are able to actively seek out their mother and themselves
initiate feeding.   (Schneirla *et al* (1963) also reports this
behaviour in kittens.)   Sit-nurse comes about when kittens nuzzle,
and then attach to the nipples, when their mother is sitting.

Contrasting patterns of change between families in behaviour
related to feeding   The patterns of change that occur in different
families in the measures - half-sit + on-side-lie, on-nipple, on-
nipple in half-sit + on-side-lie, and on-nipple in sit were

examined in a longitudinal fashion (ie across the 6 week period), in 3.8, Part 3.   In this way it was possible to gain further insight into the relationships between these measures.   Families were classified according to broad similarities and differences in their scores on the measures.

In Groups 1 and 2, the decreases that mothers show in their half-sit + on-side-lie percentage scores, prior to week 6, tend to be less dramatic than in Groups 3 and 4 (Figure 3.4).   Group 1 mothers show a fairly steady decline in half-sit + on-side-lie and, after an initial drop, Group 2 mothers' scores remain quite stable until about the end of the 5th week.   However Group 3 mothers all show very low scores on half-sit + on-side-lie around the 4th and 5th weeks, and Group 4 mothers (C1 and C7) show drops in half-sit + on-side-lie in weeks 3 and 4, and week 5 respectively.   Only the litters of Groups 3 and 4 show on-nipple in sit to any great extent, as illustrated by the areas between the slashed (on-nipple) and dotted (on-nipple in half-sit + on-side-lie) lines in the graphs in Figure 3.4.   It is when the decreases in half-sit + on-side-lie (detailed above, and illustrated by the solid lines in Figure 3.4) occur in the families of Groups 3 and 4 that the on-nipple in sit scores suddenly increase.   In Group 3 (where half-sit + on-side-lie scores drop more steeply), the on-nipple in sit scores are higher than in Group 4.

In Group 2 (with the exception perhaps of B5) and Group 4, whose half-sit + on-side-lie scores are high at the end of week 5, there are fairly sharp drops in these scores in the 6th week. However unlike the sharp decreases that occur in earlier weeks (in the families of Groups 3 and 4) these 6th week decreases in half-sit + on-side-lie, are not accompanied by any sudden increases in

on-nipple in sit.

Unlike Group 4 mothers, Group 3 mothers' scores on half-sit +
on-side-lie tend to remain fairly low following their decreases in
weeks 4 and 5.   In Group 4, half-sit + on-side-lie scores rise,
after their decreases, to approximately the same levels as before the
decreases (which are described above).   Whereas Group 3 litters con-
tinue to use on-nipple in sit into week 6, this is not found in the
Group 4 litters.

The mothers' rôle in weaning   To summarise the findings from
the Groups of mothers discussed above - early decreases in half-sit +
on-side-lie (ie prior to the 6th week) are accompanied by increases
in on-nipple in sit.   This might be expected.   If mothers are
attempting to begin weaning their kittens at an age where they are
still dependant on milk as their major food source then it is not
surprising that the kittens attempt to counteract this by attaching
to the nipples more often when their mother is sitting.   If the
mothers continue to have low scores on half-sit + on-side-lie then
the kittens continue to use on-nipple in sit;   nevertheless weaning
does appear to be commencing.   (Group 3 litters' on-nipple scores
in week 6 are all decreasing.)

Decreases in half-sit + on-side-lie in week 6 may likewise mark
the start of active weaning by the mother, but with a different
response at this stage from the kittens - no sharp increase in on-
nipple in sit.   This is probably due to the fact that the kittens
are now taking solid food.   On the other hand, the mothers'
decreases in half-sit + on-side-lie may be a response to kittens
lessening demand to spend time on the nipple.   Now that the kittens
are eating solid food they attempt to obtain milk less.   In 4.2
factors which may be causing individual differences in mother-kitten

relationships are discussed in detail.

It is also interesting that where the mothers decrease their half-sit + on-side-lie scores very steadily over the 6 weeks, there tends to be no stage at which kittens use on-nipple in sit very extensively. For example, in Group 1, the only family where on-nipple in sit is observed much at all, is C6 in weeks 5 and 6. This could be due to the fact that the mother's half-sit + on-side-lie scores decrease very steeply in these weeks (- contrast with B5 and A1). The behaviour of the mother and kittens in families B5 and A1 seems to be quite finely tuned to one another. This could perhaps be compared to the quality of rhesus monkey mother-infant interaction which Hinde and Simpson (1975) term 'meshing'.

As reported in the qualitative results (3.1.2), crouch and lie are body positions in which the nipples are concealed and it was suggested that mothers take up these positions to prevent their kittens from attaching to the nipples. In the first 3 weeks mothers hardly use these positions at all but in the later weeks some mothers begin to use crouch and lie positions quite extensively (3.6.4, Part 3). In weeks 4, 5 and 6 there was found to be a significant negative relationship between mothers' mean weekly percentage scores on half-sit + on-side-lie and their scores on crouch + lie (Table 3.16). Therefore the mothers who use crouch + lie most are the mothers who use half-sit + on-side-lie least. This suggests that those mothers are indeed trying to limit their kittens access to the nipples. Lying close to the ground as a means of preventing nursing has also been observed in the Olympic marmot, in the late stages of weaning (Barash, 1973).

Factor analysis on maternal measures (3.8, Part 1) also provided information on the body positions crouch and lie. In weeks

4-6, they tended to be negatively correlated with the measures - on-side-lie, in litter box, and the vocalisation brrp. The negative relationship with on-side-lie had already been revealed by the regression analyses in 3.6.4, Part 2. The other two results are not unexpected. It is logical that a mother who uses crouch and lie positions should also avoid the litter box - the place where the kittens spend most of their time. Brrp is a friendly greeting and 'calling' vocalisation (3.3.4 and Moelk, 1944, 1979) - it seems unlikely that mothers who are avoiding contact with their kittens would use it.

Differences between mothers in permitting access to the nipples

It is apparent from both qualitative and quantitative data that in weeks 4-6 there are some mothers who try to restrict their kittens' access to the nipples and others who still allow their kittens almost unlimited access. To what extent such differences in maternal behaviour affect kittens' total on-nipple scores is difficult to assess as there is no single measure of maternal prevention of nipple contact that can be correlated with kittens' on-nipple score. Mothers can apparently reduce their kittens' scores on on-nipple in half-sit + on-side-lie by spending less time in these positions. However if the mother allows her kittens to attach to the nipples while she is sitting, this can perhaps compensate for their reduced opportunities to suck in the former positions. The mother can however limit their on-nipple in sit scores by various means - for example by standing up and leaving them. In a cage it is impossible for the mother to use the ultimate deterrent to nipple attachment - leave the kittens completely. Therefore however much the mother tries to limit them, the kittens can usually, through persistence, find some opportunities to attach to the nipples, although these are

probably reduced.

It should be borne in mind that whether a mother restricts her kittens' access to the nipples, or allows them to suck freely, the kittens themselves must be responsible for a proportion of the individual variation that exists between litters, in their on-nipple scores. For example, litters may exhibit differences in the frequency with which they initiate feeding interactions, and also differences in the frequency with which they terminate feeding inter-actions. Such differences between litters could depend on many factors, including whether the kittens are still obtaining milk from their mother, and, related to this, the extent to which they are nutritionally and socially independent of her.

It was expected that the individual variation exhibited in the feeding relationship in different families would be reflected in certain other aspects of kitten behaviour, such as their activity, frequency of play, and consumption of solid food. Several studies have indicated a relationship between milk sucking and general activity, and the onset and frequency of play (Koepke and Pribram, 1971; Bateson and Young, 1980) but there were found to be no signi-ficant differences between litters on either play or activity measures. This result is discussed more fully in 4.2.3.

Kittens' eating of solid food The eating of solid food by kittens was rather rarely recorded during scan sampling. In most litters kittens were seen eating by week 5 (this conforms with Moelk's observations, 1979) but it tended to occur rather infrequently and sporadically. The chances of it being recorded during scan sampling were therefore small. Since very little quantitative data were being collected on eating, notes were kept in the diary on such events as the first observation of eating in a

litter and the eating of large quantities of food.

Analysis of variance showed that there is an increase over weeks 4-6 in litters' percentage scores on eating, but no significant differences between litters were revealed (Table 3.3). However it is worth mentioning an interesting observation that was recorded in the diary. Three litters were seen eating large quantities of food - C3, week 6; C8, week 5; and B1, week 6. Of these C3 and C8 were known to have mothers who showed sharp decreases in half-sit + on-side-lie before week 6. Since their kittens still spent considerable time on-nipple (except on one day when C8 kittens on-nipple score dropped to zero - Figure 3.4) the observation of them eating large quantities suggests that they were nevertheless receiving very little milk. A further speculation is that the change in their mother's behaviour was related to her lactational state. The relationship between mothers' lactational state and the behaviour of both mothers and kittens is discussed more fully in 4.2.2.

4.1.4 Conclusions: The bases of individual differences in the mother-kitten relationship

Timing of changes in the relationship The development of the feeding relationship in cats was divided into three stages by Schneirla *et al* (1963) (as explained in 1.4). The individual differences in mother-kitten relationships that are described in the present study can, to a large extent, be thought of in terms of differences in the timing of the stages that Schneirla *et al* described. According to their schema, the first stage in the relationship, characterised by the mother initiating the majority of feeding interactions, occupies the first 20 days. However, qualitative results in this study reveal that in several families kittens are

responsible for the initiation of a considerable proportion of feeding interactions before the 3rd week; and quantitative results demonstrated that some mothers nursed their kittens in half-sit + on-side-lie much less than others during this time. It seems therefore that in some litters at least, the second stage (of Schneirla *et al*) is reached earlier than in others, and the first stage is accordingly shorter.

Once kittens are mobile, they are able to actively initiate interactions by approaching their mother anywhere in the cage, and as Schneirla *et al* suggested, by about day 20 most kittens can do this. In the second stage, which is supposed to run from day 21 to 30, mother and kittens are considered to share the rôle of initiator in feeding interactions. However in this study, it was found that some mothers have virtually ceased to initiate nursing sessions, and are not always responsive when their kittens attempt to do so. These families have apparently reached the third stage in the relationship earlier than expected, according to Schneirla *et al*. There were other families who even by week 6 had not passed into the third stage of the relationship (which is meant to start at day 31), where kittens are responsible for initiating the majority of feeding interactions (Schneirla *et al*). In these families the mothers are still making themselves actively available for nursing, as well as always responding positively to their kittens' attempts to make nipple contact.

In conclusion, one of the fundamental differences between individual mother-kitten relationships appears to be in the timing of developmental changes in the relationship, or more simply, in the timing of weaning. (Weaning here refers to its behavioural manifestation in particular and not to the termination of lactation -

although the two must be closely correlated.) Altmann (1980) came
to a similar conclusion in her study of baboons. She found that one
of the main differences between mother-infant pairs was in the time
course of the various stages of their relationship, including weaning.

Quality of maternal care The quality of care that a mother
exhibits in weeks 1-3 does not appear to characterise a developmental
stage in the relationship, since many mothers never exhibit low
quality care. However there is a suggestion that some of the low
quality care mothers do show improvements in the quality of their
care over the 3 weeks.

Factors which may determine quality of care are considered in
4.2. One strong possibility is that a mother's personality, and
particularly her reactivity to external events, plays an important .
rôle in the quality of her care.

4.2 FACTORS WHICH MAY CONTRIBUTE TO INDIVIDUAL DIFFERENCES IN
MOTHER-KITTEN RELATIONSHIPS

4.2.1 General Introduction

In 4.2 various factors which may affect the mother-kitten
relationship and hence account for some of the individual differences
between families are discussed. In 4.2.2 the variables - litter
size, sex ratio, and kitten death in a litter - whose effects were
investigated through statistical techniques, are examined. In the
sub-sections that follow, the contributions that the mother's milk
yield, nutritional state, and personality make to individual dif-
ferences in mother-kitten relations are considered. No direct
evidence was available on milk yield and nutritional state, neverthe-
less there is indirect evidence to suggest that these factors play an
important rôle. Qualitative information was collected on personality

differences in mothers and it is argued that these do influence the mother-kitten relationship, but that their effects probably interact with those of milk yield and nutritional state.

4.2.2 Litter size, sex ratio, and the occurrence of kitten death in the family

None of the variables - litter size, sex ratio, or kitten death in litters, accounts for appreciably large proportions of the variances in quantitative measures of either maternal or litter behaviour (3.6.3 and 3.7.2). Nevertheless the variables did have significant (although minimal) effects on some of these measures. The results are now summarised and interpreted where possible.

Litter size

Larger litters are associated with higher percentage scores on the maternal measures - shift, lick, paw, stand, and eat.

That mothers with larger litters shifted more, is not an unexpected finding. Mothers shift in half-sit and on-side-lie positions, and in doing so, appear to be trying to reposition themselves, so that their kittens are better situated in relation to the ventral surface. With a larger number of kittens to accommodate at the ventrum, the mother must have to shift more often.

Lick scores are not corrected for litter size, and therefore it was not surprising to find that mothers with larger litters have higher lick scores. However, Priestnall (1972) in his study of mice, found that there were no significant differences between licking scores of mothers raising litters of 2, 5, and 8 pups; but when lick scores were corrected for litter size, he found that pups in smaller litters received significantly more licking than those in

larger litters.

It is not immediately obvious why pawing should be affected by litter size. Pawing by the mother seems to be chiefly related to being in an excited state (3.3.3).

Eating and standing are closely related behavioural measures (as shown by factor analysis - 3.8, Part 1), since a mother either stands, or sits, when she is eating. Mothers with larger litters have higher energy demands than those with small litters, and an obvious expression of this is their eat scores. Stand scores of mothers with large litters are probably high therefore due to the high eat scores.

Lie, and crouch + lie, are negatively associated with litter size, so mothers with small litters have higher scores on these measures. There is no apparent reason for this finding.

The only litter measure on which litter size has an effect is still by self. The relationship is a negative one, which would be expected. The fewer the kittens there are in a litter, the more likely it is that one should be observed on its own.

Sex ratio

None of the effects of sex ratio could be said to have been expected but they are of interest nevertheless. A greater proportion of females in litters is significantly associated with higher scores on on-side-lie and purr while a greater proportion of males is significantly correlated with higher scores on half-sit, lie and crouch + lie. As far as kittens' scores are concerned, a greater proportion of females is associated with higher on-nipple scores and a greater proportion of males with more huddling.

Kitten death

It should be considered that death may both affect, and be the effect of, certain aspects of maternal and kitten behaviour. As with sex ratio, it is difficult to interpret many of the results. The occurrence of death was correlated with high scores on the maternal behaviours crouch + lie and shift; and low scores on sit, half-sit, brrp, purr, and paw. As there were only 3 litters in which deaths occurred, these results must be treated with some caution.

No other study detailing the effects of litter size, sex ratio, and kitten death on mother-kitten relations in the cat has been made, therefore it is not possible to compare results. However the observation of Schneirla *et al* (1963) that the amount of time spent nursing is proportional to the size of the litter does not seem to be in agreement with the results from this study. Perhaps this is due to the small range of litter sizes used here. No statistical tests were performed to discover whether any of the qualitative differences in mother-kitten relationships were caused by litter size, sex ratio, or kitten death. However it has been suggested (2.2.2) that the quality of maternal care that mothers B2 and B4 exhibited in week 1, may have caused the deaths of kittens in their litters. It is suggested that effects of litter size and sex ratio on qualitative aspects of mother-kitten relationship would have been minimal, if they existed at all.

4.2.3   Milk yield and nutritional state of mother

1   Studies relating milk yield and nutritional state to
     maternal behaviour

In 4.1.2 it is suggested that individual differences in
mothers' milk yield at particular stages in their kittens' develop-
ment may contribute to some of the differences observed in mother-
kitten relationships.   Both direct and indirect evidence is avail-
able which indicates that there is a relationship between milk yield
and the behaviour (before and during weaning) of both mother and
young (Arnold *et al* 1979; Gallo *et al* 1980).   The mother's nutri-
tional state is known to affect her milk yield in sheep (Arnold *et al*
1979), but it is not known whether nutritional state or milk yield
more directly affects the relationship with the young.

In 1.6.7, a study of the effects of protein restriction on
maternal and kitten behaviour in the cat is briefly described
(Gallo *et al* 1980).   It is now discussed in more detail.   The con-
trol group of mothers in the study was fed a balanced diet during
gestation and the first fortnight of lactation, whilst the experi-
mental group was given a protein restricted diet.   The differences
between the two groups of mothers were recorded during qualitative
observations of the reunion of mother and kittens after a separ-
ation, on days 2, 7 and 12 after parturition.   Control mothers
quickly rushed to their crying kittens and retrieved them to the cor-
ner of the nest box where the litter was normally kept.   Their kit-
tens ceased to cry upon being retrieved.   The mothers then settled
down on their sides, and began to groom and encourage their kittens
to nurse, which they soon did.   At reunion, protein restricted
mothers often walked past their young and crouched in the home corner
alone - they did not appear eager to retrieve or comfort their young.

In spite of this the kittens sometimes managed to reach their mothers. When they did so, their mothers remained sitting and the kittens had great difficulties in attaching to the nipples. If nipple attachment did occur it was usually brief because the mother frequently disturbed her kittens by changing position. These kittens continued to cry after reunion, unlike the control kittens, possibly because they received little comfort from their mother. It was not known exactly how much milk was available to the kittens since milk yield was not measured directly, but presumably the kittens may also have been crying from hunger.

It is useful to translate the descriptions of behaviour patterns shown by the mothers above into the terms used in the present study. Hence, at reunion control mothers readily took up half-sit and on-side-lie positions for their kittens and were very attentive towards them. In contrast, protein restricted mothers remained sitting when their kittens attempted to make nipple attachments (with the result that sit-nurse sometimes occurred), were very inattentive, and showed disturbed behaviour, as manifested by their repeated position changing.

2 <u>Possible effects of milk yield and nutritional state on mother-kitten relationships in this study</u>

By comparing the behaviour of protein restricted, and control mothers, to the patterns of behaviour shown by individual mothers in this study, it may be possible to decide whether the nutritional and lactational states of the last mentioned could be contributing to the differences in their behaviour.

Apart from diet, there are other factors (including genetical factors) which can probably affect a mother's milk yield and

nutritional state. Therefore, even although the cats in the present study were all fed the same diet on a more or less *ad lib* basis (2.1.3) they could, nonetheless, have differed in their individual milk yields.

Effects on weaning behaviour and its timing In weeks 4-6, it was found that some mothers begin to nurse their kittens mainly in the sit position, let their kittens initiate the majority of feeding interactions, and also use a number of tactics to avoid nursing their kittens, eg crouching at a distance from the kittens, or standing up soon after the kittens attached to the nipples thus disrupting sucking. Such behaviour is similar to that shown by the protein restricted mothers in the study of Gallo *et al* (1980). It therefore seems possible that its occurrence in mothers in the present study may have been a response to a low nutritional state or a diminishing milk yield, or both. Furthermore the differences in timing of weaning that mothers show during the 4-6 week period (4.1.4) could be due to individual differences in nutritional state (and/or milk yield), with mothers whose nutritional state is poorer showing a tendency to wean their young earlier. This would agree with Trivers (1974), who proposed that mothers who are in poor condition become the limiting factor in nursing earlier than mothers in good condition, presumably because the cost of a given amount of milk is considerably higher when the mother is in poor condition, while the benefit to the offspring remains more or less unchanged. Perhaps like sheep (Arnold *et al* 1979), mother cats begin to limit their infants' access to the nipples when milk production falls below a specific level.

There was one mother, C8, who showed more extreme behaviour than all the others when trying to discourage her kittens from

making nipple attachment.   Reference to her diary summary (Appendix
A), reveals that during weeks 4-6 she was aggressive when her kit-
tens approached her, she avoided them much of the time, she almost
never took up half-sit or on-side-lie, and that she only sometimes
allowed her kittens to attach to the nipples when she was sitting.
The fact that this mother had the highest mean weekly percentage
scores (of all mothers) on eat in weeks 4 and 5, and the second
highest score in week 6, suggests that her behaviour may have been
the result of nutritional stress.   In week 4 especially, but also
in the later weeks, her kittens persistently followed her around
crying, attempting to make nipple contact.   (They sometimes did not
try to make nipple contact but just rested beside their mother.)
The distressed behaviour of these kittens may be comparable to the
behaviour of the protein restricted group kittens in the study of
Gallo *et al* (1980), although the latter kittens were of course much
younger.

As mentioned in 4.1.3, kittens generally behave differently in
relation to whether their mothers showed an early decrease in half-
sit + on-side-lie (ie prior to the 6th week) or a later decrease (in
week 6).   The kittens of the former type of mother (C1 and C7 of
Group 4 and C3, C5 and C8 of Group 3) who show early decreases,
exhibit increased scores on on-nipple in sit.   As suggested earlier
this may be because prior to the time that their mothers show a
sharp decrease in half-sit + on-side-lie the kittens have been
totally nutritionally dependant on their mother (or at least almost
totally);   they therefore continue to try to make nipple attachments
in attempts to obtain milk even although their mothers discourage
them.   Even if the kittens are not receiving much milk it is poss-
ible that they receive comfort from non-nutritive sucking.   It has

been demonstrated that kittens do exhibit non-nutritive sucking, at least when they are bottle fed (Kovach and Kling, 1967); and in snow leopard cubs, non-nutritive sucking is believed to occur prior to nutritive sucking during nursing (McVittie, 1978).

By week 6, the kittens in all litters have begun to eat solid food and so probably have less need for milk. They also seem generally less dependant on their mother for social contact. The behaviour of the mothers in families C1, C7, C2, C4 and B5, who show a late decrease in half-sit + on-side-lie, may in fact be a response to the decreasing amounts of time that their kittens choose to spend on the nipple (as suggested in 4.1.3). It certainly does not appear that these mothers in any way try to limit their kittens access to the nipples, as demonstrated by the observation that they all continue to take up half-sit and on-side-lie positions with little (C2) or no (C1, C7, C4, B5) prompting from their kittens (3.2.2). The kittens in litters C1 and C7 (Group 4) may have already been encouraged to switch to a mainly non-milk diet by their mothers' earlier decreases in half-sit + on-side-lie. However in Group 2 litters (C2, C4 and B5), since the kittens have apparently not been driven to eat solid food by restrictive behaviour on their mothers' part, their transition from a milk diet is probably more gradual and prompted mainly by their mothers' diminishing milk supply and their own growing nutritional needs.

It seems, in conclusion, that differences in nutritional state and milk yield may be at least partially responsible for the individual differences between families in behaviour associated with weaning.

Effects on half-sit + on-side-lie behaviour in weeks 1-3   Now it has to be considered whether mothers also possibly differ in

their nutritional states and milk yields during the period from week 1 to week 3 and, if so, whether this could affect their behaviour during this time.

In a study of sheep (Ewbank, 1967) it was found that twin lambs who were receiving less milk from their mothers (as demonstrated by their lower weight gains) sucked more frequently than twins who were receiving larger quantities of milk during the early weeks of lactation (weeks 1-6). A similar finding was made in the present study when 5 litters of high weight gain (Group A) were found to have significantly lower on-nipple scores than 5 litters of low weight gain (Group B) in weeks 2 and 3 (3.6.5). Gallo *et al* (1980) demonstrated that low weight gain in litters is probably a result of the mothers' low milk yield (and possibly also the quality of the milk); they found that the kittens of protein restricted mothers gained weight more slowly than kittens of control mothers. It seems reasonable to deduce that the mothers of the Group B litters (3.6.5) had lower milk yields than the Group A mothers. However, no differences were found between the scores on half-sit + on-side-lie or sit-nurse of the mothers in the two groups. There would appear to be, therefore, no simple relationship between milk yield and these measures of maternal behaviour during the early weeks of lactation.

Effects on quality of maternal care in weeks 1-3 Whether nutritional state and milk yield might have affected the quality of maternal care mothers exhibited in weeks 1-3 has also to be considered. Some of the characteristics that low quality care mothers exhibited are quite similar to those observed in protein restricted mothers (Gallo *et al* 1980). General comparisons are that both low quality care mothers (this study) and protein restricted mothers

(Gallo *et al*) did not make access to the nipples easy for their kittens and are inattentive towards them.   As explained above, there is some evidence to suggest that Group A mothers had higher milk yields than Group B mothers, however there is found to be little correlation between the quality of care a mother shows and her supposed milk yield during this period.   For example, both C2 and C3, who show high and low quality care respectively, have kittens with low weight gains (Table 3.17).   Overall there appears to be no correlation between quality of care and the group of which mothers are members.

The results do not eliminate the possibility that being in a poor nutritional state and having a relatively low milk yield could affect the quality of care a mother gives her young during the first few weeks.   However they do suggest that other factors must also influence quality of care, such as general differences in the behaviour of individual mothers that could be termed differences in personality (1.6.6).   The effects of personality differences are discussed in 4.2.4.

It is worth considering whether milk yield directly affects maternal behaviour or whether the mother is chiefly responding to changes in her nutritional state.   Then, if milk yield is not entirely dependant on nutritional state, but is at least partly genetically determined, it is possible to imagine the case where a mother is in good physical condition but is nevertheless low yielding.   Such a mother might be expected to provide her young with high quality care in spite of her relatively low milk production.

Effects on play and activity   It has been suggested that there is a relationship between kittens' on-nipple behaviour and the

quantity of milk kittens are receiving. Two studies (Koepke and Pribram, 1971; Bateson and Young, 1980) have shown that in later weeks there is also a relationship between milk sucking and kittens' general activity and play behaviour. In the present study, although different litters varied in their on-nipple scores, there were no significant differences in their play and activity scores. In order to interpret this finding, the results of Koepke and Pribram (1971) and Bateson and Young (1980) are now described and discussed.

Koepke and Pribram compared the frequency of play in 2 groups of kittens. One group was allowed access to a lactating female during the first 6 months after birth, whilst the other group was allowed only to suck from a non-lactating female. (Both groups of kittens were fed by stomach loading.) The dry-sucking group reached an earlier and higher peak of play, at 9 weeks, than the milk-sucking group who peaked at 16 weeks. Bateson and Young (1980) separated kittens gradually from their mothers between 31 and 35 days and therefore before natural weaning would normally have been completed. When compared with siblings who had been left with their mother, it was found that the early weaned kittens were more active, and showed higher peaks of both social play (at 38-49 days) and object play (at 50-61 days).

There are several possible reasons for there being no differences in the play or activity scores of the litters in the present study. Since observations were only made up to the kittens 6th week (day 42), it is perhaps unlikely that differences in the amounts of milk that kittens in different litters might have been receiving from their mothers at this stage would have been reflected in significant differences in the frequency of their play or their

activity.   Even if some mothers had stopped lactating, the effects
on their kittens' behaviour would probably not be apparent until
later weeks.

4.2.4   Personality of mother

Effects on quality of maternal care in weeks 1-3   In 1.6.6 a
number of primate studies were cited in which it was demonstrated,
or at least suggested, that general personality differences in
mothers are related to individual differences in their maternal
behaviour (Jay, 1963; Altmann, 1980; Stevenson-Hinde *et al* 1980).
The possibility that personality differences in cat mothers may be
reflected in their maternal behaviour is now considered.

In 3.4 mothers were described as differing in the quality of
care they exhibit towards their young in weeks 1-3.   The charac-
teristics which are used to decide whether mothers show high or low
quality care are the following.

1   The exposure of the ventral surface in half-sit and
     on-side-lie positions.

2   The orientation of the mother's body relative to
     her kittens in half-sit and on-side-lie positions.

3   The mother's attentiveness towards her kittens.

So, for example, low quality care mothers show poor ventral exposure,
sometimes orientate themselves inappropriately relative to their
kittens, and are generally inattentive.

It has already been suggested that although a mother's
nutritional state and milk yield may have some influence on the
quality of her care, other factors are almost certainly of import-
ance.   One supposition was that personality differences might con-
tribute to the differences in the quality of their care.   It was

recorded that the low quality care mothers tend to be more reactive (either showing disturbed or excited behaviour) than high quality care mothers to external stimuli, such as the observer's presence (3.4).   It may be that reactivity in the early weeks after parturition reflects a general tendency to being reactive to external stimuli.   If a mother is reactive to events going on around her, then it is easy to see how this might disrupt her interactions with her kittens.   She would be distracted from attending to them, and responding to their needs and difficulties.

Although quality of care is believed to be related to a mother's reactivity, it is not considered that high quality care merely occurs by default, ie when the mother does not exhibit the trait of reactivity.   Rather, high quality care appears to be a positive trait, which reflects a particular sensitivity or responsiveness of the mother towards her kittens.

Effects on timing of weaning: interaction with effects of nutritional state and milk yield   Personality differences, in mothers, in addition to differences in nutritional state and milk yield, may have contributed to the variation between families in the timing of weaning.   This is suggested by the observation that a mother's physical condition (which presumably mirrors her nutritional state) is not always a good predictor of her behaviour towards her kittens in the weeks when nutritional weaning would be expected to be occurring.   For example, it has been observed in the colony (personal observation) that a mother who is in relatively poor physical condition (ie who is very thin and whose coat is in poor condition) allows her kittens to make nipple attachments and other physical contact (such as in play) for longer, ie until the kittens are older, than other mothers who appear to be in a

considerable better nutritional state. In such a case it would seem that the mother's tendency to be tolerant of her kittens (which might be considered a reflection of her personality) must have over-ridden the tendency to reject their attempts to interact with her, even although she was in poor condition.

Following on from this argument, it may have been the case that some of the mothers in the present study who were still allowing their kittens almost unlimited access to the nipples (and even initiated nursing sessions) were not behaving in this way chiefly because they still had relatively high milk yields - and were in reasonable nutritional state - but because of a tolerance for their kittens. B1 may have been one such mother, since although she was assessed as tolerant in weeks 4-6 (Table 3.1), there is some evidence to suggest that she may have been in poor physical condition. In weeks 5 and 6 it was reported that her movements around the cage were rather slow (Appendix A). Since the present study, several cases of such behaviour have been witnessed in the colony, in mothers with kittens of about 5 weeks of age. The mothers were diagnosed to be suffering from calcium deficiency by the staff of the Unit. The cats were given a daily subcutaneous injection of 2 ml of 'Astracalc 6' (supplied Astrachemicals Ltd), which contains 20% calcium borogluconate. The treatment was given daily until an improvement was seen in the cats' condition. One mother, who was observed particularly closely during and after treatment, showed improvements in her coat and general body condition (ie gained weight) within a few days of the start of treatment. This particular mother had been very intolerant of her kittens prior to the treatment but she became more tolerant afterwards; she allowed them to attach to the nipples in half-sit and on-side-lie and play around

her.

Unfortunately no direct measures were made of mother B1's physical condition and weight changes, but the above findings give strength to the argument that interactions between personality and nutritional state must be taken into account when considering the timing of weaning in individual families.

In their study of the effects of protein restriction on mother-kitten interaction in cats Gallo *et al* (1980) made no mention of individual differences in mother-kitten relations within either the control or protein restricted groups. A study of this kind however would have been ideal for investigating the relationship between nutritional state and personality differences between mothers. The animals within each group would have been strictly comparable in terms of nutritional state, since not only were the mothers in each group fed the same diet, but the diet of each mother was made up according to her metabolic body size.

Although it has been argued that personality differences in mothers may have been related to the quality of care they exhibited in weeks 1-3, and to the timing of weaning, it is not known how, or indeed whether, personality differences would have affected mothers' scores on half-sit + on-side-lie in the first 3 weeks and therefore this is not discussed further.

4.2.5   Conclusions: factors affecting the mother-kitten
         relationship

In summary, it has been shown that litter size, sex ratio, and kitten death only influence quantitative measures of maternal and litter behaviour to a very limited extent. The nutritional state and milk yield of mothers are factors which are indicated to be of

considerable importance in the timing of weaning in different
families. It is considered that personality differences between
mothers affect both the quality of care that different mothers
exhibit in weeks 1-3, and the timing of weaning in different
families. The interactions of the effects of nutritional state,
milk yield and personality, are discussed. The extent to which
genetic or experiential factors contribute to the individual dif-
ferences in mother-kitten relationships is beyond the scope of this
study.

4.3 THE EFFECTS OF INDIVIDUAL DIFFERENCES IN MOTHER-KITTEN RELATIONSHIP ON THE KITTENS' DEVELOPMENT

In 4.1.4 it is concluded that the main types of individual dif-
ferences that can exist in the mother-kitten relationship are dif-
ferences in the quality of care that mothers exhibit in the early
weeks, and differences in the timing of weaning. In 4.3 the pos-
sible consequences of such differences on the development of the
kittens are briefly discussed. Since the kittens were
observed only up until their 6th week, no direct evidence is avail-
able on long-term effects. These may only be speculated upon.

4.3.1 The effects on kitten survival

There is some evidence to suggest that quality of maternal
care, especially in the first week, may affect the survival of the
kittens, since (as reported in 3.4), 2 out of the 3 low quality care
mothers, B2 and B4, had litters in which there were kitten deaths,
but a kitten death occurred in only one out of 5 of the high quality
care mothers, B5 (Table 3.1). Further, there was nothing to
suggest that the death of B5's kitten was the result of her

behaviour.   In 2.2.2 it is argued that B2 and B4 were at least partly responsible for their kittens' deaths.

It is obvious that more research is needed into the importance of quality of maternal care to kitten survival, since the evidence presented above is from a small sample.   It is interesting however that in pigs (Blaxter, 1961), it is reported that the post-natal survival of piglets depends to a large extent on the care with which the sow lies down beside the young.   Many piglet deaths are caused by the sow lying on them.   Mothers B2 and B4 in this study both trapped their kittens underneath and behind their bodies in week 1.

4.3.2   The effects on play and activity (after week 6)

Although differences in play and activity scores were not found between litters in weeks 4-6, since families seemed to vary in the time that weaning began, it would be expected from the findings of Koepke and Pribram (1971) and Bateson and Young (1980)(4.2.3) that later differences in the timing of the onset and peaks of social and object play would have occurred in different litters.   What import-ance such differences might have with respect to later social behaviour is hard to say, especially within the laboratory régime. The social groups in which the young cats are reared (2.1.2) are not comparable to those normally found in cat society as it has been described in more natural settings (Laundré, 1977;   Dards, 1978;   MacDonald and Apps, 1978;   Corbett, 1979).

4.3.3   The effects on maternal behaviour of female offspring

Altmann (1980) has some evidence (from a small sample of animals) to suggest that female baboons adopt the same maternal styles as their mothers.   However since maternal style is closely

correlated with social rank and daughters tend to have the same rank as their mothers, Altmann could not say whether the most important determinant of a female's maternal style was her own rank, her mother's rank and/or her mother's maternal style. The picture is almost as complicated for cats. If a female did happen to show the same patterns of maternal behaviour as her mother (eg in the quality of the care she gave, or when she began weaning her kittens) then it would be difficult to know whether this was due to having inherited the same lactation pattern as her mother, or having the same type of personality (which could be partly genetically and/or partly non-genetically inherited).

4.4 CRITIQUE OF THE METHODS USED TO STUDY INDIVIDUAL DIFFERENCES IN MOTHER-KITTEN RELATIONSHIPS IN THE DOMESTIC CAT

The main aim of this section is to critically examine the methods of data collection and data analysis that were used in this study of individual differences in mother-kitten relationships. Within the section some results presented in Chapter 3, but not so far brought into the discussion, are considered. (The chief reason for their omission from the discussion up to this point is because they were not central to any of the main arguments presented but provided only supplementary information on maternal behaviour.)

4.4.1   The data

It was found that qualitative data on the families was not only extremely useful in helping to interpret some of the results from quantitative data but that it was itself a valuable source of information on individual variation in maternal behaviour. Since the work was in a sense pilot work, it was not possible to have foreseen

the importance of the information collected in diary form and not enough was known about the behaviour of mother cats before the study began, to have designed a protocol for collecting such information quantitatively. However, much of the qualitative data gathered would lend itself to collection quantitatively, as explained below, and thus would provide more concrete evidence on certain aspects of individual differences in maternal behaviour.

In some studies of human maternal behaviour subjective assessments of the quality of mother-infant interactions are quantified by using ratings. Thus, for example, Ainsworth and Bell (1969) assessed mothers on a number of different aspects of maternal care, such as 'mother's perception of the baby', 'mother's delight in the baby', and 'mother's acceptance of the baby', using 9-point rating scales. This method of assessing mothering styles has not tended to be used in non-human maternal behaviour studies. Hinde and Simpson (1975) were interested in assessing rhesus monkey mothers on such qualities of the mother-infant relationship as 'maternal warmth'. Unlike Ainsworth and Bell (1969) however, they did not rate mothers subjectively but instead attempted to express levels of maternal warmth in terms of mothers' scores on a number of behavioural measures which together they considered to characterise the trait. In this way their method perhaps retained more objectivity. Like Ainsworth and Bell (1969), Stevenson-Hinde *et al* (1980) utilised their own subjective impressions of individual rhesus monkey mothers and applied ratings to them. However they were not assessing the animals' maternal behaviour but rather the general behavioural characteristics of individual mothers, so again their method is not strictly comparable to Ainsworth and Bell's.

In describing the quality of maternal behaviour in the cat

however it is felt that the method of Ainsworth and Bell could be applied. Instead of recording, for example, that a mother was 'particularly attentive' or 'very intolerant', she could be rated on a scale (eg of 3 or 5 points) on each of these measures. Likewise, how well a mother exposes her ventral surface in the various nursing positions, and how she orientates herself relative to her kittens in these positions, could also be quantitatively rather than qualitatively assessed. Exposure of the ventrum depends on the positioning of the legs and the orientation of the ventrum relative to the floor (3.2.1). It would be possible to rate each, the leg positions and the ventral orientation on (for example), a 3-point scale. Hence if a mother's ventrum was maximally exposed she would receive a total score of 6. A mother's orientation relative to her kittens could be recorded by scoring kittens not just as still beside mother but also stating whether they were in front or behind her. Many of the suggestions given above for ways of quantifying data that were collected qualitatively in this study are being used in a study now in progress by the author in collaboration with J M Deag and A Manning.

The sampling method used to collect quantitative data was scan sampling and its main limitation, as explained in 2.2.4, was that the dynamics of interactions between mothers and kittens could not be recorded. Thus no quantitative data were collected on who initiated and terminated interactions and how they did so, or on durations or frequencies of behavioural events. However, the qualitative reports revealed that one of the main sources of variation between families was in the nature of feeding interactions at various stages in the kittens' development. For example, by week 6 in some families, the kittens were responsible for initiating

almost all sucking interactions whereas in others the mother was still initiating many of these by taking up half-sit and on-side-lie positions beside her kittens without prior prompting from them.

In conclusion, it would seem to be worthwhile collecting quantitative data on interactive events in order that the differences between families could be expressed with more precision. To this end, in the study now in progress, the sampling method used allows for a complete record of mother-infant interaction to be obtained.

4.4.2   The analysis of the data

The two main questions to be asked of the data were

1   What is the nature of individual variation in mother-kitten relationships?

2   Can mothers (or families) be considered to fall into groups which characterise different types of mother-kitten relationship?

With the qualitative data it was relatively easy to distinguish the ways in which mother-kitten relationships varied and to describe them, and it was possible to classify mothers and place them in groups that were more or less exclusive. Using the quantitative data in the same way was less simple.

Analyses of variance demonstrated that mothers differed on a large number of behavioural measures and that kittens in different litters differed on rather fewer measures. The next step was to find a more economical and informative way of expressing the differences between mothers and between litters.

Relationships between measures of feeding behaviour were investigated using regression analysis, however, this was only

possible because there were relatively few measures to be considered (half-sit + on-side-lie, sit-nurse, crouch + lie, on-nipple in half-sit + on-side-lie). The results from these analyses formed the basis for the understanding of individual variation in the feeding relationship. However, in order to examine relationships between a larger number of behavioural measures (including the feeding measures listed above), factor analysis was employed. This method of analysis has been used in a number of studies of individual variation in behaviour as discussed in 3.8.

Factor analysis revealed many associations between maternal measures but only associations that were stable over several weeks are discussed here. The most interesting grouping of measures is perhaps that of half-sit, paw, purr, walk, and excited/disturbed, which occurred in weeks 3-6. Mothers who score highly on these measures can perhaps be thought of as rather excitable and reactive. Purring is believed to be associated with high levels of arousal (Moelk, 1944) and other behavioural categories seem quite likely expressions of the same. (Mothers who have low scores on these measures would show contrasting behaviour and presumably would be rather quiet and unreactive.) It is puzzling why this particular grouping of measures was not associated with one another in weeks 1 and 2. Nonetheless, factor analysis appears to have revealed a new grouping of measures, characterising a maternal trait hitherto unrecognised by the analysis of qualitative data.

Another combination of measures, however, does seem to characterise a trait already revealed by examining the qualitative data. That is the grouping of the measures crouch, lie, in between (the boxes), and in other box (ie not the litter box). These are generally associated together in weeks 4, 5 and 6 and could perhaps

be thought of as embodying a maternal trait of intolerance to feeding interactions. As already explained, this trait was also discovered through analysis of the qualitative results (3.3.5).

Finally one other association of measures is worth mentioning - that of eat, groom, and lick (in a number of weeks). This finding supports the report (in 3.3.2) that licking often occurs immediately after the mother has taken a mouthful of food. Kittens are perhaps introduced to the smell and taste of solid food by this behaviour pattern.

In summary then - factor analysis revealed one maternal trait which had not been recognised in the analysis of qualitative data, and another maternal trait which confirmed a finding already made from qualitative data.

It is interesting to speculate briefly on further uses of factor analysis. If quantitative ratings had been available on aspects of maternal behaviour for which only qualitative information was available, then these could have been incorporated into the factor analysis. For example, instead of scoring a mother as simply being in the on-side-lie position, her rating on ventral exposure could be incorporated in the score. Mothers' ratings on tolerance and attentiveness could also be included in their data sets. Applying factor analysis to such data could then give information on, for example, whether mothers who received high ratings on ventral exposure also tended to be attentive. It can be seen that there would be great advantage in having quantitative assessments of aspects of maternal behaviour on which only qualitative data was collected.

A useful method of grouping mothers and their litters, at least with regard to their feeding relationship, resulted from examination

of the changes that occurred in mothers' and kittens' behaviour over the 6 week period (3.8). Although the data were quantitative, classification of families was carried out without the aid of statistical procedure. Altmann(1980) used a similar procedure in classifying baboon mothers as *laissez-faire* or restrictive. Using what seemed to be an arbitrary division, she classed mothers who stopped restraining their infants before they were more than 1 month old as *laissez-faire* and mothers who only stopped restraining their infants when they were 1½ months or older as restrictive. Mothers of each maternal style were then compared on a number of measures and differences between the two groups expressed without the use of statistics (Altmann, 1980, pp 132). In both Altmann's study and this study it may have been possible to apply statistics to the results if data on larger numbers of mothers had been available (there were only 12 in each study). Mothers could have been divided into groups using the original criteria and then the groups could have been tested for differences. In the case of the type of data collected in this study on cat mothers analysis of variance might be a suitable test; for example a highly significant inter-action effect between groups and days would indicate that there were inter-group differences in the ways in which scores on half-sit + on-side-lie change. Further statistical tests would be required to describe the differences between the groups more precisely.

To conclude, the types of data collected and the types of analyses performed in this study, are rather different to those used in other studies of individual differences in mother-infant relation-ships. The main reason for this was perhaps because prior to the study, very little was known about individual differences in the maternal behaviour of the cat, and the methods for describing

primate behaviour were not wholly appropriate, not least because the cat has more than one infant.

4.5 BROAD IMPLICATIONS OF THE RESULTS: THE CAT OUTSIDE THE LABORATORY SITUATION

That cats do vary in their abilities as mothers, outside the laboratory as well as in it, has been suggested by MacDonald and Apps (1978) in their study of farmyard cats. Of two sisters who reared their young together, it was felt by the observers, that one was more 'conscientious', and that without her attention, her sister's kittens would have died. In the present study the kittens of low quality care mothers had problems in locating and attaching to the nipples, and in two out of the three litters in which mothers were considered to show low quality care there were kitten deaths. Although these deaths could not be unequivocally related to the mothers' behaviour, it was considered that the kittens died as a result of maternal neglect. The less conscientious mother in MacDonald and Apps' (1978) study could perhaps have been charac- terised as a low quality care mother.

It is interesting to consider the finding that low quality care mothers were more reactive than high quality care mothers to events going on around them. If a free-ranging or feral cat mother was reactive, then it might lead to her abandoning the young at an age when they were unable to survive without her. It may be that if differences in quality of care are to be found in cats which are living outwith the protective environment of the laboratory, then their main effects on the kittens are on their chances of survival.

When timing of weaning is considered, it might be predicted that cats living a free ranging or feral existence would show more

variability than the cats in this study. Food would generally not be so freely available to them and therefore more variation in mothers' nutritional state during lactation would be expected. If food was scarce early weaning would probably occur. Such a relationship between food availability and weaning has been demonstrated in Bighorn sheep (Berger, 1979). From the kittens' standpoint the effects on their lives of being weaned early or late must be of great importance, firstly in terms of their ability to feed themselves but perhaps also in terms of their social development. For example, for kittens reared in a rich social group of the composition Fagen (1978) described (1.3.3), the age at which they are weaned might influence their social relationships with group members. This could conceivably affect whether they remain in or disperse from the group. Young males commonly emigrate from the natal group, while females tend to stay (Fagen, 1978). However females do sometimes emigrate, and it would be interesting to know more about the social development and social relations within the group of such females prior to their departure. A study of individual differences in mother-kitten relationships in group living free ranging cats like those described by Laundré (1977) and Dards (1978) would be of great value.

4.6 SUMMARY OF DISCUSSION

1   Individual differences in the mother-kitten relationship are expressed in terms of the quality of care the mother shows in weeks 1-3, and the timing of weaning.

2   Litter size, sex ratio and kitten death are considered to have had little effect on mother-kitten relationships in this study, although it is argued that low quality care may

influence kitten survival in week 1.

3   Although direct evidence is not available, it is con-
sidered that the milk yield and nutritional state of mothers
influence the timing of weaning.   It is not clear whether milk
yield or nutritional state affect the quality or quantity of
maternal care in weeks 1-3.   An experimental study where
direct measurements of milk yield and maternal nutritional
state can be made would be of great value in order to effec-
tively assess the influence of these factors upon mother-kitten
relationships.

4   The personality of a mother is considered to affect the
quality of care she exhibits in weeks 1-3, and the timing of
weaning.   It is thought that the effects of personality may
interact with those of nutritional state and milk yield.   If
nutritional state could be controlled experimentally then the
importance of personality could perhaps be more easily
assessed.

5   Possible effects of differences in quality of care, and
differences in timing of weaning, on kitten development are
considered.   For example, the short-term effects on kitten
play and activity, and long-term effects on maternal behaviour
of female offspring, are discussed.

6   The qualitative and quantitative methods of data collec-
tion and analyses that were used in this study are discussed.
Suggestions for future work are made, including the quantifi-
cation of the qualitative measures used here.

7   The occurrence of individual differences in mother-kitten
relationships in domestic cats living independently, or semi-
independently of man is considered.   Factors which may cause

such differences, and possible effects on kittens' behaviour
and survival are discussed.

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APPENDIX A   <u>Edited diary entries - weekly summaries of the</u>
             <u>behaviour of mothers and kittens in each family</u>
             .

In the summaries below the reporting style that was used in the
diary itself is not altered.   M = mother, K = kitten, Ks = kittens.

FAMILY: Cl

<u>Week 1</u>

In on-side-lie M's legs are rather curled up so ventral surface
is not completely exposed.   Ks have some difficulties in locating
and attaching to nipples.   Ks are sometimes trapped behind M when
she is in on-side-lie.   M is, however, responsive to Ks' diffi-
culties and shifts (sometimes rolling) her body so Ks can then reach
her ventrum.   M is attentive, a bit excitable, and sometimes reacts
to my presence.

<u>Week 2</u>

M is attentive and excitable.   M responds to K crying when it
is behind her by carrying it in her mouth round to her ventral sur-
face.   Responds to Ks' nuzzling by shifting her body and thus making
her ventrum more accessible.   When Ks are on-nipple M is always in
half-sit or on-side-lie.   M vocalises: brrp and brrp-cry a lot;
spends some time walking around cage.   Towards end of week Ks seen
pawing each other and rolling on backs.   One climbs up edge of box.

<u>Week 3</u>

M less attentive and spends more time away from Ks.   She still
takes most of the initiative in feeding and gets into on-side-lie
before Ks begin nuzzling.

<u>Week 4</u>

M still gets into on-side-lie for Ks and thus initiates feeding,
and also allows Ks to attach to nipples whenever they initiate by
nuzzling.   M walks around quite a lot.   Vocalises (brrp) to K who
is walking around crying.   Ks follow M around.   They all climb out
of box now and play quite a lot.

<u>Week 5</u>

M still spends much time in on-side-lie when Ks are on-nipple
and when they are asleep beside her.   M sometimes sits next to Ks
when they are asleep and licks them, and when they wake up they
begin to nuzzle her and she gets into on-side-lie.   Lively play and
Ks now eating some solid food.

Week 6

M still initiates contact with Ks and gets into on-side-lie or sits beside them. Ks seem more independent, especially towards end of week, when they are rarely seen on-nipple, or still, by mother.

FAMILY: C2

Week 1

M spends a lot of time in on-side-lie beside Ks - legs stretched away from body and ventral surface well exposed. Ks therefore have easy access to nipples. M sometimes tucks her head in close to Ks' bodies when in on-side-lie. If Ks nuzzle M when she is sitting she quickly gets into on-side-lie. M not reactive to my presence.

Week 2

M gets into on-side-lie very carefully and does not disturb Ks at all. M is very attentive, she hardly ever leaves Ks and is often in on-side-lie beside them. Towards end of week M is still spending almost all her time with Ks but now sits more often, and sit-nurse is observed. M not reactive to my presence. Ks not very active (contrast with C1 Ks) and huddle when M leaves them.

Week 3

M with Ks most of time. Feeds Ks in sit-nurse quite a lot. Ks not very active and huddle when M leaves them.

Week 4

M sits beside Ks, licking them, quite a lot. If they nuzzle she goes into half-sit or on-side-lie quite rapidly. Spends a lot of time with Ks. Ks interact playfully on occasion - pawing and biting, but do not climb out of box.

Week 5

M still spends much time with Ks - almost never leaves them to rest by herself. When Ks nuzzle, she quickly goes from sit to on-side-lie. M also observed in on-side-lie beside Ks even when they were asleep. M licks Ks quite often and is watchful of them as they move around and interact. Ks playing more now but play is not vigorous fast moving play but mainly pawing, rolling and stand on. After playing Ks go to M and nuzzle her and then attach to the nipples.

Week 6

M gets into on-side-lie whenever Ks nuzzle - she never avoids them. Ks play vigorously in nest box - mainly roll and stand on

play - do not race around cage although they do use whole cage for non-play activity.

FAMILY: C3

Week 1

M and Ks moved from one cage to another at start of week (see Footnote at end of Appendix).   M adopts on-side-lie position in which ventral surface is not well exposed.   M is not careful when she gets into on-side-lie beside Ks and Ks sometimes get trapped behind her or she lies on them.   Ks often have difficulties locating nipples and sometimes behave as if they are too weak to even try to reach M's ventrum.   Often only one K is seen on-nipple at a time - possibly because there is not much room at the ventral surface (see above).   When Ks nuzzle M when she is sitting she quite often remains sitting and sit-nurse is observed.   Not very attentive M - she goes to sit alone sometimes.   Reacts to my presence with disturbed response.   This was especially noticeable in the 1st observation session.

Week 2

M spending more time with Ks but often in sit rather than on-side-lie.   In on-side-lie nipples not exposed well because of position of legs and orientation of body.   Ks seem to be locating and attaching to nipples more easily however.

Week 3

M spending more time in on-side-lie beside Ks, especially towards end of week, but the position is still rather curled up and the 3 Ks are rarely all on nipple together.   M licks Ks more now. Ks pawing and biting each other and M.

Week 4

M now spends almost all her time with Ks.   Allows Ks to attach to nipples when they attempt to but generally remains sitting. When Ks are asleep M often sits or crouches beside them.   If Ks wake up and M is not beside them they move to her to make contact.   Ks out of box and are eating solid food.

Week 5

M spends much of her time in sit and sit-nurse - allows Ks to attach to nipples whenever they attempt to but she always remains sitting.   M is quiet.   She watches Ks sometimes and makes brrp vocalisations to them - when they are playing.   K play is very

vigorous and includes running around the whole cage.

Week 6

M still allows Ks to attach to nipples when she is sitting.
When Ks are asleep she sometimes lies down beside them. Very watch-
ful of Ks when they play around her. Ks now eating large quantities
of solid food.

FAMILY: C4

Week 1

M quite excitable and reactive. In on-side-lie ventrum is well
exposed - legs are stretched out. Licks Ks and grooms self quite
often. Paws Ks when in on-side-lie or sitting next to Ks. Leaves
Ks quite often and sits in other box grooming herself.

Week 2

On-side-lie as week 1. M is out of contact with Ks quite a lot
of the time, M sometimes walks about and cries. Ks pawing one
another.

Week 3

M gets into well exposed on-side-lie whenever Ks nuzzle her but
she does spend quite a lot of time sitting next to Ks grooming her-
self. Paws Ks a lot. M is quite restless and walks around - Ks
cry when she does this. Ks are now showing pawing and rolling play
but are not out of nest box.

Week 4

M still initiates feeding by getting into on-side-lie beside
Ks. Spends a lot of her time with Ks in on-side-lie or sitting when
they are asleep. Ks playing is in nest box and consists mainly of
pawing, rolling and stand on rather than vigorous running.

Week 5

M still gets into on-side-lie frequently for Ks. She often
arouses them from sleep by pawing them. Ks spend their time in con-
tact with M or playing.

Week 6

M still initiates feeding by taking up on-side-lie for Ks - they
rapidly attach to the nipples. M walks around the cage while Ks are
playing. Ks' play is very active - running and back arching around
the whole cage. M makes brrp and brrp-cry vocalisations often.

FAMILY: C5

Week 1

M changes position often when in on-side-lie and thus disturbs Ks when they are on-nipple. However Ks generally have no problems in locating and attaching to nipples. M reacts to my presence - sometimes stands up.

Week 2

As in week 1, M changes her body position regularly which disturbs Ks. M responds to Ks' crying when she is away from nest box by returning and making brrp vocalisations.

Week 3

M in sit-nurse and on-side-lie with Ks on nipple quite a lot. Often when in sit-nurse M reacts to my presence by standing up and thus disturbs Ks (they lose the nipples). Ks not yet out of nest box, not yet steady on feet but some pawing and rolling. Ks spend most time asleep or on-nipple. M almost never leaves nest box.

Week 4

As in week 3, M is in sit-nurse and on-side-lie with Ks on-nipple quite a lot but often stands up and dislodges Ks from nipples. Ks not yet out of nest box.

Week 5

Ks attached to nipples most often when M in sit but M sometimes takes up on-side-lie. Smallest K constantly trying to make nipple attachment. Other 2 Ks play more than smallest K.

Week 6

M restricts Ks' access to nipples by crouching and also by standing up (observed when smallest K nuzzles). Ks still spend some time on-nipple when M is sitting. Ks hardly play at all and spend much time asleep either huddled or still by M when she is crouched beside them.

FAMILY: C6

Week 1

M spends almost all her time beside Ks in on-side-lie - ventrum exposed although legs slightly curled up. Ks have some problems locating and attaching to nipples but spend long periods attached to them. Towards end of week M sits sometimes and does not spend such long periods in on-side-lie. M paws Ks when in on-side-lie. M a

little reactive to me at beginning of week (growls).

Week 2

M in half-sit or on-side-lie most of time and initiates most feeding interactions. Reacts with disturbed behaviour if I go too close to cage.

Week 3

M very attentive - always with Ks in half-sit or on-side-lie. Takes initiative in feeding by taking up these positions before Ks nuzzle. Paws and purrs when Ks on-nipple. Ks not out of box but are pawing each other and actively moving around.

Week 4

M sits beside Ks much of time. Ks not playing much. One or two Ks out of nest box and eating solid food.

Week 5

M sits beside Ks much of time. Ks showing a lot of rolling and pawing play in nest box.

Week 6

M only once seen initiating a feeding session by getting into on-side-lie. On the whole she rarely gets into either on-side-lie or half-sit, and M is not always responsive to Ks' attempts to attach to nipples, eg one K follows M around crying, she turns and gently bites it, eventually she takes up half-sit beside Ks. M avoids Ks when they are playing, turning her back on them and taking up crouch position. M moves away when Ks paw her. Ks are quite active in their play.

FAMILY: C7

Week 1

Apart from first day when M is disturbed as a result of being moved from one cage to another (Footnote at end of Appendix), M is not reactive and spends much time with Ks in stretched out on-side-lie (legs away from ventrum). Ks have no difficulties in attaching to nipples. M stays with Ks in on-side-lie even when they are asleep.

Week 2

M has stretched out on-side-lie as week 1, gets into this position beside Ks even when they are asleep. If M is sitting beside Ks and they nuzzle her she goes into half-sit and then on-side-lie for them. After eating M always grooms self and licks

kittens.

Week 3

Although M still often goes into half-sit and then on-side-lie
when Ks nuzzle her, she also sometimes remains sitting and sit-nurse
takes place.   M quite often sits beside Ks when they are asleep.
When M is absent Ks are usually huddled asleep.   M eats quite a lot.

Week 4

By mid-week some of Ks seen outside litter box.   M seen feeding
Ks in on-side-lie outside litter box.   Ks actively playing with each
other and also paw and bite M - she licks them in response or does not
react.   After play Ks go to M and nuzzle - M gets into on-side-lie.

Week 5

M allows Ks to attach to nipples whenever they attempt to.   She
sometimes remains sitting but still often gets into half-sit or on-
side-lie.   M stays with Ks for some time after they have come off
the nipple and have fallen asleep.   Ks show a lot of active playing
and M often sits near them.   She is very tolerant of Ks pawing her
and climbing on her.   After playing Ks always seek M and initiate
feeding.

Week 6

M still readily gets into half-sit or on-side-lie for Ks when
they nuzzle her in sit.   She also still returns to Ks after eating
and often gets into half-sit beside them.   Ks play very actively
and often paw and climb on M.   M is very tolerant of this.

FAMILY: C8

Week 1

M and Ks are moved to a new cage (Footnote at end of Appendix)
but M settles down quickly.   She stays with Ks almost constantly and
is very attentive.   M licks and paws Ks a lot and also rests her
head on Ks and rubs her face against them.   M sometimes reacts to my
presence - shifts her body and may stand up thus disturbing Ks who
cry in response.   M eats a lot of food.

Week 2

M gets into half-sit around Ks when she returns from eating.
Ks are usually wakened and begin to nuzzle and then attach to
nipples.   M licks Ks a lot especially after eating.   M is friendly
towards me and sometimes reacts to my presence.

Week 3

M seeks contact with Ks and when they are asleep she either sits next to them, licking them, or sleeps next to them curled up in on-side-lie. If Ks begin to nuzzle M stretches out her legs to make access to the nipples easier. At end of week M is seen in crouch position, and Ks are seen nuzzling M when she is standing.

Week 4

M paces around cage a lot. She leaves Ks and sits away from them. Ks are walking unsteadily and follow M around, crying. They cry almost continually. M strikes at Ks and yowls at them. Ks retreat from her. Ks sleep huddled together. They do play some-times. Ks are eating solid food. M is friendly to me.

Week 5

Ks seek and follow M a lot. They are eating a lot of solid food by end of week but still attempting to attach to nipples. M sometimes allows Ks to do so when she is sitting but never gets into half-sit or on-side-lie for Ks. M never seeks contact with Ks. Ks make all approaches. K that was ill disappears (2.2.2 under Deaths) - must have been eaten by M. M yowls at Ks when they play. Towards end of week M allows Ks to remain attached to nipples for longer periods and even licks them.

Week 6

Ks are opportunistic and seek contact and attempt to attach to nipples whenever the chance arises. M generally avoids contact with Ks. They quietly edge closer to M when she is resting alone, but often, once they have made contact with M, she moves away from them. Ks play a lot. M yowls at them.

FAMILY: B1

Week 1

Attentive M. She spends most of her time with Ks in stretched out on-side-lie position (legs way from body) but also seen in half-sit and sit. Ks seen once to have problems locating nipples. M not reactive to my presence but seems slightly wary of me. Licks Ks.

Week 2

M is quiet and with Ks almost constantly. M has a stretched out on-side-lie position and Ks have easy access to nipples. M rests with Ks when they are asleep - sitting or in on-side-lie beside

them.   Licks, purrs and grooms quite often.   Occasionally paws Ks.

Week 3

M in half-sit and on-side-lie a lot.   Very attentive.   Purrs when Ks on-nipple.   M makes brrp vocalisations when she returns to Ks after being out of the litter box.   She immediately settles down beside Ks.   Ks pawing and rolling on backs with one another, not yet steady on feet.

Week 4

No diary record.

Week 5

Ks steady on feet now and both M and Ks are active around the cage.   M makes brrp vocalisations to Ks when they play and is very watchful of them.   Ks play very vigorously.   After playing Ks go to M and nuzzle - she purrs loudly and takes up half-sit and then on-side-lie position.   After being on-nipple Ks sleep and mother generally stays with them.   M does occasionally rest along crouched on cage floor.   At end of week M is moving around very slowly making a quiet throaty vocalistion (crrow - Appendix B).

Week 6

M still gets in half-sit and on-side-lie when Ks nuzzle her. She purrs and licks Ks while they are on-nipple.   Ks always nuzzle and attach to nipples after playing.   M rests with Ks when they sleep but also rests alone sometimes.   M is tolerant of Ks when they play around her.   She is still moving around rather slowly.   Ks eat solid food hungrily.

FAMILY: B2

Week 1

Although M is in on-side-lie a lot her ventral surface is not well exposed.   Her legs are curled close to her body and she some-times orientates her body so her ventrum is close to the floor.   She is unresponsive to Ks' attempts to make nipple contact and Ks some-times become exhausted in their searching.   When M gets into on-side-lie Ks are sometimes trapped behind her for long periods - she does not respond to their attempts to escape.   (Four kittens (out of 6) died in this first week, apparently from either dehydration, lack of nourishment, or being suffocated - 2.2.2).   M cries a lot and stands up and walks about sometimes.   When she returns to Ks she does not immediately assume on-side-lie - she often sits and grooms herself

while Ks cry and try to locate her nipples. Sometimes M shows
ambivalence in her behaviour - one moment being very unresponsive to
Ks and the next watching Ks intently and pawing them.

Week 2

M stays with Ks almost all the time and is in on-side-lie a lot.
However Ks still have some difficulties in making nipple attachments.
M does not shift to make nipple location and attachment easier for
Ks. Ks sometimes become exhausted after nuzzling for long periods.
M cries a lot and does not purr when Ks are on-nipple. M sometimes
shows disturbed behaviour (apparently not as a reaction to my
presence).

Week 3

No diary record.

Week 4

M in on-side-lie a lot but could not be called attentive. Ks
on-nipple a lot. When M walks around cage Ks follow her, crying.
When they reach her they nuzzle - M usually gets into half-sit. M
cries a lot.

Week 5

M very restless and paces around the cage. M avoids Ks but
they follow her. Whenever M rests Ks approach and nuzzle - they
initiate all contact including nipple attachments. Ks not seen
playing much.

Week 6

M rests in on-side-lie quite a lot and Ks take opportunity to
go to her and attach to nipples. M terminates contact between her-
self and Ks far more often than they do. M walks around crying a
lot and Ks follow her. Ks do not play much, and when not seeking
contact with M, they sleep, huddled together.

FAMILY: B3

Week 1

M is friendly to me and reacts to my presence. M leaves Ks
often. In on-side-lie ventrum is well exposed but Ks are often
disrupted when on-nipple by M standing up and sometimes leaving. Ks
sometimes become exhausted by these disruptions apparently because
they must continually relocate the nipples. However nipple location
and attachment itself causes them no problems. M sits beside Ks and
quite often only takes up on-side-lie after Ks have nuzzled her or

moved around her, crying.   Once M is in on-side-lie she becomes more attentive and paws and licks Ks, and purrs.

Week 2

M is inattentive - she spends much time sitting and often out of contact with Ks.   She looks out of cage and not at Ks.   In on-side-lie M sometimes traps Ks behind her.   Often Ks seem too exhausted to attempt to locate her ventrum.   Ks attach to nipples when M is sitting and in half-sit as well as on-side-lie.   M purrs when Ks are on-nipple.   M is less reactive to me now.   Ks huddle when not with M.

Week 3

M spending more time in on-side-lie (and sometimes taking up the position without Ks nuzzling first).   M not reactive to my presence now and is quite calm.   M spends quite a lot of time sitting grooming herself.   Rather an inattentive mother.   Ks pawing and rolling on backs but not yet steady on feet.

Week 4

M spends much time sitting alone grooming but does get into half-sit or on-side-lie for Ks when they nuzzle.   M purrs when Ks on-nipple.   Ks not very active or playful.

Week 5

Sit-nurse observed but M also gets into half-sit and on-side-lie for Ks.   M sits a lot of the time.   M watches Ks when they play and vocalises to them (mrrn - Appendix B).

Week 6

Sit-nurse observed but M also gets in half-sit and on-side-lie. M purrs when Ks on nipple.   After playing Ks go to M, nuzzle and attach to nipples.

FAMILY: B4

Week 1

M in on-side-lie almost all the time but does not shift to make access easy for Ks - they have problems in locating the nipples. M pays no attention to Ks and sometimes almost lies on top of them. M hardly ever changes her body position.   M is rather disturbed by my presence - backs away slightly.

Week 2

M stays in on-side-lie for long periods, ventrum better exposed than week 1.   Ks have easy access to nipples but do spend long

periods, still, beside M.   M shows a little more responsiveness and lifts one K (in her mouth) round to her ventral side when it is behind her.   She also curls around Ks and licks them.

Week 3

As previous weeks - M in on-side-lie a lot, Ks still beside her a lot.

Week 4

No diary record.

Week 5

Although M still spends long periods in on-side-lie she does sometimes leave Ks.   When she returns she gets into on-side-lie beside them.   Ks spend much time on-nipple, or still, beside M and when they are active they are not very lively.

Week 6

When Ks are active this seems to make M active - she walks around making brrp and brrp-cry vocalisations and rubs against Ks.   Although Ks are active they are not very playful.

FAMILY: B5

Week 1

M in half-sit or on-side-lie almost all the time and Ks have easy access to nipples because ventrum is well exposed.   Ks can easily attach to nipples even when M is sitting.   M not reactive to me except if I am very close to cage - she is then friendly and some-times moves.   M paws Ks a lot.

Week 2

M in half-sit and on-side-lie a lot.   Remains in on-side-lie even when Ks come off nipple.   Purrs when Ks are on-nipple and paws them a lot.   Spends a little more time grooming herself now. Quiet mother.   She is sometimes reactive to me.

Week 3

M spends almost all her time in half-sit or on-side-lie, with Ks, or sitting grooming herself.   If Ks attach to nipples when she is sitting she gets into half-sit.   Paws Ks and purrs a lot.

Week 4

M never leaves Ks for very long periods.   M takes up on-side-lie beside Ks when they are asleep - when they wake they can immediately attach to nipples.   Ks play and are seen out of litter box for first time.

Week 5

M in half-sit or on-side-lie beside Ks most of time but once
seen resting alone on floor of cage.   When M returns from eating she
takes up on-side-lie beside Ks.

Week 6

M still spends much time in half-sit and on-side-lie beside Ks
but does sometimes rest alone.   When Ks play M either ignores them
or paws and bites them rather excitedly.

FAMILY: B6

Week 1

M with Ks almost constantly in half-sit or on-side-lie - in both
positions ventrum is well exposed, and Ks have easy access and are on
nipple a lot.   M is quiet and not easily disturbed although seems a
little timid of me and backs off slightly.   Paws and licks Ks
occasionally.

Week 2

M still spends almost all her time in half-sit or on-side-lie
beside Ks.   She licks Ks a lot and purrs sometimes.   By end of week
M leaves Ks a little more readily.   M seems timid of me.

Week 3

M more active now and walks around occasionally but still gets
into half-sit and on-side-lie for Ks a lot.   Paws, licks and purrs
when Ks on-nipple.   Ks walking around unsteadily and pawing and
rolling each other.   M seen clasping a K in her paws and rolling it
over.   M and Ks usually active at same time.   M purrs almost con-
stantly even when Ks not on-nipple.

Week 4

M still initiating nipple attachment by taking up on-side-lie
beside Ks.   If Ks attach when M is sitting she takes up half-sit for
them, and paws, licks and purrs.   Ks playing and seen out of litter
box.   Ks paw mother quite a lot.   M seen resting alone.

Week 5

M spends almost all time with Ks.   M initiates nipple attach-
ment by taking up half-sit beside Ks.   M also responds quickly by
taking up half-sit if Ks nuzzle when she is sitting.   Purrs, paws
and licks when they are on-nipple;   sits in contact with them when
they are not on-nipple.

Week 6

As week 5, M still initiates nipple attachment and allows Ks to do so.   M still seeks contact with Ks but sometimes rests alone.   M and Ks active together - M walking around purring, sometimes making brrp vocalisations to Ks and sometimes rolling on her back playfully.

FAMILY: B7

Week 1

M is very attentive - always looking at Ks and when in on-side-lie she shifts her body so that Ks have better access to nipples. Ventrum well exposed.   M paws and licks Ks, and curls around them in a protective fashion.   Responds to Ks' cries and if they nuzzle her when she is sitting she quickly takes up on-side-lie.   When Ks are asleep M sometimes leaves them (towards end of week at least).   M makes brrp vocalisation in response to Ks cries.   M sometimes stands up in response to my approach but then immediately resumes her original position.

Week 2

M is very attentive - spends much time in on-side-lie and often rests her head on Ks.   If sitting and Ks nuzzle, M quickly responds by taking up half-sit and then on-side-lie.   When Ks are asleep M often sits close to them.   M purrs constantly.

Week 3

No diary record.

Week 4

Ks nuzzle M when she is standing and sitting and she almost always gets into half-sit or on-side-lie for them to attach to nipples.   Ks active and playful and M active at same time.   M purrs when Ks are with her and brrps when they are playing.   Ks now eating solid food.

Week 5

M spends much time with Ks and positively seeks contact with them.   Often M takes up on-side-lie beside Ks when they are asleep - when they wake they can immediately attach to nipples.   Ks showing rolling and pawing play together.   Ks eating some solid food.

Week 6

M sometimes rests away from Ks now but still takes up on-side-lie beside them.   Ks play a lot and M walks around more or less ignoring them.

FAMILY: B8

Week 1

M attentive at start but towards end of week she leaves Ks
occasionally.   On-side-lie is stretched out and Ks have easy access
to nipples, but when one K was trapped behind M, it was some time
before she shifted so that it could locate her ventrum.   M is not
generally reactive and is only slightly disturbed if I go very close
to cage.

Week 2

M is not very responsive to Ks when they are searching for
nipples - she does not shift to help them.   However, generally, her
position allows easy access to nipples.   If Ks nuzzle when M is
sitting she usually takes up half-sit quickly.   M quite often leaves
Ks and rests alone or walks around.   Ks huddle together asleep.

Week 3

M quite often leaves Ks when they are asleep but she still
readily takes up half-sit or on-side-lie for them to make nipple con-
tact.

Week 4

No diary record.

Week 5

M spends a lot of time away from Ks and is rather restless,
crying sometimes.   Towards end of week she begins to avoid Ks.   Ks
huddle together and do not follow her around.   Usually when M goes
to Ks and they nuzzle her she takes up on-side-lie and lets them
attach to nipples.   Later in the week she is less responsive.   She
sometimes leaves when Ks nuzzle or leaves shortly after Ks have
attached to nipples.   When Ks come off nipples M assumes a position
in which her nipples are less accessible.   When Ks are actively
playing around M avoids them.

Week 6

Ks playing actively.   M sleeps away from Ks, on floor.

FAMILY: A1

Week 1

M is rather reactive and shifts about and rolls, disturbing Ks
who are on-nipple.   M spends quite a lot of time in on-side-lie and
also uses half-sit position when Ks are on-nipple.   M paws Ks.

Week 2

On-side-lie is stretched out and ventral surface exposed but M is reactive to me and rolls about and disrupts Ks when they are on-nipple.   M spends quite a lot of time sitting grooming herself and paying little attention to Ks.

Week 3

Ks actively playing - pawing, rolling and stand on.   They are out of litter box now.   After playing they settle beside M and initiate nipple attachment.   M goes from sit to half-sit.   M seems less reactive now and spends much time in half-sit and on-side-lie.

Week 4

M is quieter now.   She gets into half-sit from sit-nurse and also takes up on-side-lie in which ventrum is well exposed.   Spends more time with Ks now.   Ks are very playful and active.

Week 5

When Ks nuzzle and attach to nipples while M is sitting, she takes up half-sit or on-side-lie for them.   Ks are active and play-ful and M is active and walks around at same time.   Ks seek contact with M to rest with her as well as to attach to nipples.

Week 6

No diary record.

Footnote

Three of the mothers - C3, C7 and C8, were not housed in the observation room when they gave birth.   They therefore had to be moved to cages in this room, a day or two after parturition.   Moving the families was carried out with the minimum of disturbance.   The kittens were transferred in their litter box, with the mother, if she would remain in the box;   otherwise she was carried separately. The family were given the sanitary tray and food dish from their original cage.   The first observation session had to be run on the same day as the families were moved but they were given some time to settle before the session was begun.

APPENDIX B   Descriptions of vocalisations recorded

Vocalisations

The most frequently recorded vocalisations were brrp, brrp-cry, cry, and purr; rather less frequently, hiss, growl, and yowl were recorded; and in addition some vocalisations were recorded which were apparently characteristic of individual cats and seemed to be variations on brrp and brrp-cry, these were crrp, mrrp, crrow and mrrow.   These latter were termed 'various vocalisations'.

Moelk (1979) divided sounds uttered by the cat into 3 main types.   She did this by ear and did not use sound spectograph analysis.

1   Sounds made through the nose with the mouth closed (purring and mhrn murmurs).

2   Sounds made as the mouth opens and then closes, producing a pattern of vowels (basically a:ou).

3   Sounds made with the mouth held tensely open (strained intensity cries such as growling and hissing).

In an earlier paper Moelk (1944) described how these 3 types of sound can be patterned to give 16 different vocalisations.   However she simplified this in her 1979 paper, explaining that the basic adult vocalisation is a vowel pattern opening from a murmur - mhrn-a:ou (a combination of sounds 1 and 2).   She suggested that most vocalisations can be described as a modification of this pattern with each half of the sound being subject to variation from one to zero.

On the basis of Moelk's simplified classification of vocalisations it was thought that brrp, brrp-cry and cry were all variations on her mhrn-a:ou calls.   Brrp was thought to be equivalent to a mhrn murmur, brrp-cry, a murmur followed by a vowel sound, and cry the same as brrp-cry but with more emphasis on the vowel sound than the murmur.   It was also realised that 'various vocalisations' were also variations on mhrn-a:ou.   Purr, as in Moelk's purr, was recognised as a pattern of murmur sounds.   With reference to Moelk (1944), growl was thought to be equivalent to the growl she described, yowl was thought to be equivalent to anger wail, and hiss equivalent to spit.

Since brrp-cry and cry could not be translated precisely into

Moelk's terminology, it was decided that the original names given to vocalisations in this study would be those used in the text.

APPENDIX C   Changes across the 6 weeks in means of maternal and litter measures

Details of the maternal and litter behavioural measures that show significant changes across weeks (Tables, 3.2, 3.3, 3.20 and 3.21), are presented here.   Mean weekly percentage scores (for all mothers, and for all litters) are given for each measure, each week, as illustrated in Figure C(1)-(9).

The results presented above are now briefly considered and compared with those available from other studies.   Both mothers and litters show a decrease in their scores in the litter box, although for mothers the decrease is greater, probably due to the fact that some of the mothers, at least, are trying to avoid their kittens. Haskins (1975) found considerably greater decreases by both mothers' and litters' scores in the litter box.   However his families were accommodated in individual rooms and not cages and presumably therefore had a greater choice of locations.

Haskins also collected information on the following measures: half-sit + on-side-lie (thought to be equivalent to Haskins' lactation position), shift, lick, kitten play, and kitten huddling. (Haskins' nuzzle and suckle scores are not equivalent to nuzzle and on-nipple in this study because he had difficulty in distinguishing these two measures one from another, and consequently scored them together.)   Of the above measures, most showed approximately the same patterns of change in each study.   The mean weekly scores were not however strictly comparable in the two studies because they were expressed differently.   (Haskins' scores were expressed in terms of proportions of 10 second blocks in which each measure occurred.)

A few of the measures recorded in this study that are of

particular interest are now mentioned. The maternal vocalisation

purr which is usually associated with nursing rises up to the third

week after which it decreases. This fits in with the fact that in

weeks 4, 5 and 6 both sit-nurse, and half-sit + on-side-lie are

decreasing. The brrp vocalisation which is often used when the

mother is calling to her kittens in a friendly manner (Moelk, 1979)

increases across the weeks. This is in keeping with the fact that

the kittens are becoming more mobile, and from week 4 are able to

leave their mother and explore the cage.

It is interesting that the two maternal measures, excited/dis-

turbed, and paw, which have been shown to be associated with one

another using factor analysis (3.8), exhibit such similar patterns

of change over the 6 weeks. The fact that they decrease is

reflected in the diary records of several of the mothers (Appendix A)

who become less reactive to the observer with time.

FIGURE C(1)   Illustrates weekly means for the measures
               in litter box (mothers), half-sit + on-
               side-lie, and on-side-lie.   Analysis of
               variance was performed on litters' in
               litter box scores, only for weeks 4-6
               (3.7.1).   As illustrated by the dotted
               line, kittens generally did not leave the
               litter box until week 4.   The solid line
               from week 4 onwards shows the mean in
               litter box score thereafter.

FIGURE C(2)   Illustrates weekly means for the maternal
               measures: sit, sit-nurse and shift.
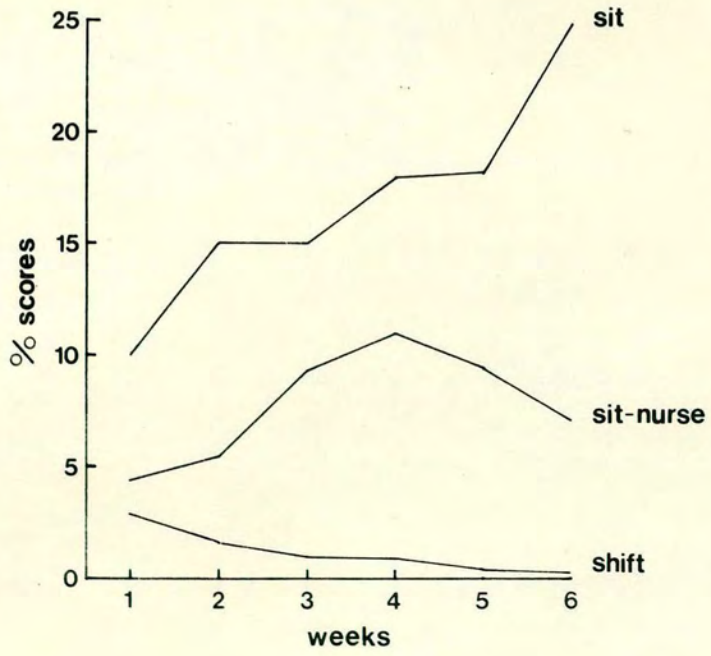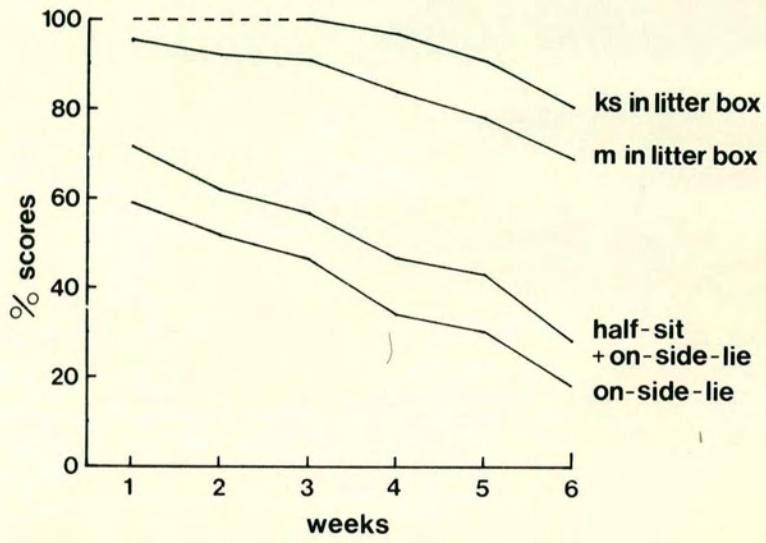
FIGURE C(3)   Illustrates weekly means for the maternal
              measures: crouch, lie, and crouch + lie.

FIGURE C(4)   Illustrates weekly means for the maternal
              measures: stand, walk, eat, and drink.
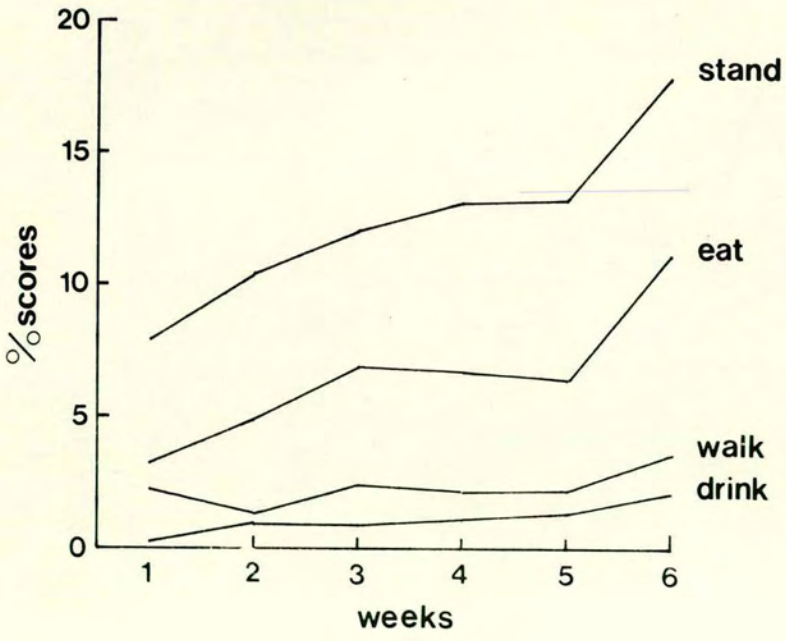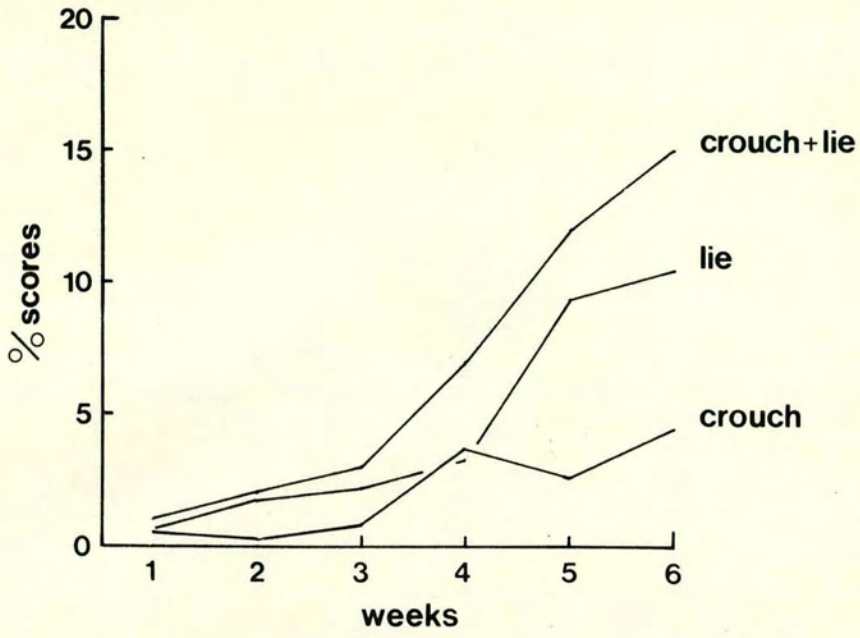
FIGURE C(5)   Illustrates weekly means for the maternal
              vocalisations: brrp, brrp-cry and purr.
              Mother B2 did almost all the crying.
              Since no data are available for her in
              week 3, means for this measure are not
              plotted.   Means for weeks 1, 2, 4, 5
              and 6 are 4.4%, 3.8%, 3.0%, 1.2% and
              1.0% respectively.

FIGURE C(6)   Illustrates weekly means for the maternal
              measures: groom, lick, paw, and
              excited/disturbed.
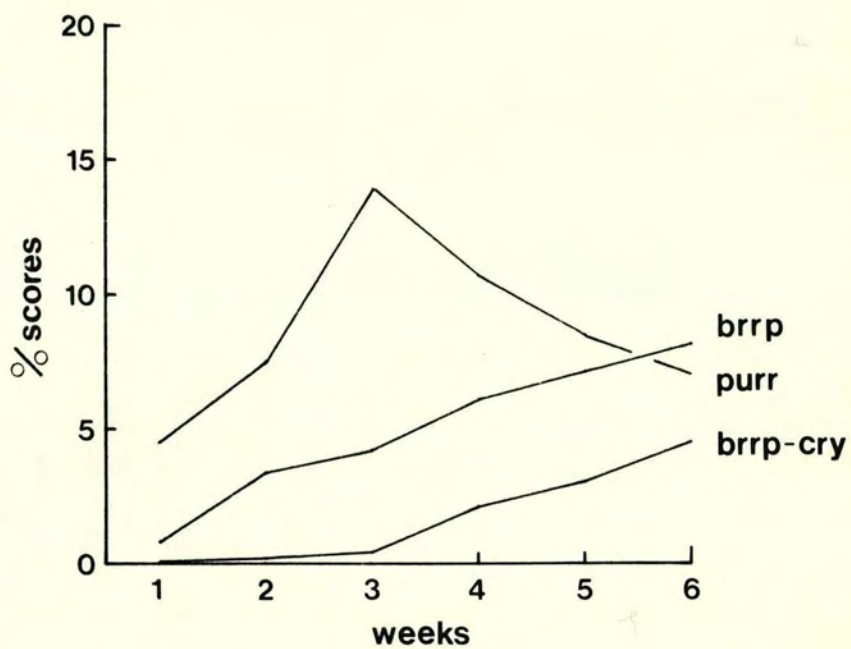
FIGURE C(7)   Illustrates weekly means for the litter
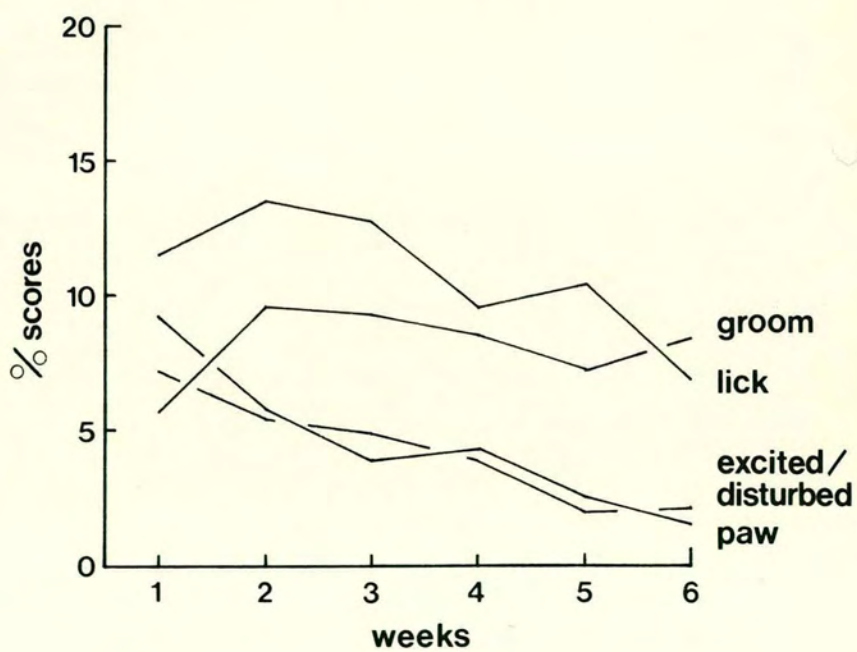measures: nuzzle, on-nipple, on-nipple
in sit, on-nipple in half-sit + on-side-
lie, and still by mother.
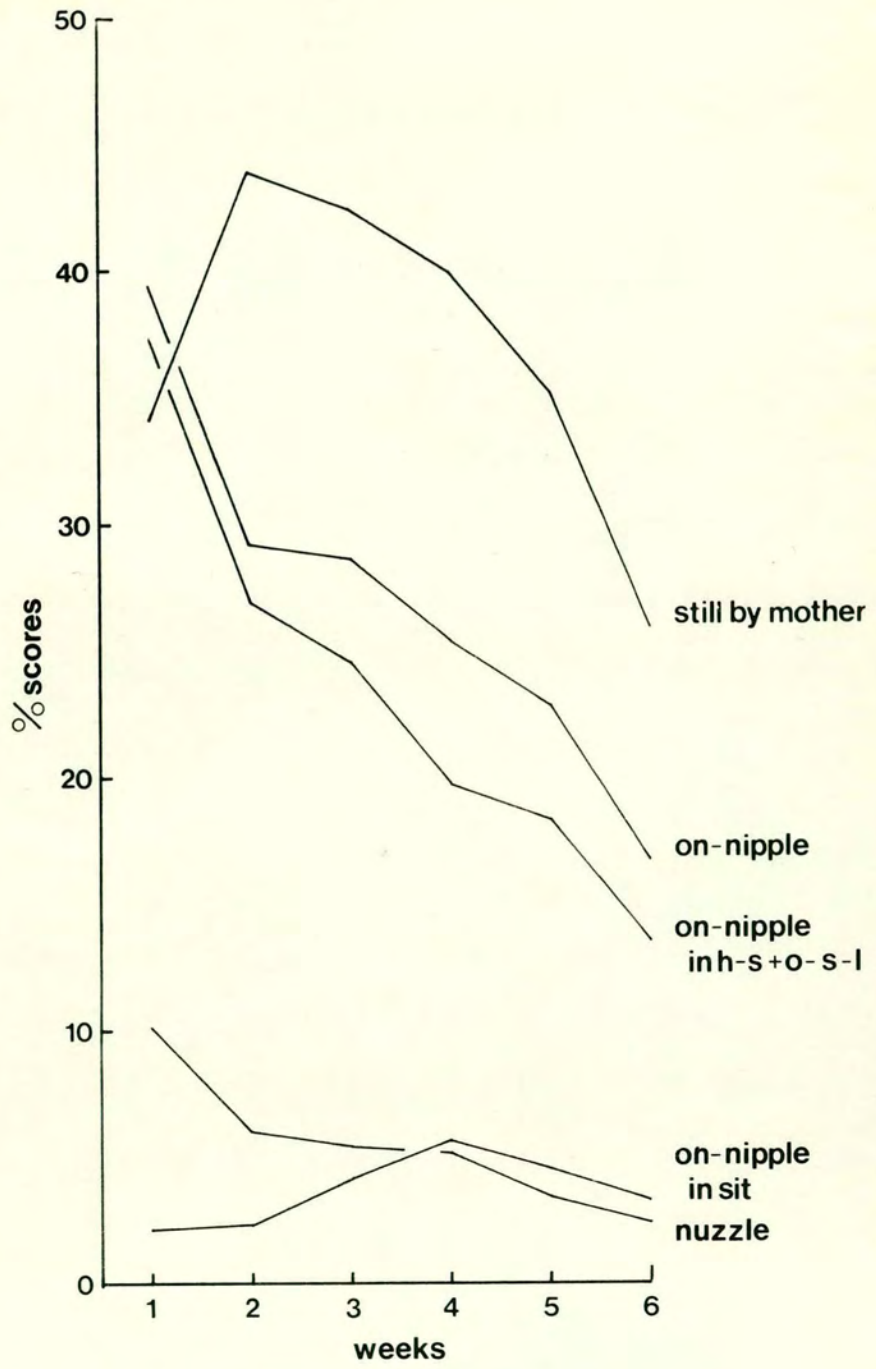
FIGURE C(8)   Illustrates weekly means for the litter
               measures: huddle, active and play.
               Analysis of variance was performed on
               active, and play scores from weeks 4-6
               only (3.7.1)

FIGURE C(9)   Illustrates weekly means of the litter
               measures: still by self, vocalise and
               eat.   Kittens did not begin eating
               solid food until week 4 (analysis of
               variance was performed on scores from
               weeks 4,5 and 6 - 3.7.1).
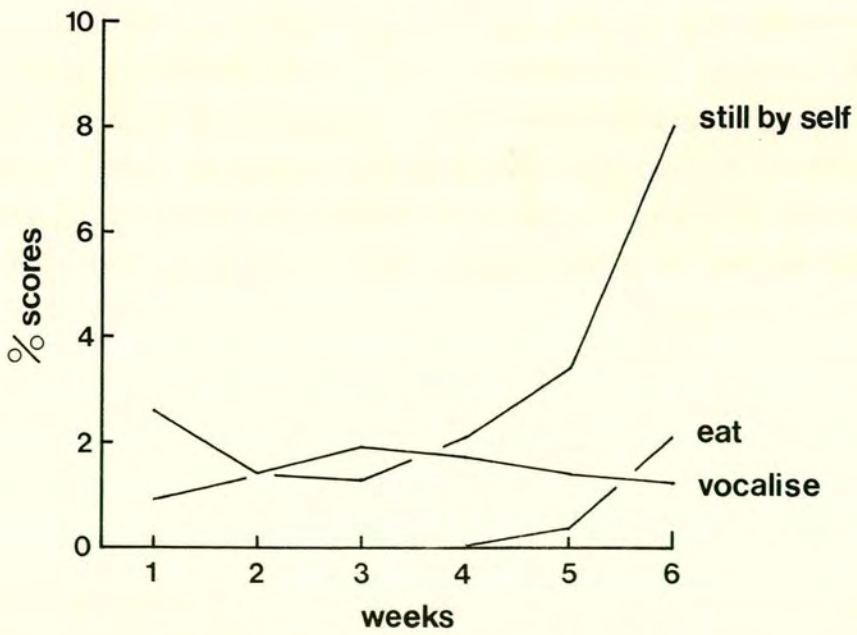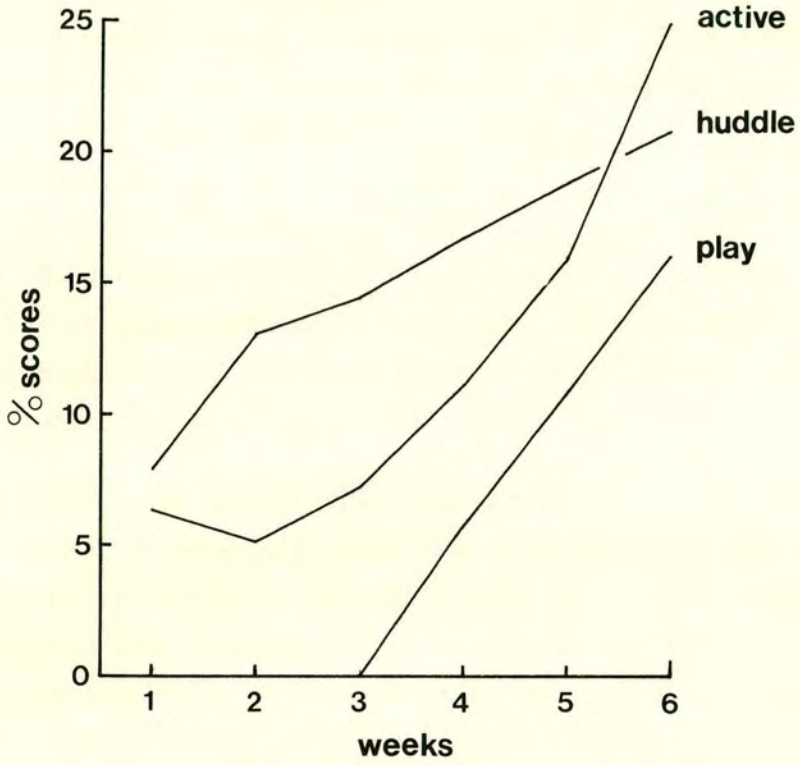
APPENDIX D   <u>Derivation of on-nipple in sit, and on-nipple in</u>
<u>half-sit + on-side-lie scores</u>

Virtually all on-nipple behaviour occurred when mothers were in
sit-nurse, half-sit or on-side-lie.   Only once or twice in the
entire study was a kitten seen on-nipple when its mother was standing.
For the purposes of the following calculations therefore, the few
occurrences of on-nipple in stand are ignored.

As stated in the text, on-nipple was scored independently of the
mother's body position, and therefore on-nipple in sit, and on-nipple
in half-sit + on-side-lie scores had to be derived.   By definition,
when a mother was in sit-nurse she had one or more kittens attached
to her nipples.

To derive a litter's on-nipple in sit score for a session, the
following procedure was carried out.   The mother's total sit-nurse
+ half-sit + on-side-lie score was calculated and then the proportion
that sit-nurse was of that total was calculated,

ie $$\frac{\text{sit-nurse}}{\text{sit-nurse + half-sit + on-side-lie}}$$

The litter's on-nipple score was then multiplied by this proportion
to give the amount of on-nipple that occurred in sit-nurse, ie on-
nipple in sit, for the litter.   The litter's on-nipple in half-sit +
on-side-lie score could then be calculated by subtracting the on-
nipple in sit score from the on-nipple score.

The derivation rests on the assumption that the proportion of
on-nipple in sit to on-nipple is the same as the proportion of sit-
nurse to sit-nurse + half-sit + on-side-lie.   However this assump-
tion may lead to on-nipple in sit scores being slightly underesti-
mated.   This is because it is known that for every sit-nurse score
there is at least one kitten on-nipple.   Half-sit and on-side-lie
on the other hand are scored independently of whether there are kit-
tens attached to the nipples or not.   Through the derivation pro-
cedure, half-sit and on-side-lie may effectively be credited with
more on-nipple scores than actually occurred in these positions.
However these effects may be counterbalanced; during nursing ses-
sions, when the mother is in half-sit or on-side-lie, more kittens
tend to be attached to the nipples at any one time than during sit-
nurse sessions.   This observation is in agreement with the sugges-
tion made in 3.2.1 that in the sit position, accommodation for

kittens at the ventrum is rather cramped.

To conclude therefore, it would seem that the derivation procedure, for on-nipple in sit and on-nipple in half-sit + on-side-lie scores, gives fairly good approximations to the true scores. Obviously in future work it would be preferable to use actual scores. It was due to the way in which check sheet scores were totalled that raw data were not directly available on the above derived measures.

In the regression analyses performed in 3.6.3 (under the heading of Half-sit + on-side-lie) it may seem that the proportional relationship between mothers' scores on the X axis and their litters' scores on the Y axis is purely a result of the derivation procedure. This is not the case. For each family the litter's score on on-nipple in half-sit + on-side-lie is indeed proportional to their mother's score on half-sit + on-side-lie. However the litter's on-nipple score, from which their on-nipple in half-sit + on-side-lie is derived, is independent of the mother's half-sit + on-side-lie score. Therefore, the size of the on-nipple in half-sit + on-side-lie score is not entirely dependent on the mother's score, although it is proportional to it. In each family, the proportional relationship that exists between sit-nurse, and sit-nurse + half-sit + on-side-lie, is independent of the same relationship in any other family. The results of the regression analyses are therefore not merely the product of the derivation procedure for on-nipple in sit and on-nipple in half-sit + on-side-lie.

APPENDIX E   Normality tests for data used in analyses of variance and regression analyses

In this appendix, tests made for the normality of the data used in analyses of variance (3.6.2 and 3.7.1) and regression analyses (3.6.3 and 3.7.2) are reported.

1   Analyses of variance

One of the underlying assumptions of the analysis of variance is that residuals are normally distributed.   Residuals should therefore be calculated and tested for normality before the results of such analyses are taken as valid.   (It is worth noting however that Sokal and Rohlf (1969) consider that only if the distribution of residuals is very skewed would there be a marked effect on the significance level of the F-test or on the efficiency of the design.)

Residuals were calculated for the following selection of the most important behavioural measures - sit-nurse, half-sit + on-side-lie, on-nipple, and on-nipple in half-sit + on-side-lie.   The goodness of fit to a normal distribution of each set of residuals was tested using the Kolmogorov-Smirnov test.   This test is based on the absolute differences between observed and expected cumulative frequency distributions (Sokal and Rohlf, 1969).

In the test, the Kolmogorov-Smirnov statistic K-S D is calculated.   If the data (ie residuals) is normally distributed then K-S D will be less than the critical value $1.358/\sqrt{n}$ (where n is greater than 100) (Sokal and Rohlf, 1969).

Behavioural measure	K-S D	Normality
Sit-nurse	0.1457	non-normal
Half-sit + on-side-lie	0.0323	normal
On-nipple	0.0563	normal
On-nipple in sit	0.0601	normal

Critical value for K-S D = $1.358/\sqrt{387}$ = 0.0690

The non-normality of the sit-nurse residuals is thought to be due to the large number of zero scores in the sit-nurse data.   In the early weeks in particular, some mothers rarely showed sit-nurse behaviour and often have zero scores.   The same is true for the measures crouch + lie and on-nipple in sit.   Hence it is predicted that the

residuals of these measures would not be normal.

Since transforming the original data does not overcome the problem of many zero scores (see 2 below) and hence renders the residuals normal, a non-parametric test was employed instead of analysis of variance. Kruskal-Wallis one-way analysis of variance was used to individually test the effects of differences between mothers (or litters) and the effects of differences between weeks on the measures below.

Kruskal-Wallis results

Measure	χ^2(mothers/litters)df = 16	χ^2(weeks)df = 5
Sit-nurse	113.44***	15.53**
Crouch + lie	57.62***	34.89***
On-nipple in sit	107.88***	13.61*

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

The results show that there are significant differences between mothers (or litters) and between weeks for the three measures. The conclusions therefore do not differ from those of the analyses of variance in Tables 3.2 and 3.3.

2   Regression analyses

As with the analysis of variance, one of the assumptions of regression analysis is that the residuals should be normally distributed.

Of the regression analyses in which the effects of litter size, sex ratio and kitten death are examined, those involving litter size are of greatest interest. The variables sex ratio and kitten death are of less interest, especially the latter, since only 3 litters have kitten deaths.

Residuals are calculated from the regressions (with litter size) of selected important maternal and litter measures. The residuals are tested for normality as described in the previous section.

Measure	K-S D	Normality
Half-sit + on-side-lie	0.0640	normal
Crouch + lie	0.3387	non-normal
On-nipple	0.0527	normal
On-nipple in half-sit + on-side-lie	0.0685	normal
On-nipple in sit	0.2343	non-normal

Critical value for K-S D = $1.358/\sqrt{387}$ = 0.0690

Crouch + lie and on-nipple in sit have non-normal residuals and it is predicted that this would also be the case for sit-nurse since the data on this measure contains many zero scores.

Neither an arcsine nor a square root transformation renders the data normal. The non-parametric Spearman rank correlation test is therefore used to examine the effect of litter size on the above measures. In the Table below, the results of this test are compared with those of the regression analyses (Tables 3.4 and 3.7).

Measure	Spearman rank (n = 203) correlation coefficient	Regression analysis F ratio
Sit-nurse	0.015	0.68
Crouch + lie	- 0.264**	6.59*
On-nipple in sit	- 0.021	0.50

** $p < 0.01$, * $p < 0.05$

The conclusions from the two tests are similar.

It is also of interest to discover whether litter size may be of particular importance in the later weeks (4-6) when weaning is probably occurring. The effect of litter size is examined using regression analysis, or where appropriate, Spearman rank correlation, for the following measures = sit-nurse, half-sit + on-side-lie, crouch + lie, on-nipple, on-nipple in half-sit + on-side-lie, on-nipple in sit. Only crouch + lie is found to be significantly affected by litter size in weeks 4-6 (Spearman correlation coefficient = - 0.278, $p < 0.001$).

APPENDIX F   <u>Correlations between different weeks of mean weekly</u>
<u>percentage scores of selected maternal and litter</u>
<u>measures</u>

As explained in 3.6.2 and 3.7.1, the results from the two-way
analyses of variance indicate that differences between mothers and
differences between litters are, in general, consistent across weeks
for measures examined.

In order to examine developmental changes in some of the
important behavioural measures in more detail, correlations (Pearson
product-moment) are run between different weeks for the selected
measures. Mean weekly percentage scores are correlated between
weeks for the following measures - sit-nurse, half-sit + on-side-lie,
crouch + lie, on-nipple, on-nipple in half-sit + on-side-lie, on-
nipple in sit.

In general, the correlations do no more than lend support to
the results from the analyses of variance. However correlations
between different weeks for the measure half-sit + on-side-lie are
of some interest.

Half-sit + on-side-lie: Pearson product-moment correlation coefficients

Week	1	2	3	4	5	6
1		0.567*	0.077	0.656**	0.514*	0.493*
2			0.477	0.464	0.469*	0.402
3				0.190	- 0.013	- 0.229
4					0.742***	0.652**
5						0.845***
6						

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Mothers' scores at week 3 are not correlated with their scores in any
other week, whereas between most other pairs of weeks there are sig-
nificant positive correlations. This finding suggests that during
the third week the mothers may be changing their behaviour in dif-
ferent ways, or at different rates, relative to one another. Such
differences between mothers may indicate differences in the onset of
weaning behaviour. However further evidence would be required to
substantiate this suggestion.

APPENDIX G   Further analysis of kitten weight data

In this appendix mean kitten weight gains in all 6 weeks are presented and used in various analyses.   In 3.6.5 only weight gain in weeks 2 and 3 are examined.

A complete weight record was not collected for the kittens of all litters.   However, by extrapolation from known weights, it is possible to estimate kitten weights where data is missing.   Data is missing from weeks 1-4 only.   Since kitten weight gain is known to be almost linear during this period (Innes, 1980), the method of estimation is probably quite accurate.   Birth weights were estimated for each kitten in the same way.   Hence a complete record of mean kitten weight gains for each week is given below.

Mean kitten weight gains (grams)

Week	1	2	3	4	5	6
Litter C1	98*	82	45	92	72	167
C2	31*	28	25	78	95	124
C3	40*	37	35	47	90	132
C4	43*	48	32	60	81	83
C5	65*	37	27	42	58	60
C6	24*	29	38	55	98	106
C7	26*	25*	24*	13	54	112
C8	20*	19*	6*	13	100	153
B1	68*	70*	75*	97*	102*	152
B2	53*	65*	63*	58*	58	103
B3	70*	70	93	78	133	120
B4	100*	105*	110*	78*	80*	75
B5	92*	92	72	63	102	110
B6	53*	77	83	70	68	106
B7	78*	77*	90*	93*	50	122
B8	92*	98*	92*	92*	93	55
A1	69*	69	76	75	71	69

* weight gains calculated from estimated weights

Pearson product-moment correlation coefficients were run between mean kitten weight gains each week.

Week	1	2	3	4	5	6
1		0.917***	0.744***	0.690***	− 0.021	− 0.209
2			0.891***	0.725***	0.014	− 0.237
3				0.706***	0.090	− 0.294
4					0.145	− 0.015
5						0.244
6						

Up until week 4 there are significant positive correlations between weight gains each week. However in weeks 5 and 6, when kittens are switching to a solid food diet, this relationship breaks down.
Rate of weight gain in weeks 5 and 6 is independent of rate of weight gain in earlier weeks. This finding could be related to that of Bateson and Young (1980) who discovered that at about day 30 kittens show a discontinuity in their rate of weight gain − they suddenly gain weight more quickly. The timing of the discontinuity and the extent of the change of rate of weight gain varies from litter to litter. Such variation could account for the results of the present study. If kitten weight gain changes in different ways in different litters in weeks 5 and 6 then this would explain the lack of correlation between these weeks and earlier weeks.

It is also of interest to examine the relationship between maternal behaviour related to feeding, and kitten weight gain. Mean kitten weight gain is therefore correlated with mothers' mean weekly percentage scores on the measures − half-sit + on-side-lie and sit-nurse.

Mean kitten weight gains

	Week	1	2	3	4	5	6
Half-sit + on-side-lie	1	0.381	0.521*	0.468*	0.436	− 0.155	− 0.391
	2		0.469*	0.501*	0.256	− 0.322	− 0.020
	3			0.284	0.119	− 0.089	− 0.098
	4				0.418	− 0.028	0.098
	5					− 0.109	0.053
	6						− 0.047

* $p < 0.05$

Mean kitten weight gains

	Week	1	2	3	4	5	6
Sit-nurse	1	-0.316	-0.472*	-0.468*	-0.346	-0.185	0.101
	2		-0.601**	-0.557*	-0.464	-0.085	0.184
	3			-0.512*	-0.375	-0.273	-0.140
	4				-0.395	-0.195	-0.216
	5					-0.003	0.121
	6						0.133

** $p < 0.01$, * $p < 0.05$

It can be seen that for both measures, the relationship between maternal behaviour and kitten weight gain extends only up until week 3. In week 4 some kittens begin to take solid food, therefore this breakdown in the relationship is not surprising. It is interesting that mothers who show more half-sit + on-side-lie have kittens who have greater weight gains, and that sit-nurse is negatively correlated with weight gain. The latter result might indicate that mothers who have less milk are less inclined to nurse their kittens, and show this by remaining sitting when their kittens are on-nipple rather than taking up half-sit or on-side-lie positions.

In future it would be useful to weigh mothers as well as kittens since it would be interesting to examine correlations between maternal weight and maternal behaviour.