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# The effects of litter-size variation on the development of play behaviour in the domestic cat: litters of one and two

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**Abstract.** In many litter-bearing species, litter-mates interact with each other in a variety of ways during early life. In the domestic cat, *Felis catus*, social play is a prominent form of interaction between litter-mates. The present study investigated how the lack of a litter-mate affected the development of kitten play and of the mother–kitten relationship. The subjects were 14 litters of domestic kittens living with their mothers in large indoor cages. Seven litters contained two male kittens, and the other seven contained single male kittens. Social interactions within the families were observed from day 22 to day 83 after birth. Single kittens played a more active part in maintaining close proximity to their mothers and directed more playful behaviour at them than did kittens with a sibling. Although single-kitten mothers avoided their offspring more than did mothers of litters of two, they also directed much higher levels of play behaviour at them. Despite the marked difference in the mother–kitten play relationship in the two litter types, single kittens experienced quantitatively less social play than did kittens with siblings. As the kittens grew older, single-kitten mothers showed higher levels of aggression towards their young than did mothers of litters of two.

In many mammalian litter-bearing species in which litter members remain together for some time, litter-mates may play with each other, compete for access to solid food and mother's milk, establish dominance relations, huddle to keep warm, and explore the environment together (e.g. rats, *Rattus norvegicus*, Meaney & Stewart 1981; Mongolian gerbils, *Meriones unguiculatus*, Elwood & Broom 1978; domestic cats, *Felis catus*, Barrett & Bateson 1978; wolves, *Canis lupus*, Fox 1972; coyotes, *Canis latrans*, Bekoff 1977). It seems likely therefore that the absence of a litter-mate may cause changes in the behavioural development of the single offspring, particularly in species where interaction between litter-mates is a prominent part of social development (see Bekoff 1981; Suomi 1982).

Some indirect evidence that this may be the case comes from studies of non-litter-bearing species. Harlow and colleagues (Harlow & Harlow 1969) have suggested that the presence of peers is necessary for the 'normal' social development of captive rhesus monkey infants, *Macaca mulatta*, kept alone with their mothers. Similarly, Hinde and co-workers (Hinde & Spencer-Booth 1967a; Hinde 1983) have shown that the lack of other group members with which to interact can cause changes in the quality of the developing mother–infant relationship in captive rhesus monkeys.

Descriptions of differences in the social experience of single versus multiple offspring in litter-bearing species are rare (e.g. Elwood & Broom 1978) but deserve attention since litter size may vary according to environmental conditions (Lack 1954) sometimes resulting in the existence of single-offspring litters. Developmental studies comparing litters of single and multiple offspring will show how the presence or absence of a sibling affects social experience. Since early social experience may have long-term effects on adult behaviour, such studies may provide us with hypotheses about how such litter-size variation influences adult behaviour. These sorts of study represent the first step in elucidating the importance of the presence of a sibling in allowing normal social development in litter-bearing species.

In the domestic cat, one prominent feature of the behaviour of developing kittens is social play (West 1974; Barrett & Bateson 1978; Caro 1981a). In families of two or more kittens, social play between litter-mates is much more common than between kittens and their mothers (Mendl 1986). The purpose of the present study was to examine how the absence of a sibling affected the development of

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play behaviour in kittens reared with their mother alone, and what effect it had on the development of the mother–kitten social relationship when compared to that seen in two-kitten families. Families containing two male kittens were compared with those containing one male kitten. Single-kitten litters occur naturally in the domestic cat, sometimes as the result of disease and predation causing a drop in litter size (Hall & Pierce 1934; Nelson et al. 1969; G. Kerby, personal communication; personal observation). Kitten play behaviour, general kitten activity, mother–kitten proximity relations and mother–kitten play, and agonistic interactions were recorded.

## METHODS

### Subjects, Housing and Care

The subjects were 14 litters of domestic kittens from 10 different mothers. Each litter was culled to the required composition within 2 or 3 days of birth. The single-kitten group consisted of seven litters of one male kitten from seven different mothers. The two-kitten group consisted of seven litters of two male kittens from seven different mothers, four of whom were also used in the single-kitten group. All mothers had previously given birth to at least four other litters. Original litter sizes and sex-ratios (before adjustment to the required litter compositions) did not differ significantly between the two groups of litters, and nor did maternal age or the number of previous litters to which mothers had given birth (Mann–Whitney *U*-tests, $P > 0{\cdot}10$). Each litter was sired by one of three fathers.

The kittens were born and reared in a laboratory colony and were housed with their mothers from birth in large indoor trapezoid-shaped pens with a floor area of 8·8 $m^2$. The short side of each pen was 1·1 m in length and the long side was 4·0 m long, with two radiating walls of length 3·8 m. Set into the short side was a door, and set into this was a darkened sheet of Perspex (0·3 m × 0·74 m) which provided an effective one-way screen. The long side of the pen had a translucent window (4·1 $m^2$) in it. Each pen, in addition to receiving daylight, was artificially lit for 14 h each day (0600–2000 hours).

Each pen contained a plastic nest box, a litter tray, two food bowls, one water bowl and six corks which were scattered around the floor for the kittens to play with. In addition, each pen contained a carpet-covered wooden scratching post, 1·13 m high.

Mounted on the long back wall of each pen was a wooden shelf (the 'back shelf') 2·7 m long, 0·26 m wide and 0·65 m off the ground. Below this was a wire grille of length 2·6 m and height 0·28 m covering two wall-mounted 500-W tube heaters. These heaters were thermostatically controlled and maintained the pen temperature above 15°C. This was necessary since pen temperature fluctuated, to some extent, with external temperature. Mounted on one of the radiating walls was another wooden shelf (the 'high shelf') 0·7 m long, 0·24 m wide and 0·84 m off the ground. Kittens could reach the back shelf when they were around 7 weeks old, but they could reach the high shelf only when they were 10 or 11 weeks old. Mothers and kittens in one pen were not able to see those in another, although a limited degree of auditory and olfactory contact was possible.

Every morning (0800–0900 hours) the litter trays were emptied, the cats fed and the pens cleaned. All families experienced an ad libitum supply of food and water. Kittens were weighed and checked daily, and mothers were weighed weekly. The cats were used to, and apparently undisturbed by, the presence of humans.

### Observation Schedule

Each family was observed in its home pen from day 22 to day 83 after birth (day 0 = birth). This period was split up into 10 5-day age blocks followed by two 9-day age blocks, such that each family was observed on days 22, 27, 32, . . . 67 and days 74 and 83 (each ± 2 days).

On each observation day, three 40-min observation sessions were made per family, giving a total of 2 h of observation per family per age block. The three sessions took place at different times of day: the first between 0930 and 1100 hours, the second between 1130 and 1300 hours and the third between 1400 and 1530 hours.

### Recording Methods and Behavioural Categories

Five min prior to the start of each observation, I entered the family's home pen and gently placed the kittens 0·5 m in front of the nest box. This was done to minimize any variation in behaviour caused by the fact that the kittens might either be alert or fast

asleep just prior to each session, and it acted to standardize the starting point of each observation.

Observations were made from outside the pen through the one-way screen. When 5 min had elapsed data collection began. Data were recorded using the Madingley Interactive Computer for Recording Observations ('MICRO', Styles 1980). This consists of a keyboard event recorder system that can record the order of interactions and events and also the times, relative to the start of the watch, at which they take place.

The behaviour of all individuals in the family was recorded simultaneously. Using MICRO, it was possible to record when a behaviour had been performed, who had performed it and, where relevant, to whom or what it had been directed. All observations were made by myself. The behaviour patterns recorded are defined below together with a note indicating whether they were recorded as frequencies or durations.

*Kitten activity*

(1) Inactive (duration): time spent by an individual lying still with its eyes closed or almost closed (Bateson & Young 1981).

*Proximity relations and locations*

(2) Approach (frequency): each occurrence of movement by an individual from at least two kitten body lengths away from another individual to less than two kitten body lengths away from that individual (Martin 1986).

(3) Leave (frequency): each occurrence of movement by an individual from less than two kitten body lengths away from another individual to at least two kitten body lengths away (Martin 1986).

(4) On back shelf (duration): time spent by an individual on the back shelf.

(5) On high shelf (duration): time spent by an individual on the high shelf.

*Play interactions*

(6) Paw/pat/bite (frequency): each occurrence of a pawing/patting/biting movement directed at another individual/mobile object which lasts no longer than 1 s and also involves no grasping or holding of the individual/mobile object. This excludes any occurrences which are defined in the Hit/bite category (incorporates Cat Contact and Object Contact, Barrett & Bateson 1978).

(7) Wrestle (duration): time spent by an individual holding/grabbing another individual/mobile object, sometimes kicking at it with the back legs (incorporates Hold Cat, Hold Object and Rake, Bateson & Young 1981).

(8) Stalk (frequency): each bout of low crouching with hindlegs treading, or creeping (or running briefly) with belly close to the ground and head low towards another individual/mobile object (Barrett & Bateson 1978).

(9) Chase (frequency): each bout of running after another individual/mobile object with the chased individual running away from the chaser for at least a distance of 1 m.

(10) Hold/bite object (frequency): each bout of an individual holding an immobile object in the forepaws, with hindquarters slightly raised, and biting/chewing at it.

(11) Self play (frequency): each bout in which the individual chases its own tail.

*Agonistic social interactions*

(12) Growl (frequency): each low rumbling vocalization uttered by an individual (see Moelk 1944).

(13) Hiss (frequency): each sharp hissing vocalization directed by one individual at another. The subject faces the individual, draws its lips back to expose its teeth and produces the sound (Moelk 1944, Spitting).

(14) Hit/bite (frequency): each rapid and vigorous pawing or biting movement directed by one individual at another, often with claws exposed. This is preceded by or followed by or is simultaneous to an incidence of growling or hissing by the subject.

*Derived scores*

The following scores were derived from the primary categories listed above.

(15) Kitten–mother proximity (duration): the total amount of time spent by mother and kitten less than two kitten lengths apart. Calculated as the time elapsed between the time at which one individual approached another and the time at which the two individuals subsequently separated.

(16) Alone (duration): the total amount of time spent by an individual greater than two kitten lengths away from any other individual.

(17) Percentage of kitten–mother approaches made by kitten (%KA): calculated for each kitten per watch as (Kitten Approach Mother/(Kitten Approach Mother + Mother Approach Kitten)) × 100.

(18) Percentage of kitten–mother leaves made by kitten (%KL): calculated as for %KA but using Leave rather than Approach frequencies.

(19) Kitten responsibility for maintaining proximity to mother (%KA−%KL): calculated by subtracting the Kitten Leave percentage (%KL) from the Kitten Approach percentage (%KA) to give an index of the kitten's role in maintaining proximity to its mother. Thus, if a kitten was responsible for all the approaches between itself and its mother, and none of the leaves, then the index would be given by $100\% - 0\% = +100$, whereas if it was responsible for 75% of the approaches but also 75% of the leaves, then the index would be $75\% - 75\% = 0$. This index is similar to one used by Hinde & Atkinson (1970) for rhesus monkeys, and is the same as the one used by Martin (1982) in his study of cat development.

### Analysis of Results

Data were collected at three times of day for each family at each age block. A Friedman two-way analysis of variance was performed on the data for a variety of behaviour patterns and no effects of time of day on these data were detected. Therefore, data from the three watches for each age block were added together to give one data value per age block.

In two-kitten litters, the litter-mates could not be assumed to behave independently and so litter means ($N=7$) were used throughout (Abbey & Howard 1973). These values were compared to single-kitten scores ($N=7$).

A repeated-measures design analysis of variance (ANOVA) was used to analyse the data. Several measures were initially found to depart from a normal distribution and so were transformed using the square root transformation, for scores in the form of counts (frequencies and durations), and the arcsine–square-root transformation for scores in the form of percentages (Sokal & Rohlf 1981).

For the purposes of ANOVA, the study period was divided into three shorter periods. Period A comprised days 22, 27, 32 and 37, period B comprised days 42, 47, 52 and 57, and period C comprised days 62, 67, 74 and 83. Period A corresponded to the time during which weaning normally begins to occur, period B corresponded to the time during which weaning is usually completed, and period C corresponded to a post-weaning phase (Schneirla et al. 1963; Martin 1986). ANOVA was performed on data from each period separately and also on all the data from the whole study period (days 22–83). This allowed the detection of overall effects and also of those that occurred only at one particular phase of development. The ANOVA specified age as the within-subjects factor (12 or four levels depending upon the analysis), and experimental treatment (litter size) as the between-subjects factor (two levels).

For some measures, the transformation procedures described above did not rectify the departure from a normal distribution. This was usually due to zero scores, particularly at early ages, causing heavy skewing. For the purposes of ANOVA, data from the four age blocks in each of periods A, B and C were averaged to give one mean value per family per period (three values in total per family). These lumped data were tested for normality and were subsequently analysed using the ANOVA technique described above (with the age factor having three levels). Any positive effects of treatment (litter size) detected by ANOVA were further analysed using Mann-Whitney *U*-tests. These were performed on the mean scores for each of periods A, B and C in order to determine during which age periods the differences between litter types were most pronounced.

In all the ANOVA tests on factors with more than two levels (e.g. age), multivariate and more powerful univariate statistics were performed by the SPSSX program (Norusis 1985) used for analysis. The univariate statistics were used as long as Box's M test of homogeneity of variance and Bartlett's test of sphericity (Zar 1974) were satisfied. If either one of the tests was not satisfied, the less powerful multivariate statistics were used. Rarely, however, did multivariate and univariate statistics disagree about the significance of the results.

## RESULTS

The results of the analyses are given in Tables I–V. Tables I and III contain data that achieved a normal distribution while Tables II, IV and V contain data that had to be condensed before analysis.

In the following sections, the effects of litter size are considered. Litter size × age interactions are discussed only when they occur in the absence of a litter-size effect, and so provide information not

**Table I.** Results of ANOVA on inactivity and proximity measures

| | Source of variation and age ranges of analysed data | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Litter size | | | | Age (days) | | | | Litter size × age | | | |
| Measure | 22–83 (1, 12) | A 22–37 (1, 12) | B 42–57 (1, 12) | C 62–83 (1, 12) | 22–83 (11, 132) | A 22–37 (3, 36) | B 42–57 (3, 36) | C 62–83 (3, 36) | 22–83 (11, 132) | A 22–37 (3, 36) | B 42–57 (3, 36) | C 62–83 (3, 36) |
| K Inactive | 3·24 | 4·21 | 0·90 | 0·77 | 2·80 | 7·28** | 1·69 | 0·11 | 0·57 | 0·28 | 0·28 | 1·00 |
| **Proximity relations** | | | | | | | | | | | | |
| K–M Proximity | 2·92 | 1·57 | 3·61 | 1·97 | m64·50* | 14·47*** | 1·05 | 0·87 | m6·20 | 0·84 | 1·56 | 0·63 |
| K Approach M | 7·13* | 0·00 | 8·00* | 15·50** | m1233·50*** | 22·54*** | 4·37** | m0·22 | m21·54* | 0·39 | 0·23 | m1·10 |
| K Leave M | 2·92 | 0·10 | 4·60 | 7·10* | 9·53*** | m17·30*** | 4·12* | 0·48 | 1·02 | m0·93 | 0·17 | 0·54 |
| M Approach K | 0·08 | 0·03 | 0·13 | 0·24 | m1·16 | 0·91 | 1·26 | 0·60 | m2·05 | 1·27 | 0·61 | 0·10 |
| M Leave K | 4·86* | 0·08 | 6·80* | 5·78* | m2·95 | 3·96* | 1·73 | m0·53 | m0·93 | 1·80 | 0·09 | m0·36 |
| % Approach between M and K by K (%KA) | 2·57 | 0·23 | 3·12 | 2·31 | m10·96 | 16·95*** | 4·65** | 2·66 | m0·94 | 0·07 | 1·77 | 0·04 |
| % Leave between M and K by K (%KL) | 0·63 | 0·00 | 1·32 | 0·05 | 11·01*** | m6·57** | 9·73*** | 0·02 | 1·28 | m2·08 | 0·59 | 0·47 |
| %KA − %KL | 3·72 | 0·29 | 6·05* | 1·34 | m5·36 | 6·05** | 0·27 | 1·72 | m5·28 | 3·49* | 1·88 | 0·14 |
| K Alone | 8·96* | 12·20** | 9·81** | 3·87 | m17·14 | m9·64** | 1·58 | 1·65 | m0·88 | m3·22 | 4·18* | 0·45 |
| M Alone | 0·58 | 0·89 | 0·49 | 0·12 | m34·94* | 11·64*** | 1·40 | 0·43 | m3·63 | 0·92 | 1·06 | 1·25 |

M = mother; K = kitten.

'm' denotes a multivariate *F*-ratio. All other *F*-ratios are univariate. Univariate and multivariate degrees of freedom (uni.)/(multi.): (1, 12)/(1, 12); (11, 132)/(11, 2); (3, 36)/(3, 10).

* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

**Table II.** Results of ANOVA on proximity measures

| Measure | Source of variation: Litter size (1, 12) | Age (2, 24) | Litter size × age (2, 24) |
|---|---|---|---|
| M on back shelf | 0·59 | 32·86** | 0·31 |
| M on high shelf | 3·48 | m4·44* | m2·20 |

M = mother.
'm' denotes a multivariate *F*-ratio. All other *F*-ratios are univariate. Univariate and multivariate degrees of freedom (uni.)/(multi.): (1, 12)/(1, 12); (2, 24)/(2, 11).
* $P < 0.05$; ** $P < 0.001$.

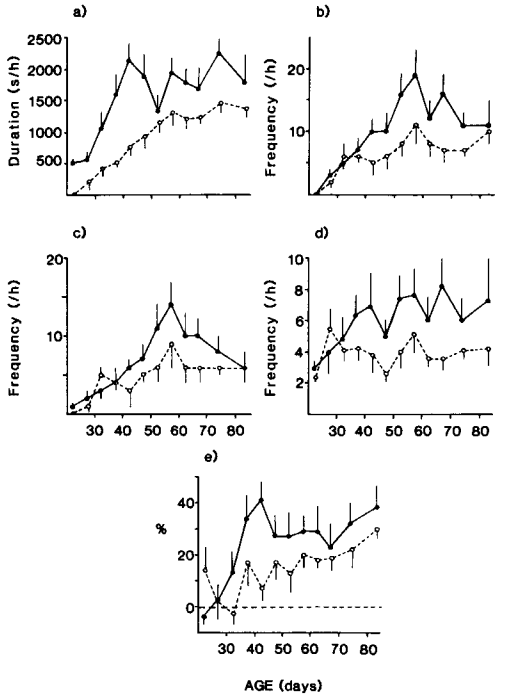


**Figure 1.** Changes with kitten age in five measures of mother–kitten proximity relations: (a) kitten alone, (b) kitten approaches mother, (c) kitten leaves mother, (d) mother leaves kitten, (e) index of kitten responsibility for maintaining proximity to mother (see text for details). Mean scores for the single-kitten group ($N = 7$) are shown as closed circles joined by solid lines, and for the two-kitten group ($N = 7$) as open circles joined by broken lines. Litter-mean scores were used for kitten behaviour in the two-kitten litters. Error bars denote one SEM. Note that the *y*-axis scales and units of measurement differ.

detected by the litter-size factor. Age-related changes have been discussed in detail elsewhere (West 1974; Barrett & Bateson 1978; Caro 1981a; Martin 1986; Mendl 1986) and are not considered here.

### Kitten Activity

There was no significant difference in the amount of time that kittens from litters of one or two spent lying inactive during any of periods A–C (Table I).

### Proximity Relations and Locations

The results are presented in Tables I and II. Single kittens and the average kitten in a litter of two spent similar amounts of time next to their mothers, and mothers of both litter types spent similar amounts of time alone. However, due to the absence of siblings, single kittens spent much more time alone than did the average kitten in a litter of two (Fig. 1a). This effect of litter size applied to the overall data ($P < 0.05$) and also to periods A ($P < 0.01$) and B ($P < 0.01$). During period C, there was no difference. By this time kittens in litters of two were also spending a lot of time on their own.

Single kittens showed higher overall scores of approach behaviour towards their mothers than did the average kitten in a litter of two ($P < 0.05$), in particular during periods B ($P < 0.05$) and C ($P < 0.01$; Fig. 1b). Single kittens left their mothers more often than did the average kitten in a litter of two, during period C ($P < 0.05$) only (Fig. 1c).

Mothers of both litter types did not differ in the frequencies with which they approached their offspring. However, single-kitten mothers left their offspring more often than did two-kitten mothers overall ($P < 0.05$) and during periods B ($P < 0.05$) and C ($P < 0.05$; Fig. 1d).

For both the percentage scores (%KA and %KL as defined above), there were no significant differences between the two litter types. For the approach–leave index (%KA − %KL), there was an effect of litter size during period B ($P < 0.05$). Single kittens were more responsible for maintaining proximity to their mother than were kittens in litters of two at this age, a trend that was evident during most of the study period (Fig. 1e). There was also a litter size × age interaction effect on this measure during period A ($P < 0.05$), and this corresponded to the rapid increase in the kittens'

**Table III.** Results of ANOVA on measures of social and object play

| | Source of variation and age ranges of analysed data | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Litter size | | | | Age | | | | Litter size × age | | | |
| Measure | 22–83 (1, 12) | A 22–37 (1, 12) | B 42–57 (1, 12) | C 62–83 (1, 12) | 22–83 (11, 132) | A 22–37 (3, 36) | B 42–57 (3, 36) | C 62–83 (3, 36) | 22–83 (11, 132) | A 22–37 (3, 36) | B 42–57 (3, 36) | C 62–83 (3, 36) |
| Social play | | | | | | | | | | | | |
| K Wrestle C (/K) | 26·89*** | 22·76*** | 4·45 | 10·64** | 4·40*** | 9·71*** | 0·83 | 1·12 | 1·86* | 3·43* | 1·41 | 1·13 |
| K Paw/pat/bite M (/K) | 65·70*** | 13·82** | 66·75*** | 43·82*** | m58·97*** | m14·08*** | m0·54 | 3·13* | m29·07* | m6·67** | m0·05 | 1·66 |
| K Paw/pat/bite M (/M) | 23·16*** | 3·90 | 25·39*** | 12·57** | 5·62*** | 13·65*** | 0·65 | 2·80 | 1·82 | 4·14* | 0·08 | 1·15 |
| K Paw/pat/bite C (/K) | 1·85 | 0·35 | 5·98* | 0·40 | m25·71* | m25·02*** | 0·46 | 2·33 | m2·15 | m2·13 | 0·19 | 0·84 |
| C Paw/pat/bite K (/K) | 76·30*** | 32·81*** | 16·48** | 27·36*** | 5·30*** | m23·06*** | 0·17 | 1·04 | 0·78 | m8·89** | 0·36 | 0·45 |
| Object play | | | | | | | | | | | | |
| K Paw/pat/bite O | 1·21 | 1·16 | 0·22 | 1·06 | 9·79*** | m21·74*** | 1·84 | 1·32 | 0·71 | m0·64 | 0·37 | 1·61 |

M = mother; K = kitten; C = conspecific; O = object.
'm' denotes a multivariate *F*-ratio. All other *F*-ratios are univariate. Univariate and multivariate degrees of freedom (uni.)/(multi.): (1, 12)/(1, 12): (11, 132)/(11, 2); (3, 36)/(3, 10).
* $P<0·05$; ** $P<0·01$; *** $P<0·001$.

**Table IV.** Results of ANOVA and Mann–Whitney *U*-tests on social play measures

| Measure | ANOVA: source of variation | | | Mann–Whitney *U*-tests on periods A, B and C for data with positive overall litter size effects | | |
|---|---|---|---|---|---|---|
| | Litter size (1, 12) | Age (2, 24) | Litter size × age (2, 24) | A 22–37 | B 42–57 | C 62–83 |
| K Wrestle M (/K) | 113·10*** | 11·80*** | 9·42*** | 4·50* | 0·00*** | 0·00*** |
| K Wrestle M (/M) | 67·91*** | 8·74*** | 6·47*** | 9·00* | 0·00*** | 0·00*** |
| M Wrestle K (/K) | 22·15*** | m17·72*** | m14·82*** | 16·00 | 0·00*** | 2·00** |
| M Wrestle K (/M) | 19·48*** | m17·55*** | m13·63*** | 16·00 | 0·00*** | 3·00** |
| C Wrestle K (/K) | 49·94*** | 5·24* | 2·70 | 0·00*** | 4·50* | 3·00** |
| M Paw/pat/bite K (/K) | 63·30*** | m14·30*** | m12·36** | 6·00* | 0·00*** | 0·00*** |
| M Paw/pat/bite K (/M) | 45·61*** | 8·98*** | 4·79* | 7·00* | 0·00*** | 3·00** |
| K Stalk M (/K) | 41·70*** | 50·54*** | 26·66*** | 7·50* | 0·00*** | 1·00** |
| K Stalk M (/M) | 23·74*** | 33·91*** | 11·43*** | 12·50 | 0·00*** | 5·50* |
| M Stalk K (/K) | 4·47 | m0·79 | m0·79 | | | |
| M Stalk K (/M) | 4·47 | m0·79 | m0·79 | | | |
| K Stalk C (/K) | 0·00 | m19·34*** | m4·39* | | | |
| C Stalk K (/K) | 41·01*** | 3·95* | 2·19 | 7·50* | 2·00** | 0·50*** |
| K Chase M (/K) | 3·21 | m1·98 | m1·63 | | | |
| K Chase M (/M) | 3·03 | m2·83 | m1·80 | | | |
| M Chase K (/K) | 1·79 | m2·54 | m0·97 | | | |
| M Chase K (/M) | 1·01 | m2·64 | m1·33 | | | |
| K Chase C (/K) | 17·47*** | 12·99*** | 5·01* | 24·00 | 5·50* | 6·00* |
| C Chase K (/K) | 18·73*** | 19·89*** | 7·50** | 21·00 | 2·50** | 5·00* |

M = mother; K = kitten; C = conspecific.
ANOVA: 'm' denotes a multivariate *F*-ratio. All other *F*-ratios are univariate. Univariate and multivariate degrees of freedom (uni.)/(multi): (1, 12)/(1, 12); (2, 24)/(2, 11).
Mann–Whitney *U*-test ($N = 7, 7$): tests on litter means for each of periods A, B and C. *U*-values are given.
* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

responsibility for maintaining proximity to their mother which occurred in single-kitten families, but not so clearly in families of two kittens.

Mothers of the two groups did not differ in the amount of time they spent on the back shelf and the high shelf.

## Social Play Interactions

Four measures of social play behaviour were recorded: wrestling, paw/pat/biting, stalking and chasing. These were analysed in the following ways: as the amount performed by the average kitten in a litter to (1) its mother, and (2) both its mother and sibling (if it had a sibling); as the amount received by the average kitten from (1) its mother, and (2) both its mother and sibling; as the total amount (1) received by the mother from, and (2) performed by the mother to, all her kittens.

Significance levels of the results are given in Tables III and IV.

*The amount of social play performed by kittens*

(1) Single kittens spent much more time directing wrestling behaviour towards their mother than did the average kitten in a litter of two (Fig. 2a). This difference was significant during each of periods A, B and C. The same was true for the frequency of kitten paw/pat/bite and stalking behaviour directed towards the mother (Fig. 2b, c). There were no differences in the frequencies with which kittens from either litter type directed chasing behaviour towards their mother.

(2) During periods A and C the average kitten in a litter of two spent a greater total amount of time

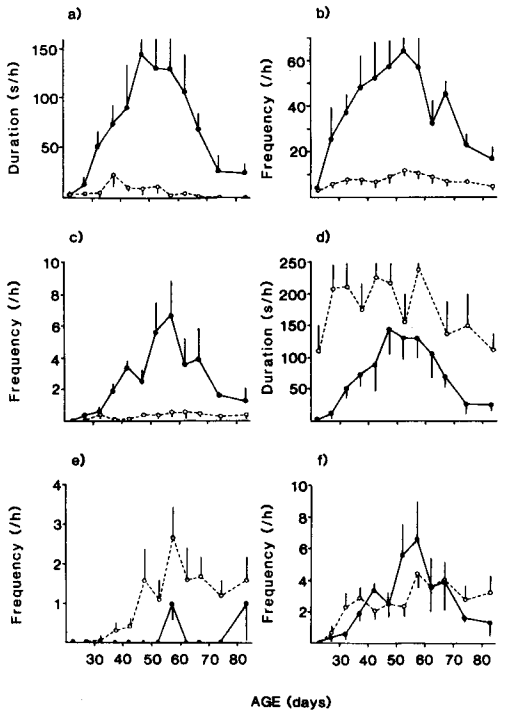


**Figure 2.** Changes with kitten age in six measures of social play behaviour: the amount of (a) wrestling, (b) paw/pat/biting and (c) stalking performed by the average kitten to its mother. The total amount of (d) wrestling, (e) chasing and (f) stalking performed by the average kitten to all the other members of its family. Note that the *y*-axis scales and units of measurement differ. See Fig. 1 for further details.

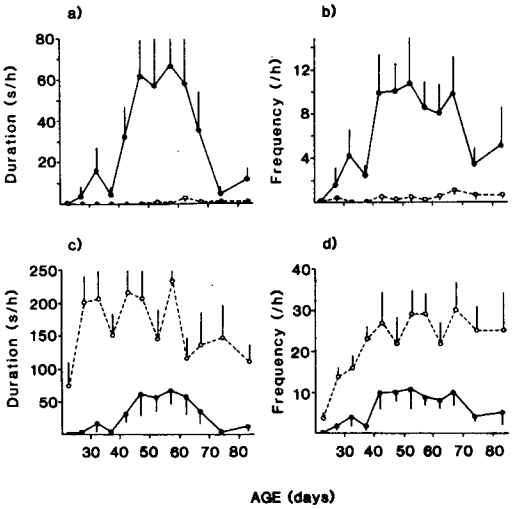


**Figure 3.** Changes with kitten age in four measures of social play behaviour: the amount of (a) wrestling and (b) paw/pat/biting received by the average kitten from its mother. The total amount of (c) wrestling and (d) paw/pat/biting received by the average kitten from all the other members of its family. Note that the *y*-axis scales and units of measurement differ. See Fig. 1 for further details.

directing wrestling behaviour towards its mother and sibling than the average single kitten spent wrestling with its mother (Fig. 2d). A similar result occurred for chasing behaviour although this was significant only during periods B and C by which time kitten–kitten chasing behaviour in litters of two had reached a high level in comparison to the lower levels of kitten–mother chasing behaviour seen in litters of one (Fig. 2e).

However, for stalking behaviour there was no significant difference between the two litter types, although there was a significant litter size × age interaction. This may have been due to the clear peak and rapid subsequent decrease in stalking behaviour in single-kitten litters which was not so pronounced in litters of two (Fig. 2f). Single kittens directed more paw/pat/biting behaviour at their mother during period B (when the measure had reached a peak) than the average kitten in a litter of two performed to both its mother and sibling.

*The amount of social play received by kittens*

(1) Single kittens received more wrestling behaviour from their mother than did the average kitten in a litter of two. This was significant during periods B and C (Fig. 3a). The same was true for paw/pat/bite behaviour, except that the difference was significant at all ages (Fig. 3b). For stalking and chasing behaviour, there was no significant difference between the two litter types.

(2) The average kitten in a litter of two received more wrestling behaviour from both its mother and sibling than the average single kitten received from its mother (Fig. 3c). This difference was significant at all ages. The same was true for paw/pat/bite (Fig. 3d), stalk and chase behaviour patterns except that in the case of chasing, the difference was only significant during periods B and C.

*The amount of social play received and performed by mothers*

(1) Mothers of single kittens received more wrestling behaviour from their offspring than

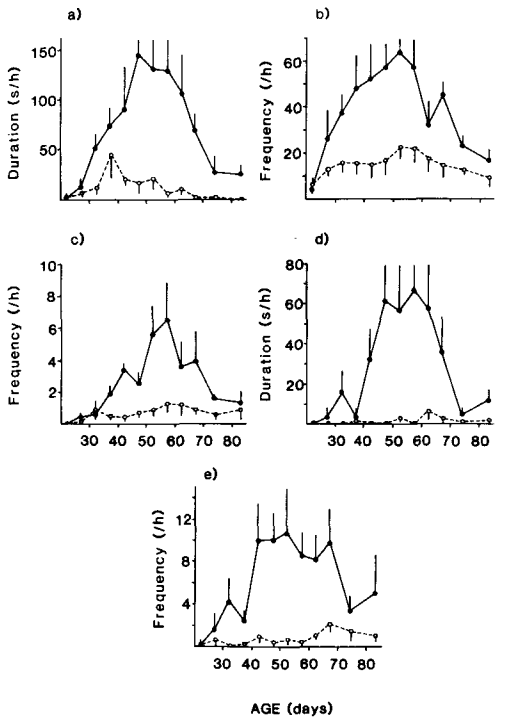


**Figure 4.** Changes with kitten age in five measures of social play behaviour: the total amount of (a) wrestling, (b) paw/pat/biting and (c) stalking received by mothers from their kitten(s). The total amount of (d) wrestling and (e) paw/pat/biting performed by mothers to their kitten(s). Note that the *y*-axis scales and units of measurement differ. See Fig. 1 for further details.

mothers of two received from both of their offspring together. This difference was significant at all ages (Fig. 4a). The same was true for paw/pat/bite and stalking behaviour except that the differences were significant only during periods B and C (Fig. 4b, c). There was no significant difference between the litter types for chasing behaviour.

(2) Mothers directed more wrestling behaviour towards single kittens than they did towards both kittens in a litter of two (Fig. 4d). This difference was significant during periods B and C. The same was true for paw/pat/bite behaviour except that the difference was significant at all ages (Fig. 4e). For stalking behaviour and chasing behaviour there was no significant difference between the two litter types.

### Agonistic Social Interactions

Results of the analysis are presented in Table V. Although maternal agonistic behaviour directed at kittens generally occurred at low levels, mothers of single kittens hit/bit their offspring more overall ($P < 0{\cdot}01$) and during period C ($P < 0{\cdot}05$) than did mothers of litters of two (Fig. 5a). The significant litter size × age interaction detected for the hit/bite measure appeared to be due to the marked increase in the occurrence of this behaviour during periods B and C in single-kitten families. Such an increase was not so clearly evident in families of two kittens where the scores were low throughout. Mothers of single kittens tended to growl more than did mothers of litters of two (Fig. 5b), although this difference was not significant. Mothers of single kittens also hissed at their offspring more often overall ($P < 0{\cdot}05$) than did mothers of two kittens (Fig. 5c).

### Kitten and Maternal Object Play and Kitten Self Play

There was no clear effect of litter size on any measure of kitten object and self play or maternal object play analysed (see Tables III and V).

## DISCUSSION

In the following discussion it should be noted that the present study examined male kittens only. Although a detailed study of the development of all-male and all-female litters of two kittens detected virtually no sex differences in a variety of behavioural measures (Mendl 1986), other studies have detected sex differences in certain measures of play behaviour (Barrett & Bateson 1978; Caro 1981b; Martin 1984), and further research is therefore required to establish whether the findings reported here can be generalized to female kittens.

### Mother–Kitten Social Play Interactions

In families containing two or more kittens, sibling–sibling play interactions occur frequently (West 1974; Barrett & Bateson 1978) while mother–offspring play interactions are relatively uncommon (Mendl 1986). In the present study, kittens reared without a litter-mate generally directed more play behaviour towards and received

**Table V.** Results of ANOVA and Mann–Whitney *U*-tests on measures of maternal aggression and object play

| | ANOVA: source of variation | | | Mann–Whitney *U*-tests on periods A, B and C for data with positive overall litter size effects | | |
|---|---|---|---|---|---|---|
| Measure | Litter size (1, 12) | Age (2, 24) | Litter size × age (2, 24) | A 22–37 | B 42–57 | C 62–83 |
| Maternal aggression | | | | | | |
| M Hiss at K | 6·60* | m3·25 | m3·25 | 24·50 | 17·50 | 14·00 |
| M Hit/bite K | 9·93** | m6·34* | m5·88* | 21·00 | 10·50 | 8·00* |
| M Growl | 3·82 | m7·38 | m2·72 | | | |
| Object play | | | | | | |
| K Wrestle O | 0·05 | 14·64*** | 3·22 | | | |
| K Hold/bite O | 0·71 | 4·35* | 1·09 | | | |
| K Self play | 1·21 | 31·61*** | 0·41 | | | |
| K Stalk O | 4·28 | m2·79 | m2·79 | | | |
| K Chase O | 0·10 | 2·69 | 0·15 | | | |
| M Wrestle O | 1·64 | m0·11 | m1·32 | | | |
| M Paw/pat/bite O | 4·28 | m2·13 | m1·48 | | | |

M = mother; K = kitten; O = object.
ANOVA: 'm' denotes a multivariate *F*-ratio. All other *F*-ratios are univariate. Univariate and multivariate degrees of freedom (uni.)/(multi.): (1, 12)/(1, 12); (2, 24)/(2, 11).
Mann–Whitney *U*-test ($N = 7, 7$): tests on litter means for each of periods A, B and C. *U*-values are given.
* $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.

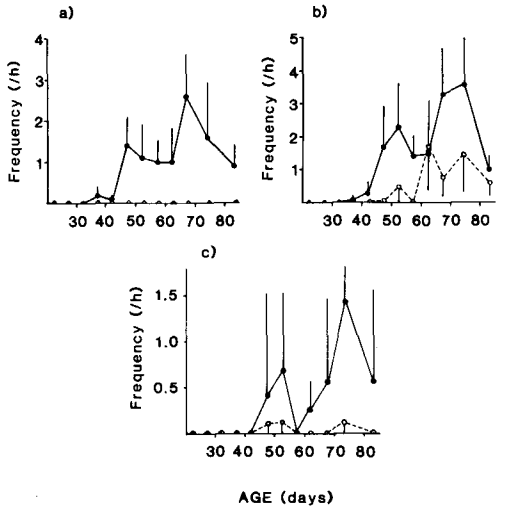


**Figure 5.** Changes with kitten age in three measures of maternal aggressive behaviour: (a) hit/bite, (b) growl, (c) hiss. Note that the *y*-axis scales differ. See Fig. 1 for further details.

more from their mother, than did offspring in families of two kittens. This suggests that in two-kitten families, kittens either preferred to play with their litter-mate rather than with their mother, or the mother actively avoided or discouraged playful interactions with her offspring.

There was no evidence to suggest that mothers of two-kitten litters actively avoided their offspring's playful interactions any more than did mothers of single kittens. In fact, if anything, there was a tendency for mothers of single kittens to show more avoidance of their offspring than did mothers of litters of two. It thus appears that the low levels of mother–offspring play seen in two-kitten litters were the result of kittens playing preferentially with each other rather than with their mother. It is quite likely that a same-aged sibling was more willing to engage in a variety of play behaviour patterns, than was the mother. Several studies have demonstrated that young individuals of a variety of species predominantly play with siblings and age-mates rather than with older individuals (e.g. Hinde & Spencer-Booth 1967b; Cheney 1978; Byers 1980; Meaney & Stewart 1981).

In the single-kitten family, it appears that the behaviour which would normally have been directed by the kitten at a litter-mate, was instead directed at the mother. Single kittens approached and left their mothers more often and played with them more. This was so for three of the four measures of social play recorded in this study, but not for chasing behaviour. Chasing behaviour involved the mother running away from the chasing kitten, or vice versa, while the other three measures of social play (wrestle, paw/pat/bite, stalk) did not involve the mother running around the pen or actively fleeing from her kitten. This difference in the nature of the play behaviour patterns may have accounted for the different findings for chasing behaviour in comparison to the other three measures.

Both mothers and kittens showed high levels of social play behaviour in single-kitten families. It is thus possible that mothers actively initiated play interactions with their single offspring as well as, or rather than, vice versa. Data on initiations of play interactions were not collected in this study. However, it was clear from personal observation that kittens and not mothers generally, although not exclusively, initiated play interactions. It was also the case that for each of the three measures (wrestle, paw/pat/bite, stalk), the levels directed from kitten to mother were higher than those directed in the opposite direction. These findings support the idea that kittens in single-kitten families, and not mothers, were mainly responsible for the increased levels of mother–kitten play interactions. It seems likely that mothers responded to the high levels of play behaviour that they received from single kittens (in comparison to that which they would have received from both kittens in a litter of two) by showing high levels of social play behaviour (wrestle and paw/pat/bite) themselves.

It is possible that in a more natural situation, single-kitten mothers would have avoided their offsprings' playful behaviour totally and would not have shown high levels of play behaviour themselves. However, although single-kitten mothers appeared to show more avoidance of their offspring than did mothers of two-kitten litters (probably due to the disturbance caused them by the single kittens' playful behaviour), they did not spend significantly more time away from them. In addition, there was ample opportunity for the mothers to avoid their kittens totally in the present study, by moving to the back shelf and high shelf, and yet mothers of single-kitten litters did not use these locations significantly more than did mothers of two-kitten litters. Furthermore, mothers could respond to their kittens' playful behaviour in an aggressive way but, even in the single-kitten families, this type of response did not become prominent until around days 50–60 of kitten life. Prior to and after this time, mothers reciprocated their kittens' playful interactions.

It thus seems that the high levels of mother–kitten play in single-kitten families were not simply a result of the laboratory environment forcing mother and kitten to remain in close proximity to each other. In support of this, it is also the case that single kittens have been seen to engage in more play with their mothers, than kittens from litters of two or more, in a study of feral cats living on farms (G. Kerby, personal communication). However, it should be noted here that if other individuals, apart from the parents, are available for interaction (e.g. older siblings), the effects of being a single offspring may not be as pronounced as those described in the present study (see Suomi 1982).

### Kitten Experience of Play Behaviour

Although single kittens played more with their mothers than those in litters of two, it was clear that the lack of a sibling play partner resulted in these kittens receiving less wrestling, paw/pat/biting, stalking and chasing than did kittens with a sibling. In the same way, single kittens performed in total less wrestling and chasing behaviour than did kittens who had a sibling. However, this was not so for paw/pat/bite and stalking behaviour. Of the four social behaviour patterns recorded, kitten paw/pat/biting and stalking involved the least disturbance to the mother. The mother often appeared to be totally unaware that a kitten was stalking her, and kittens often directed paw/pat/bite behaviour at the mother's tail without appearing to disturb her much. In contrast, wrestling behaviour involved the kitten grabbing, kicking and biting at the mother's body or head, and chasing behaviour involved the mother fleeing from her offspring. Mothers may thus have been less willing recipients of the more disturbing wrestling and chasing behaviour than they were of paw/pat/biting or stalking, and so may have avoided their kittens more during bouts of the former two behaviour patterns.

In addition to these quantitative differences, the quality of a single kitten's social play experience may also have been different to that of a kitten reared with a sibling. The mother was a bigger and stronger play partner than was a sibling, and probably differed in many other ways (e.g. being less active in her movements around the home pen than kittens). It was my impression that wrestling behaviour in particular occurred in a different way between mothers and kittens than it did between siblings, close ventral–ventral contact between the participants being much less common in mother–kitten interactions than in those between kittens.

There was no evidence that single kittens increased their performance of object or self play in response to their quantitative lack of experience of social play. Such a response might only be expected if the benefits of social play experience could be achieved through the performance of other forms of play. At present, the biological functions of play behaviour are unclear (Martin & Caro 1985). The extent to which the single kittens' lack of social play experience had a detrimental effect on their social development can only be elucidated through further empirical research (see below).

### Maternal Aggression

Mothers of single kittens hit/bit their offspring more often from around day 62 onwards, and showed generally higher levels of hissing behaviour, than did mothers of two kittens. Maternal aggression may have been the result of mothers becoming increasingly disturbed by the more frequent and vigorous bouts of social play directed towards them by their kittens as the kittens grew older. The fact that mothers of single kittens were not only more aggressive towards their kittens but also received much more social play from them than did mothers of two-kitten litters lends support to this idea. The peak in the levels of single kitten play directed towards the mother between days 47 and 67 may have promoted the increase in maternal aggressive behaviour in these litters. Subsequent to this period, maternal aggression increased and levels of mother–kitten play, which had previously been high, decreased rapidly. This decrease in social play may have been a direct result of the change in maternal behaviour. Although some measures of kitten–kitten social play show a drop from around day 70 onwards (West 1974; Barrett & Bateson 1978; Caro 1981b; Mendl 1986) this is nowhere near as pronounced as the drop in mother–kitten play seen in single-kitten litters.

Alternatively, or additionally, mothers of single kittens may not have been as motivated to behave in a maternal way as mothers of two-kitten litters due to the relative lack of stimulation (e.g. to the nipples) from a single kitten as compared to that provided by two kittens (Schneirla et al. 1963; rats, Ota & Yokoyama 1967). This may have resulted in a decrease in maternal tolerance of the single kitten earlier than that seen in families of two kittens.

Hinde & Spencer-Booth (1967a) noted that rhesus mothers who reared their offspring in isolation from other conspecifics became more rejecting of their young as they grew older than did mothers rearing offspring in a group situation. It was suggested that the tendency of isolate monkeys to approach and interact with their mothers at a stage when group-living young were beginning to interact with other social companions may have resulted in this increase in maternal rejection behaviour. Similar findings were described by Ingram (1977) in her study of marmoset, *Callithrix jacchus*, families of twins and singletons, and by Spencer-Booth (1968) in her comparison of twin and single offspring in rhesus monkeys. In general, therefore, the dependence of the single offspring on the mother for social interaction may result in a marked increase in maternal intolerance as the offspring grows older. This may function to distance the mother from her dependent youngster.

### The Mother–Single Kitten Relationship: Consequences for the Single Kitten

The present study demonstrated the development of a different mother–offspring relationship in families containing one kitten in comparison to that seen in two-kitten families. Although single-kitten mothers showed greater avoidance of their offspring and directed more aggressive behaviour towards them as the kittens grew older, they also played more with their offspring than did mothers of two. Single kittens experienced quantitatively less social play than did kittens with siblings and the nature of their play experience was probably qualitatively different. They also spent more time on their own. The consequences of these different forms of early social experience need to be investigated in order to determine what effect the absence of a sibling has on a kitten's social behaviour when

adult, and to what extent the behaviour of single-kitten mothers helps to overcome this absence.

Guyot et al. (1980) noted that domestic kittens, raised initially with their mother and no litter-mate and then isolated from week 6 of life onwards, appeared to have problems in responding to play signals, and generally 'did not know how to play' when placed with age-mates in a test situation. It was suggested that kittens deprived of a litter-mate did not 'learn social communication skills'. Although it is possible that the lack of a litter-mate resulted in this socially inept behaviour, it is also possible that the complete social isolation experienced by single kittens in the study was responsible for this effect. Further investigation of the consequences of being a single kitten is required in order to provide a clearer picture of the effect of the absence of a sibling, and of the changes in maternal behaviour, on social development.

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