Anim. Behav., 1990, **40**, 514–525

Play in the domestic cat is enhanced by rationing of the mother during lactation

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Abstract. The mothers of eight litters of domestic cats, *Felis catus*, were given a rationed diet after the birth of their kittens so that they received approximately 80% of the energy intake when given ad libitum food. Rationing of the whole family was maintained until the end of the period in which the family were observed. The subsequent play of the kittens was compared with that of litters of the same mothers when the families were given ad libitum food. When the mothers received rationed food, their kittens played with objects significantly more than when the mothers received ad libitum food. This was a specific effect and was not due to a general increase in the activity of the rationed kittens. Over the first 18 days after birth the extent to which mothers were unavailable to their kittens when rationed was strongly correlated with the object play of their kittens 70–84 days after birth. While the kittens in the rationed condition were well buffered from the effects of rationing, they nuzzled significantly more than those in the ad libitum condition in apparent attempts to reach their mothers' nipples.

Play is an activity that is often thought to be a luxury which can be dispensed with when food is in short supply. A number of studies both in the laboratory and in the wild have suggested that young mammals on a low plane of nutrition do play less than when they are better fed (squirrel monkeys, *Saimiri sciureus*: Baldwin & Baldwin 1976; vervet monkeys, *Cercopithecus aethiops*: Lee 1984; rock hyrax, *Procavia johnstoni* and tree hyrax, *Heterohyrax brucei*: Magin 1988). While the energy costs of play are not great (Martin 1984), an animal close to starvation presumably saves energy when it can, giving relatively low priority to play (Martin & Caro 1985).

When a young mammal is weaned earlier than is usual for the species, it might be relatively debilitated and, as a consequence, play less. However, a considerable body of evidence suggests that early-weaned domestic cats, *Felis catus*, play more than later-weaned animals. In one study, kittens from litters of four were separated gradually from their mothers, starting at 5 weeks after birth (Bateson & Young 1981). Two weeks after the beginning of separation these kittens showed significantly higher rates of object contact while playing than did their littermates left with their mothers. In a second study, cat mothers were given a single dose of bromocriptine when their kittens were 5 weeks old (Bateson et al. 1981). The drug suppressed lactation for about 24 h, thereby removing the kittens' milk supply without removing the mother. Once again object play of the kittens whose mothers' lactation had been suppressed was significantly greater than in a control group 2 weeks after the administration of the drug. In both these experiments the reduction in parental care was simulated when social play was well developed and the major influence was on object play that was not fully expressed for another 2 weeks. In a third study (Martin & Bateson 1985) three doses of bromocriptine were given to the mothers, starting when the kittens were 4 weeks old, i.e. a week earlier than in the previous experiment. In this case, cat contacts during social play were significantly greater in the kittens of mothers with blocked lactation than in those of the control group.

The general finding of these studies on the cat, namely that early weaning is followed by an increase in play behaviour, appears to contradict the findings of other studies where low food availability results in a decrease in levels of play. One possible explanation for the results obtained with the domestic cat is that direct interference with the mother–offspring relationship, designed to promote early weaning, is not equivalent to the whole family experiencing low food availability. In addition, in all the laboratory studies of early-weaned kittens carried out in our colony, kittens had access to ad libitum food supplies after they were weaned, an unlikely event when food is limited in the wild. Perhaps, then, the view that low food availability causes a decrease in play might also hold for the

Table I. The compositions and dates of birth of two litters for eight domestic cat mothers which were given an ad libitum diet for one litter and were rationed after the birth of the other litter

Mother	Litter composition		Date of birth	
	Ad Libitum	Rationed	Ad Libitum	Rationed
Penelope	MFF	MMM	6 May 1985	11 June 1984
Helen	MF	MFF	20 May 1985	25 July 1984
Chacha	FFF	MFF	15 July 1985	8 February 1985
Nina	FFF	MFF	11 September 1985	10 September 1984
Calypso	FF	FM	17 June 1984	2 August 1985
Raina	MF	MMM	7 August 1984	12 May 1985
Laura	FF	MF	3 September 1984	17 May 1985
Dixie	MMM	MFF	8 March 1985	3 August 1985

M: a male kitten, F: a female kitten.

domestic cat if it were tested appropriately. To investigate this possibility, we simulated a set of conditions that might be more characteristic of the real world than artificially interrupting the kittens' milk supply.

Several strands of evidence suggest that domestic cat mothers will generally wean their young early when the energy loss during lactation is heavy. For instance, Deag et al. (1987) have found that kittens in larger litters showed an earlier discontinuity in the rate at which they put on weight, suggesting earlier weaning onto solid food when the load on the mother is greater. And in our own colony mothers that have been off their food have weaned their young earlier (see Bateson & Young 1981; Martin 1986). Lactation imposes a heavy drain on a mother's energy reserves. In principle, she might wean her current offspring earlier or later than usual in response to the added strain of low food intake while she is nursing (Martin & Bateson 1988). What she does is likely to depend on many factors such as her current condition, the time likely to elapse before the next litter, and the rate of recovery in her condition after nursing is complete. However, in the domestic cat, it seemed likely that experimental reduction in mothers' food during lactation could be used to investigate the effects of early weaning on behavioural development.

In the present study, therefore, we encouraged early weaning by restricting the food supply of the mothers. Food restriction continued throughout the study period in order to mimic conditions likely to occur in the wild. Because the present experiment involved a relatively natural manipulation in the sense that it did not involve direct interference with the mother–offspring relationship, special attention was given to the variability in the responses of the families to rationing.

METHODS

Subjects, Housing and Care

The subjects were 16 litters of kittens from eight different mothers, living in a laboratory colony. The Rationed and Ad Libitum groups consisted of eight litters each, and each mother used in the study raised one litter when rationed and one when on an ad libitum diet. We varied the order in which the mothers reared their litters such that four mothers were put on rations for the first litter and given ad libitum food for the second, while for the other four mothers the order was reversed.

Four males sired all the litters, and the mothers used were always paired with the same male for both their Rationed and Ad Libitum litters. The dates of birth and litter compositions from 2–3 days after birth are shown in Table I; our intention was to have three kittens in every litter, but this was not always possible. Housing is described in Mendl (1988). Each family of a mother and her kittens lived on its own in one of the pens described by Mendl. These pens were cleaned out daily.

Experimental Manipulation

The cats were fed twice daily (once between 0830 and 0930 hours and once between 1530 and 1630

hours) on 'Whiskas Supermeat' moist cat food and dry 'Purina Cat Chow', and were provided with ad libitum supplies of water. The Ad Libitum families received a supply of the moist and dry cat food such that their food trays were never empty. The Rationed families received a restricted amount of food. For each Rationed family, we assessed the amount of moist food consumed by a previous family of the same mother using data collected at the Madingley cat colony. Using these figures, it was possible to supply the Rationed families with approximately 80% of the amount of moist food that they might have been expected to consume if given ad libitum supplies. Half of the moist food was provided at the morning feed and half in the afternoon. A standard amount of 50 g of dry food was provided for the Rationed families each day. The cats in the Ad Libitum group left most of the dry food. The Rationed cats took significantly more, particularly towards the end of the period of rationing. Even then, however, not all of the dry food was eaten in most cases; the cats would reduce their energy intake rather than eat their fill of this type of food.

For both the Ad Libitum and Rationed families, the amount of moist food and dry food provided were weighed at each feeding session and the two food stuffs were placed in separate trays. Prior to the morning feeds, the amounts of moist food and dry food remaining in the food trays from the previous day were weighed in order to determine how much of each type of food had been consumed by the cats. This process of controlling the Rationed group's food intake started on the day after the birth of the litters and continued up until day 84 after birth. The total metabolizable energy intake for the Ad Libitum and Rationed families was calculated using figures for both Whiskas Supermeat (3·5 kJ/g, Pedigree Pet Foods) and Purina (15 kJ/g, determined at the Dunn Nutritional Laboratory, Cambridge).

Observation Schedule and Recording Procedure

During the early period of the kittens' lives when they spent the entire day in the nestbox (day 3 to day 18), we observed each family on six occasions at 3-day intervals beginning on the third day after birth. Each watch was 45 min long and was carried out between 1300 and 1600 hours. Each session was divided into 90 intervals of 30 s.

Three weeks after birth the kittens started to leave the nestbox and became much more active. Families were observed for two 30-min sessions at 3-day intervals from day 21 to day 31, on day 35 and at weekly intervals up to day 84. Recording was especially intense during days 21–35 since this period had been identified as a time of rapid change in the kitten's behaviour (West 1974; Barrett & Bateson 1978; Caro 1981) and when weaning starts (Schneirla et al. 1963; Martin 1982, 1986). One 30-min session took place in the morning (0930–1230 hours) and one in the afternoon (1300–1600 hours) on each observation day. Each session was divided into 30 intervals of 60 s.

The observer watched the cats in the home pen through a one-way screen in the door of the pen. The items of maternal and kitten behaviour referred to in this paper were recorded by instantaneous sampling when a beeper sounded in the observer's ear (see Martin & Bateson 1986). The behaviour and locations of the mother and her kittens were recorded simultaneously using a keyboard connected to a microcomputer (Epson PX-8). The keys were coded to denote behaviour patterns, individuals, locations and postures. Sequences of key presses were stored in the computer's memory and could subsequently be read out to produce a transcript of the session or down-loaded to a BBC microcomputer for analysis.

Behavioural Measures

Mother on-side-lie: the mother lies on her side with her ventrum fully exposed (Martin 1986).

Mother unavailable: the mother adopts a posture in the nest (lying on her ventrum in the Inaccessible position or Standing, see Martin 1986) which prevents the kittens from suckling or is unavailable to them outside the nest.

Kitten ventral: the kitten lies with its head against and facing towards the mother's ventrum. The kitten's head is kept quite still or pushed against the ventrum as if it were suckling (Martin 1986).

Kitten nuzzle: the kitten lies with its head against and facing towards the mother's ventrum, moving its head from side to side as if searching for a nipple (Martin 1986).

Kitten lie: the kitten lies still.

Object contact*: the kitten paws, pats or bites an inanimate object (Bateson & Young 1981).

Cat contact*: the kitten paws, pats or bites a conspecific (Bateson & Young 1981).

Items that are not referred to in the analysis have been excluded. Those marked with an asterisk were

recorded only after the first 3 weeks. Focusing on the kittens' behaviour between 21 and 84 days meant that we could not obtain reliable data on the mothers' nursing behaviour in this later period.

Weights

Kittens were weighed for the first time on day 2 and thereafter on a daily basis except at weekends. We obtained the missing weights by interpolation. Mothers were weighed twice each week starting on day 7. To smooth out short-term fluctuations, regression equations were fitted to the measurements of mother's weight and the total weight of her kittens on successive occasions after birth. In the case of the kittens, linear regressions could be fitted to the data for the first 21 days. In the case of the mothers, polynomials were needed. From these equations we could estimate how much weight the mothers lost over the first 21 days after birth and how much the kittens gained weight.

Analysis of Data

Most measured aspects of behaviour occurred at relatively low levels and have therefore been accumulated across several watches. For purposes of analysis and presentation, we grouped the number of occurrences at the moments of sampling into a maximum of six age periods (each consisting of three observation sessions). In the case of all the behavioural measures, the data are expressed as the percentage of all instantaneous samples occurring during each age period, during which the behaviour pattern was observed. The age periods and their biological significance are described below.

Periods 1 and 2: Total dependence (3–9, 12–18). At this stage the kittens receive all their nutrition through their mother's milk and measures of the mother's maternal behaviour are relatively stable (see Deag et al. 1988). For most purposes, the data have been lumped for both periods.

Period 3: Pre-weaning (21–28). The kittens rapidly develop sensory and motor capacities and become markedly more active (see Martin & Bateson 1988).

Period 4: Weaning (31–42). A period of rapid change in maternal behaviour and the time when the majority of kittens take their first solid food (see Schneirla et al. 1963; Bateson & Young 1981; Deag et al. 1988). The kitten's responsibility for maintaining proximity to its mother is particularly likely to reach a peak at this stage (Deag et al. 1988).

Period 5: Early post-weaning (49–63). Many measures of kitten behaviour are showing rapid changes. Object play in particular may show a five-fold increase from the beginning to the end of this period (Barrett & Bateson 1978; Martin & Bateson 1988).

Period 6: Late post-weaning (70–84). Changes in many aspects of the kitten's behaviour are much less rapid. Few kittens are to be seen suckling in this period.

Kittens in the same litter were not treated as being independent for statistical purposes and so litter means for kitten behaviour are used throughout (Abbey & Howard 1973).

A repeated measures ANOVA was used to analyse most results. Each mother was used as its own matched pair when a measure of maternal behaviour was examined. When kitten behaviour was analysed, litters from the same mother were matched. In addition to the matched-pairs factor (experimental treatment) with ad libitum food compared with rationed food, the ANOVA had one within-subjects factor (age) with varying numbers of levels according to the data being analysed. All the data were examined to see whether the distributions were normal. Where necessary, scores were transformed using the angular (arcsine-square root) transformation (Sokal & Rohlf 1981). In periods 1 and 2 where data have been lumped, matched-pairs *t*-tests have been used.

On every measure, the effect of the rationing procedure was calculated for each family by calculating the following ratio

$$\text{Rationed score}/(\text{Rationed score} + \text{Ad Libitum score})$$

Each ratio provided an index of the relative performance of mothers and kittens in the two experimental procedures, and could be used to examine the extent to which different families were affected by the experimental treatment, and how the size of this effect was related to changes in their behaviour and growth. For example, if Mother A's unavailability to her kittens for nursing was increased more by the rationing procedure than Mother B's, then Mother A's unavailability ratio would be greater than Mother B's (both would be above 0·5 if the treatment resulted in a general increase in the

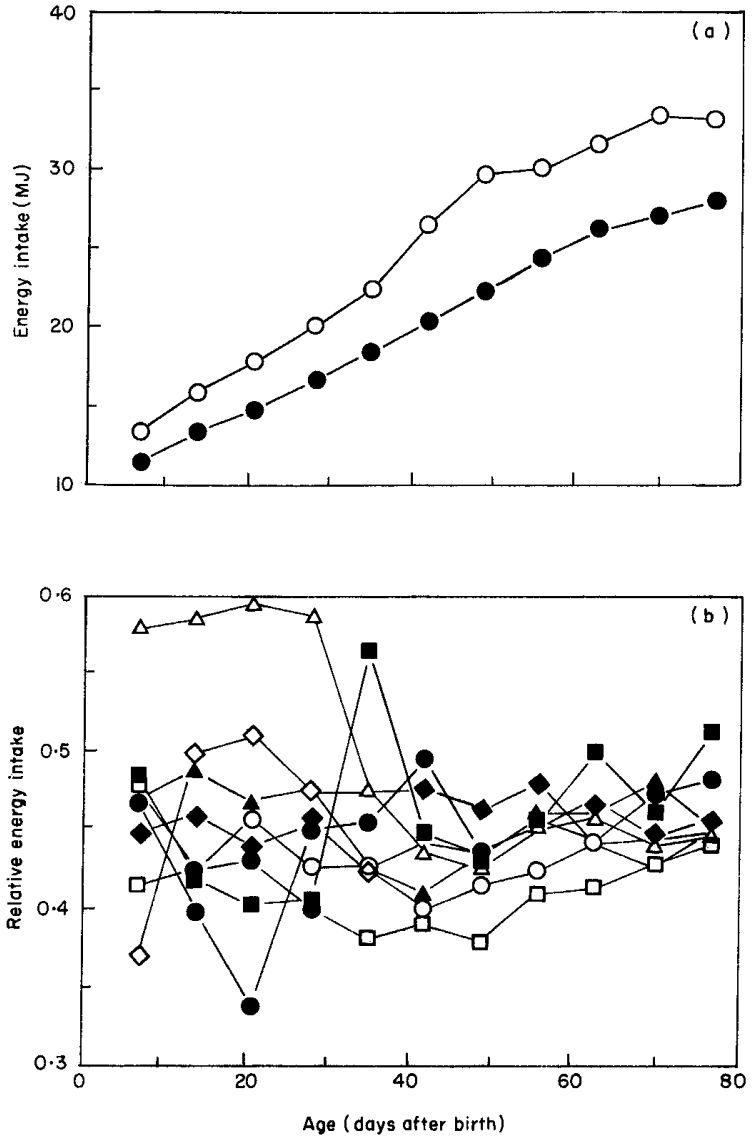

Figure 1. (a) Mean weekly energy intake of the cat families in the Ad Libitum (○) and Rationed (●) conditions in successive weeks after birth. The difference between the groups is statistically significant ($F_{1,7}=41{\cdot}8$, $P<0{\cdot}0001$) as is the interaction between treatment and age ($F_{10,70}=3{\cdot}12$, $P<0{\cdot}01$). (b) The ratio of Rationed intake to Ad Libitum plus Rationed intake for each mother (when the Rationed intake was 80% of the Ad Libitum intake, the ratio is 0·44). Note that Dixie had a higher energy intake in the first 4 weeks after birth when she was rationed. ○, Calypso; ◆, Raina; ●, Laura; ◇, Penelope; ■, Helen; □, Chacha; ▲, Nina; △, Dixie.

mothers' unavailability). In addition, if Mother A's kittens played at higher levels in the Rationed condition, relative to the Ad Libitum condition, than Mother B's kittens, then Mother A's kitten play ratio score would also be higher than Mother B's. If these rank orders were consistent across all mothers, then a significant positive correlation between the maternal unavailability ratios and kitten play ratios would be found. When associations between ratios have been analysed, Pearson correlation coefficients are quoted.

RESULTS

Between-group Differences

Mothers in the Rationed group had a lower energy intake than those in the Ad Libitum group except for Dixie (see Fig. 1). Dixie had diarrhoea in the Ad Libitum condition at the time she was nursing her kittens and was eating considerably less food than when she was rationed. The statistical analysis of the data for all the cats showed that the ration-

Table II. Statistical analysis of data using repeated measures ANOVA with each mother as its own matched pair

Variable	All cats		Excluding Dixie		Direction
	$F_{1,7}$	P	$F_{1,7}$	P	
Energy intake	41·8	0·0001	43·7	0·001	R<A
Mother weight	1·3	NS	2·3	NS	R<A
Kitten weight	0·1	NS	0·0	NS	
Kitten ventral	5·2	0·06	3·3	NS	R<A
Kitten nuzzle	15·7	0·01	22·5	0·01	R>A
Object contact	6·5	0·05	13·8	0·01	R>A
Cat contact	1·9	NS	2·5	NS	R>A
Kitten lie	0·3	NS	0·4	NS	
Corrected object contact	58·8	0·00001	50·3	0·00001	R>A
Corrected cat contact	0·3	NS	0·1	NS	

Two analyses were carried out, one using all eight mothers and one excluding Dixie. R and A refer to Rationed and Ad Libitum treatments. Corrected object contact and Corrected cat contact refer to Object contacts and Cat contacts corrected for time spent active. The following interactions were statistically significant. All cats: Energy intake $F_{10,70}=3·12$, $P<0·01$, Corrected object contact $F_{3,21}=3·42$, $P<0·05$. Excluding Dixie: Energy intake $F_{10,60}=2·02$, $P<0·05$.

ing significantly reduced the energy intake and the interaction between age and condition was also statistically significant. The interaction was much less marked when Dixie was excluded from the analysis (see Table II). Neither the mothers' weights nor the kittens' weights were significantly affected by the rationing procedure, although the trend in the mothers' weights was obscured by considerable individual variation in response to rationing (Fig. 2 and Table II).

During the period of total dependence, the rationing procedure had no significant effect on the mothers' availability for nursing, although with Dixie excluded from the analysis, Rationed mothers were observed significantly less often than Ad Libitum mothers in the Mother on-side-lie position on days 3–18, when the mother's nipples were fully accessible to her kittens (see Table III). The lowered Mother accessibility for nursing in the rationed group was accompanied by a significant increase in Kitten nuzzle (see Fig. 3 and Table II). Kitten ventral scores tended to be lower in the rationed group and the difference bordered on statistical significance.

During the 21–84 day period, kittens in the Rationed group showed significantly higher levels of Object contacts, a measure of object play, than kittens in the Ad Libitum group (see Fig. 4 and Table II). No differences were found in Cat contacts, a measure of social play (see Tables II and

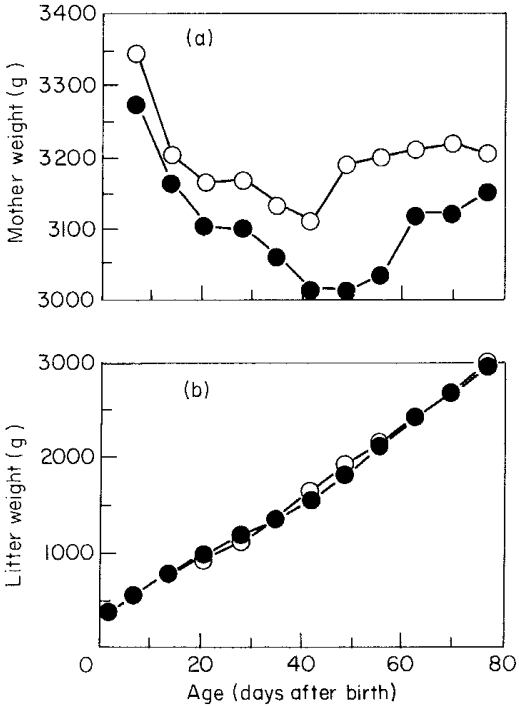

Figure 2. (a) The mean weights of mothers in the Ad Libitum (○) and Rationed (●) conditions in successive weeks after birth. (b) The mean weights of their litters (starting on day 2). Neither difference between the groups is statistically significant, using a repeated measures ANOVA ($F_{1,7}=1·3$ and 0·1, respectively).

Table III. Mean percentage scores for maternal behaviour in the Ad Libitum and Rationed conditions 3–18 days after birth

Measure	Condition	All cats		Excluding Dixie		
		%	*t*	%	*t*	*P*
On-side-lie	Ad Libitum	62·7	0·73	65·9	2·67	0·04
	Rationed	57·2		54·0		
Unavailable	Ad Libitum	17·1	0·83	14·0	2·06	0·09
	Rationed	22·6		24·4		

The scores are the percentage number of observations in which the category of behaviour was observed. Values for matched-paired *t*-tests are given alongside each group. The three right-hand columns give the data when Dixie has been excluded from the analysis.

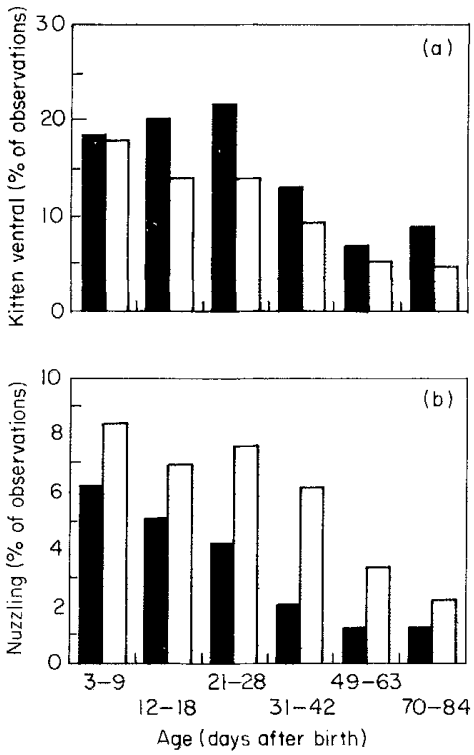

Figure 3. The percentage number of observations in which (a) Kitten nuzzle and (b) Kitten ventral occurred in different age periods after birth in Ad Libitum (■) and Rationed (□) conditions. The difference in Kitten nuzzle is highly significant, using a repeated measures ANOVA ($F_{1,7}=15{\cdot}66$, $P<0{\cdot}01$) and that in Kitten ventral borders on significance ($F_{1,7}=5{\cdot}16$, $P<0{\cdot}06$).

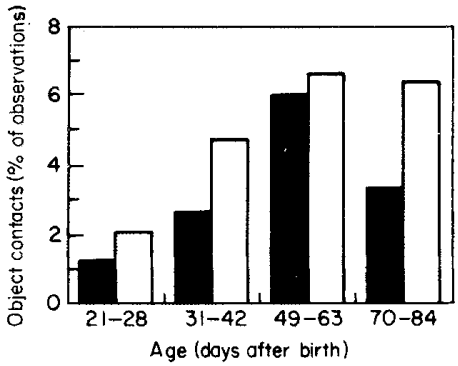

Figure 4. The percentage number of observations in which Object contacts, given by kittens in object play, occurred in different age periods after birth in Ad Libitum (■) and Rationed (□) conditions. The difference is statistically significant, using a repeated measures ANOVA ($F_{1,7}=6{\cdot}45$, $P<0{\cdot}05$). When the scores are corrected for time spent active (see Table II), the difference is much more pronounced ($F_{1,7}=58{\cdot}8$, $P<0{\cdot}0001$) and the interaction between treatment and age is also statistically significant ($F_{3,21}=3{\cdot}42$, $P<0{\cdot}05$).

IV). To check that the object play difference was not simply due to an effect on kitten activity, we compared a measure of kittens' inactivity (Kitten lie) between the two groups (see Table IV). No significant difference was found. Nevertheless, from this measure of inactivity, the kitten play scores were corrected for the number of occasions on which each kitten was not lying at each age range. When the corrected scores were compared, the difference between Rationed and Ad Libitum kittens in Object contacts was even more strongly significant than when using uncorrected scores (see Tables II and IV). No effects were found in corrected Cat contacts.

Analysis of Individual Variation

The supposed effects of the treatment differed markedly between families. In particular, the Ad Libitum kittens of Dixie, who sharply reduced her food intake when nursing (see above), played with

Table IV. Mean percentage scores for aspects of kitten behaviour not given in the figures at different age periods after birth

Measure	Condition	Age period (days after birth)			
		21–28	31–42	49–63	70–84
Cat contact	Ad Libitum	5·7	12·0	14·5	8·5
	Rationed	5·4	15·3	16·1	11·1
Kitten lie	Ad Libitum	53·7	53·5	49·6	55·4
	Rationed	60·4	55·2	48·1	44·5
Corrected object contact	Ad Libitum	2·9	5·2	12·1	7·4
	Rationed	5·1	10·6	13·5	11·9
Corrected cat contact	Ad Libitum	13·3	24·3	28·8	18·0
	Rationed	14·0	32·2	31·3	19·5

The uncorrected scores are the percentage number of observations in which the category of behaviour was observed. The corrected scores are the percentage number of observations in which the category was observed divided by (100 minus the percentage number of occasions in which Kitten lie was observed). The difference between the groups for Corrected object contacts is highly significant, using repeated measures ANOVA ($F_{1,7} = 58{\cdot}8$, $P < 0{\cdot}0001$); the interaction between treatment and age is also statistically significant ($F_{3,21} = 3{\cdot}42$, $P < 0{\cdot}05$). None of the other differences is statistically significant.

objects more than the Rationed kittens. The other mothers differed markedly in how they responded to rationing. Calypso lost more weight when she was nursing under rations but remained as available to her kittens as when she was fed ad libitum. Helen and Chacha lost more weight and made themselves less available when rationed. Raina, Penelope and Nina did not lose more weight when they were rationed but did make themselves considerably less available. Laura seemed to be unaffected by the rationing procedure, even though she clearly had a lower energy intake when she was rationed. She was able to maintain her own weight and even behaved more maternally than she did when she was on an ad libitum diet.

To examine possible effects on the kittens of the individual variation in the mothers, the difference in each measure between the Rationed and Ad Libitum conditions was converted to a ratio, as outlined in the Methods, and the relations between the ratios were then calculated. Such analysis on the small sample sizes available must be treated with some caution. Even so, the analysis does amplify the between-group comparisons. The ratio for the energy intake over the first 21 days after birth was correlated with the ratio for the loss of maternal weight over the same period ($r = 0{\cdot}83$, $df = 6$, $P < 0{\cdot}02$). The mother's energy intake ratio was strongly negatively correlated with the ratio for Kitten nuzzle in the 12–18-day period ($r = -0{\cdot}87$, $df = 6$, $P < 0{\cdot}01$), but was not correlated with the ratio for Mother unavailable ($r = -0{\cdot}17$, $df = 6$) or with the kitten weight gain ratio ($r = -0{\cdot}50$, $df = 6$). This suggests that some mothers responded to the enhanced nuzzling activity of their kittens in the Rationed condition by nursing. Finally, the relationship between the ratio for Mother unavailable (3–18) and the ratio for Object contacts (70–84) is very strong ($r = 0{\cdot}91$, $df = 6$, $P < 0{\cdot}01$; Fig. 5). The less available the mother was to her kittens during nursing, the more her kittens played with objects some 50 days later.

Possible Effects of Sex Differences

By chance the mothers had more all-female litters when they were on an ad libitum diet. (The rationing procedure started after birth and the mothers were no more likely to have all-female litters after they had been rationed than when having a previous litter.) In some studies object play in cats was higher in litters containing male kittens than in all-female litters (Barrett & Bateson 1978; Bateson & Young 1979; Caro 1981). The differences were subtle and Caro (1981) found sex differences only after 12 weeks. Even so, it was possible that the observed differences in object play in the present study were due to chance variation in the composition of the litters. In the Ad Libitum group the mean percentage of observations in which Object

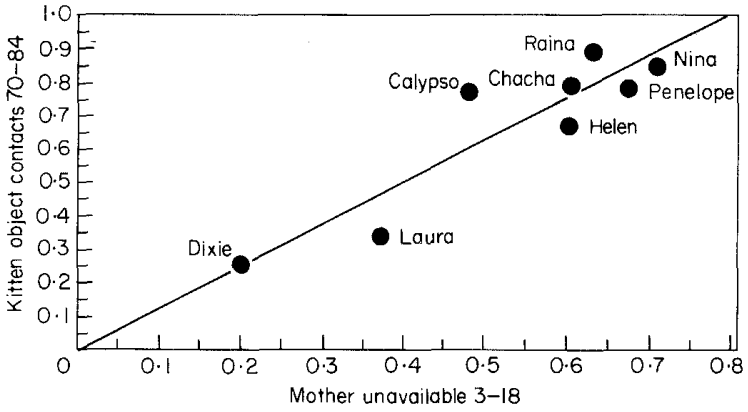

Figure 5. The association between relative unavailability of the mother to her kittens in the Rationed condition 3–18 days after birth and relative amount of object play 70–84 days after birth. Mother unavailable (3–18) and Kitten object contact (70–84) ratios are Rationed score/(Ad Libitum score + Rationed score). The correlation is highly significant ($r = 0{\cdot}91$, $P < 0{\cdot}01$).

contacts (70–84) was scored was 4·14% for the all-female litters and 2·35% for the litters with males in them. The difference was not significant and, in any event, was in the opposite direction from what might have been expected. Furthermore, when an index of sex-ratio difference was calculated (Rationed sex ratio/(Ad Libitum sex ratio + Rationed sex ratio)) the correlation between this index and Object contacts (70–84) was far from reaching statistical significance ($r = 0{\cdot}45$, $df = 6$). When the association between Mother unavailable (3–18) and Object contacts (70–84) was included in the analysis, the partial correlation coefficient between the sex ratio difference and Object contacts (70–84) was only 0·18. Therefore, sex-ratio differences between the Rationed and Ad Libitum litters did not appear to underlie the differences in object play.

DISCUSSION

Reduction in the food available to mother cats and their litters during the period of lactation significantly enhanced object play in the kittens. The rate at which kittens gained weight was well buffered from variation in their mothers' food supply, as in many other mammals including humans (Prentice & Whitehead 1987). Nevertheless, the kittens' attempts to get onto a nipple, as measured by Kitten nuzzle, was significantly greater in the Rationed group 3–18 days after birth. Furthermore, the mothers' energy intake was negatively correlated with kitten nuzzling. Perhaps, by increasing their nuzzling when the flow of milk was reduced, the Rationed kittens were able to maintain the same rate of growth as did the kittens in the Ad Libitum condition.

The influence of rationing on play confirmed the expectation based on three previous studies which manipulated directly (though artificially) the age at which kittens first took solid food (Bateson & Young 1981; Bateson et al. 1981; Martin & Bateson 1985). Comparison of the play scores with these earlier studies is not possible because different methods of scoring were used. Nevertheless, the general qualitative conclusion that the weaning process affects play has been supported. The present study confirms that an enhancement of play is not due to a higher level of general activity. It also shows that the effect is obtained in kittens whether or not unlimited food is available after weaning.

The deliberate manipulation of diet had embedded within it a small natural experiment, albeit unintended. One of the mothers, Dixie, had severe diarrhoea when she was nursing her kittens on an ad libitum diet. We subsequently discovered that she had taken less food during lactation under the supposed ad libitum conditions than when she was rationed. She was less available to her kittens when she was on an ad libitum diet; and later in development her kittens played more with objects than those reared when she was rationed. This was the opposite of what the other cats did.

The mothers' energy intake was not correlated with their weight loss, their availability to their kittens or with their kittens' weight gain. On the other hand, the kittens of rationed mothers clearly felt the treatment because they nuzzled more than the kittens in the Ad Libitum condition. Therefore, some rationed mothers probably responded to the

enhanced nuzzling activity of their kittens by giving them milk. Almost certainly, a variety of factors influence maternal behaviour. The mother's condition, the demands placed on her by her offspring and her predisposition to behave maternally probably all play their part. While these hypothetical relations require testing in more extensive studies, the present study shows that, even with a 20% reduction in energy intake, the mothers are able to compensate in various ways so that their own weight is scarcely affected and their kittens' growth is undisturbed.

Even though the influence of reduction in energy intake on weight is complicated, the link between the mother's withdrawal of care and the long-term effects on play are strikingly borne out by analysis of the individual differences. The strong inference is, therefore, that the kittens' subsequent level of play is affected by the pattern of the mothers' nursing behaviour. When rationed, the mothers tended to reduce some aspects of their maternal care in the 3–18-day period after birth. This is long before the kittens first take solid food and are able to process it effectively (Bateson & Young 1981; Deag et al. 1987). Possibly, then, the mother prepares her offspring for earlier weaning days or even weeks before they will become dependent on solid food. Such preparation would be valuable in ensuring that a whole range of necessary anatomical and physiological changes in the digestive system were timed so that the young were ready to process solid food when they were weaned. Both the mother and her offspring benefit if these changes coincide with the time when the mother's milk is insufficient for the offsprings' needs.

Bateson & Young (1981) suggested that, if the mother reduced lactation relatively early in the kitten's development, such a cue might predict that the kitten would be forced to independence at an earlier age than would have otherwise been the case. Enforced independence at an earlier age would mean that the kittens would have to start foraging at an age when they could otherwise have been playing. To avoid the ill-effects of curtailed play, the early-weaned kittens could, while they still had opportunities, play more than those that were weaned later. Such a conditional response might have evolved, therefore, because those kittens that played more in response to being weaned earlier were more likely to survive than those that did not. Admittedly, the benefits of play, which such an argument assumes to exist, remain to be tested adequately (see Martin & Caro 1985). The hypothesis is supported by evidence linking the time of weaning and the development of independent foraging. Tan & Counsilman (1985) examined the development of predatory behaviour in kittens that had experienced early, normal or late weaning. Early weaning was simulated by gradual separation from the mother starting at 4 weeks, while late-weaned kittens were left with their mothers, but were denied access to solid food until the ninth week. Tan & Counsilman found that early-weaned kittens developed predatory behaviour sooner than normally weaned kittens and were more likely to become mouse-killers at an early age.

Changing the availability of food is a much more natural way to simulate reduction in maternal care than separation of the kittens from the mother or suppression of the mother's lactation with drugs. If the way in which play develops depends on the quality of the environment, manipulation of the nutritional plane of the mother would be expected to influence how much the kittens play by affecting the age of weaning. This expectation is confirmed by the present study. In a subsequent study, levels of play in the pups of hooded rats, *Rattus norvegicus*, rationed after birth increased relative to those in the ad libitum condition (E. Smith, unpublished data).

If the mothers had been seriously starved (which was not the case in the present study), it seems likely that they would have been forced to accept a substantial loss of weight, produce less milk while they suckled, stop lactating earlier than in a favourable environment, as well as reduce other drains on their energy. Other studies suggest that all of these things would have happened. For instance, Smith & Jansen (1977a, b) fed mother cats half their ad libitum intake during the second half of the gestation period and the first 6 weeks postpartum. These cats showed less active mothering than normal and were more irritable towards their kittens. Gallo et al. (1980, 1984) fed cat mothers on a low-protein diet during late gestation and lactation and found that the social interactions between mothers and kittens were affected, with kittens generally showing fewer social interactions with their mothers and poorer attachment, as assessed by separation experiments (Gallo et al. 1980).

The kittens of severely malnourished mothers are likely to be seriously affected as well and, when malnourished themselves, probably suppress play. Smith & Jansen (1977a, b) found that kittens of

starved mothers showed growth deficits in some brain regions (cerebrum, cerebellum and brain stem). Even after rehabilitation with ad libitum access to food from 6 weeks of age onwards, they showed a number of behavioural abnormalities. At 4 months, for example, they had more accidents during free play and performed poorly on several behavioural tests (Smith & Jansen 1977c). Simonson (1979) also found a wide variety of behavioural and physical abnormalities in kittens whose mothers were restricted to 50% of normal food intake throughout gestation (see also Gallo et al. 1980, 1984).

Some of the effects of severe malnourishment may be pathological without representing adaptations to poor conditions. However, stopping play may represent the best tactic for the individual, given its circumstances. Field studies of other species have demonstrated that, when food is in short supply, play is suppressed until conditions improve (Lee 1986; Magin 1988). Such changes would certainly seem adaptive if the marginal benefits of play were less than the marginal costs (Martin & Caro 1986). The present study and a similar one on the rat (E. Smith, unpublished data) suggest, however, that a slight reduction in maternal diet leads to higher levels of play by the offspring rather than to suppression, at least in some mammals. The functional significance of such a conditional response needs to be examined under natural conditions. Even so it seems likely that, by responding to cues from the mother, the individual animal is able to move along a developmental route that is appropriate to the conditions it will encounter in later life.

ACKNOWLEDGMENTS

This work was supported by a grant from the Medical Research Council. We thank Paul Heavens for his expert help in looking after the cats. We are also grateful to Robert Harcourt, Phyllis Lee, James Serpell and Eileen Smith for their comments on earlier drafts of the manuscript.

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(Received 1 July 1989; initial acceptance 12 September 1989; final acceptance 12 October 1989; MS. number: 3419)