

in the young of many species, e.g. the cat (Bateson & Young, 1981; Martin, 1986), mouse (Fuchs, 1982), hamster (Johnson, 1989) and rabbit (Zarrow, Denenberg & Anderson, 1965). This turning point in growth is therefore a convenient and non-invasive indicator of weaning (e.g. Bateson & Young, 1981).

The course of growth and weaning in the young mammal can be affected by features of the infant itself or of its mother. For instance, large infants are weaned earlier in the cat (Deag, Manning & Lawrence, 1988). Small litters are weaned earlier in desert woodrats (Cameron, 1973) and house mice (König & Markl, 1987), but later in pigs (Boe, 1991). Males are weaned earlier than females in langurs (Rajpurohit & Mohnot, 1991), but later in elephant seals (Reiter, Stinson & Le Boeuf, 1978) and zebu cattle (Reinhardt & Reinhardt, 1981).

Empirical studies and theoretical predictions do not always agree over the differences in parenting behaviour between primiparous and multiparous mothers. In terms of raising future litters, it should be important for the mother not to over-tax herself when young (Trivers, 1974; Carlisle, 1982). In some species this combines with the effect of greater parenting experience to make multiparous females the better mothers. This is true in, e.g. pigs (Jensen & Recén, 1989) and in many species of rodents (reviewed by Smith, 1990). However, parity does not affect the maternal activities of house mice (König & Markl, 1987; see also review by Smith, 1990); and in other species, primipares seem more maternal than older mothers. Primiparous rhesus and Japanese macaques (reviewed Nicolson, 1987; Gomendio, 1988), cows (Edwards & Broom, 1982) and horses (Duncan, Harvey & Wells, 1984) suckle their infants for longer. Primiparous vervet monkeys are more protective and less rejecting (Fairbanks, 1988), and the same is true of humans (Rutter, 1981: 206).

The young animal's course of growth can also be affected by various factors prior to weaning. The transition from relying on milk to relying on solid food is not always marked by the simple change in growth rate described above. In some instances, it is preceded by a slowing or even a cessation or reversal of growth. In house mice, the young hardly grow at all for around five days prior to weaning (König & Markl, 1987), a diapause period that is longer the bigger the litter (Fuchs, 1982). In cats, too, a slowing of growth is often seen (Martin, 1986), especially if the mothers are nutritionally stressed (Bateson & Young, 1981), and litter size also affects the shape of the growth curve (e.g. Martin, 1982). Small offspring may have a particularly rough time in the period prior to weaning. In litters of golden hamsters, the weaning of runts is preceded by a longer period of poor or absent growth than is seen in their littermates, and they are older when they finally switch to solid food (Johnson, 1989).

In this study, a series of measurements were made to examine the determinants of weaning age and growth patterns in the American mink (*Mustela vison*). This species is solitary-living (e.g. Marshall, 1936; Birks, 1981). During the single annual mating season (February–March), males search for females, leaving their territories to do so. Females come into oestrus every eight days (e.g. Rice, 1967); ovulation is induced by sexual contact with the male (Enders, 1952; Dunstone, 1986). Mink separate after mating, and the female receives no help with rearing the young (kits). Implantation of the fertilized blastocysts occurs around the beginning of April, and the litter is born 28–30 days later (Enders, 1952). Females do not have a post-partum oestrus. Kits generally leave the natal territory when about four months old (Mitchell, 1961; Gerell, 1970).

Subjects and methods

The subjects of this investigation were farmed American mink of the Wild Type strain. They were kept in

typical fur farm conditions, i.e. individually housed in wire mesh cages with wooden nestboxes.¹ The cages each measured 0.75 × 0.35 × 0.35 m, and were in long, parallel rows of 200. Each pair of rows was roofed over to form a long shed, the walls of which were open to the outside. Once a day, a feeding machine was driven along each shed, and an offal-based purée was deposited on top of each cage, such that both young and adults could reach it. Water was provided *ad libitum*. The first kits were born at the end of April, and whelping continued until the end of May. The average litter size was around 6 (e.g. 6.2 in 1988; 5.9 in 1989; Mason, 1992).

The litters of 31 adult female mink were selected for study, on the basis of having all been born within the second week of May (so that the dates of weaning would not be too spread out for convenient measuring) and containing 3 or more kits. Very small litters were not considered as in cats the acceleration in weight gain at weaning is gradual and prolonged in litters of only 1 or 2 (Martin, 1982; Deag *et al.*, 1987, 1988).

The kits were weighed daily, from 2 until 6 weeks of age. Weighing was done at approximately the same time each day, between 11:00 and 13:00 h. Males and females were weighed separately. Mean male and female weights were calculated; values were also combined to give litter means. Daily weights were then recorded graphically, and the age at which the steep phase of growth commenced assessed by manually drawing the line of best fit for the accelerated growth post-weaning, and reading off the intersection of the line with the earlier growth curve. This was done without reference to the age of the mother or comparison with the graphs of other litters, to rule out any subjective bias.² The weight at 3 weeks was also selected as an (arbitrary) measure of kit weight prior to weaning.

Other measures relevant to the mother-infant relationship were also recorded, as follows. Weighing involved separating the mother from her kits. If she showed a marked reluctance to leave them, being very difficult to flush out of the nestbox, this was recorded. Vocalization by her during the process of kit weighing was also noted, as mink vocalize when they are under threat (Gilbert, 1969; MacLennan & Bailey, 1969). Enteritis in the litter, as revealed by dirty, sticky kits (Henriksen, 1988), was also recorded.

Results

The growth curves of mink litters

Kit growth was approximately linear while they were entirely dependent on their mother's milk; growth per day averaged 6.2 ± 1.4 g in the female ($n=30$; in one litter there were no females) and 7.1 ± 1.4 g in the male ($n=31$). A few weeks after birth, the rate of growth then accelerated, as weaning occurred. For females, the mean weaning age was 32.2 ± 1.9 days ($n=29$), and for males, 32.2 ± 1.6 days ($n=30$). (In one litter the change in slope of the curve was so gradual that the kits' age at weaning could not be assessed accurately, and so this was omitted from analyses.) Kits from bigger litters were lighter at weaning (see Fig. 1).

The age at which the kits were weaned was predicted neither by litter size, nor total litter weight, nor kit weight. It was, however, predicted by the birthdate of the litter: later-born kits were significantly younger when weaned (see Fig. 2). They were not significantly lighter at weaning, however.

The growth curves of the mink kits were of two types (see Fig. 3), one in which this transition was relatively smooth, and one in which weaning was preceded by a temporary cessation of growth, of between one and five days. The mean age at which kits commenced this growth pause was for male

¹ These conditions, although legal, are clearly not ideal. This research was actually carried out as part of a wider study of the welfare of farmed mink. This study used existing fur farms rather than caging additional animals for research purposes.

² A computer algorithm method (cf. Deag *et al.*, 1987) could not be used as several cases involved insufficient points in a straight line immediately prior to weaning (see Results).

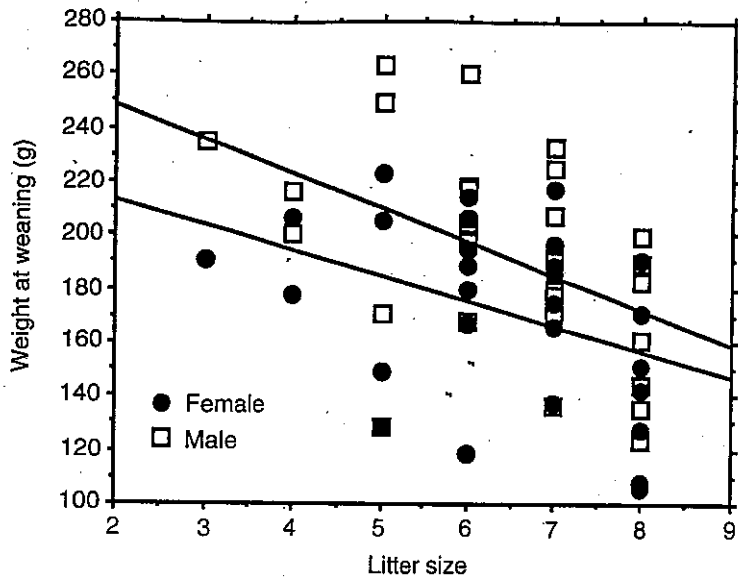


FIG. 1. Litter size and the mean weight of mink kits at weaning. Female kits: $R = -0.39$, $P = 0.034$ ($n = 29$); male kits: $R = -0.46$, $P = 0.010$ ($n = 30$).

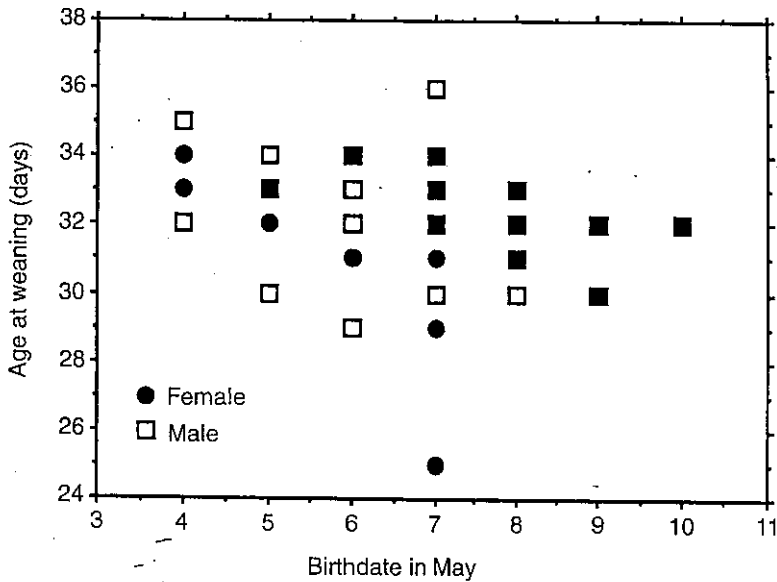


FIG. 2. The birthdate (in May) of mink kits and their mean age at weaning. Female kits: $\tau = -0.30$, $P = 0.021$ ($n = 29$); male kits: $\tau = -0.31$, $P = 0.015$ ($n = 30$).

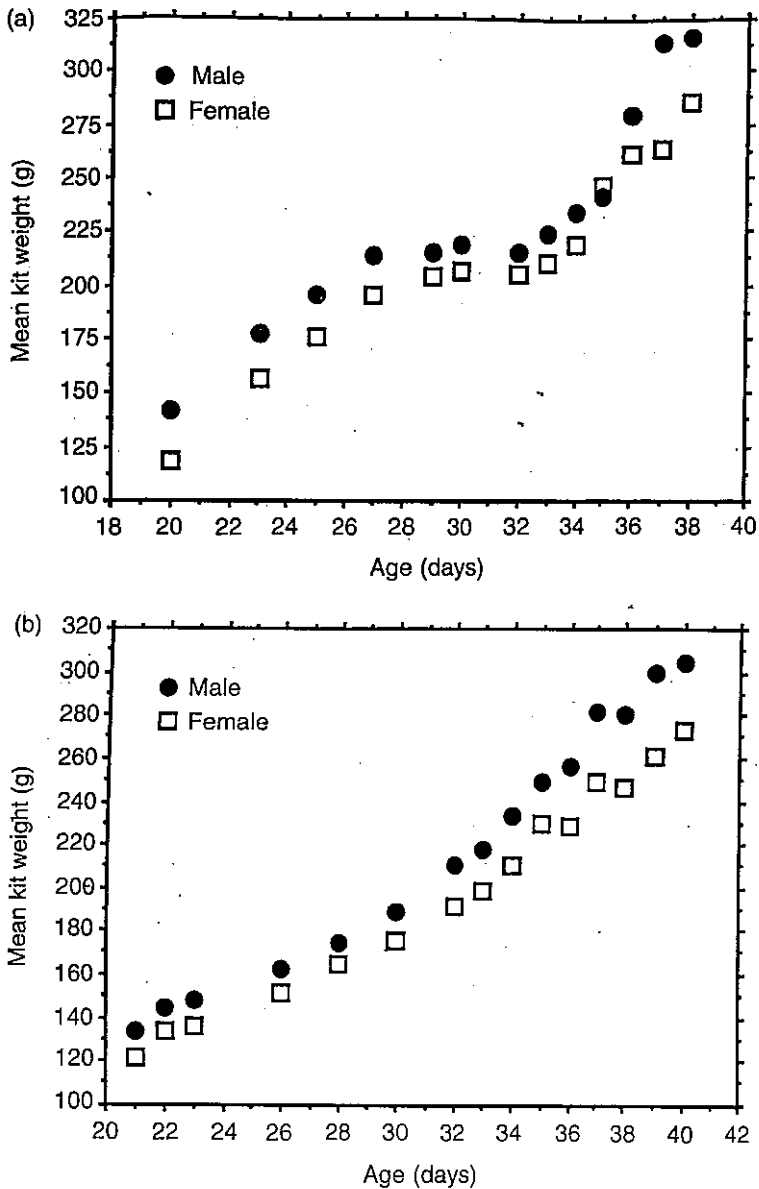


FIG. 3. Examples of the typical growth curves of mink litters: (a) with growth pause; (b) without growth pause.

kits, 28.3 ± 1.3 days ($n=14$), and for female, 28.3 ± 1.7 ($n=11$). The growth pause seemed to be a time of vulnerability; five of the six litters with enteritis had experienced a growth pause ($G=6.34$, $d.f.=1$, $P<0.02$), and in four of these litters illness occurred actually during it, just after the start of the pause.

What factors predicted the presence of this period of arrested growth? Cessation of growth indicates that kits were not obtaining enough milk to meet their growth needs. This might be

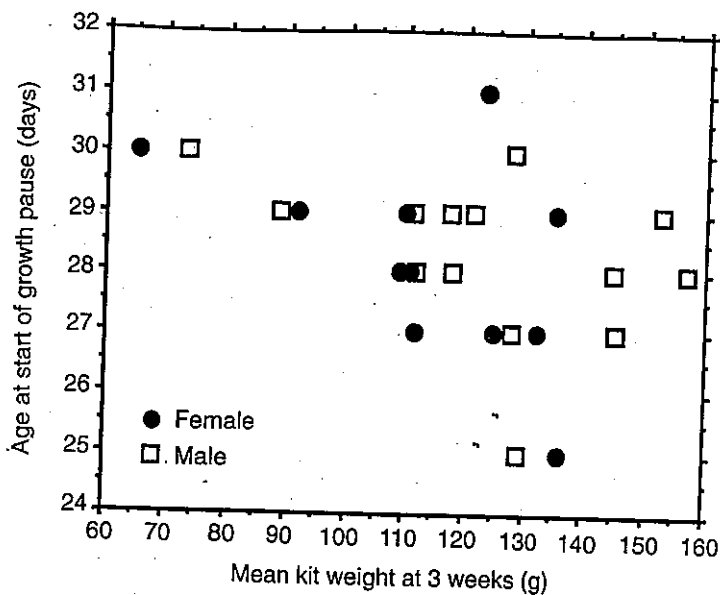


FIG. 4. The mean weight of the mink kit (at 3 weeks of age, when reliant on milk) and the age at which it ceased growing, pre-weaning: female kits: $\tau = -0.47$, $P = 0.045$ ($n = 11$); male kits: $\tau = -0.37$, $P = 0.065$ ($n = 14$).

because the growing kits outstripped their milk supply, as their requirements became too great for their mother. The energetic demands of lactation correlate with the total litter mass (Gittleman & Oftedal, 1987), so mothers with heavy litters might be particularly prone to being over-stretched in this way. However, litters with a growth pause were neither heavier nor larger than litters without (unpaired t ; $P > 0.10$), nor did they consist of a greater proportion of males (Mann-Whitney; $P > 0.10$). Neither did total litter size, weight or proportion of males predict the timing of the growth pause: heavy, large or male-biased litters did not cease to grow any earlier than other litters.

However, an attribute of the kits as individuals did predict the age at which the growth pause commenced: among litters with a growth pause, the timing of the pause was predicted by kit weight. There was a trend for heavier males to cease growing at an earlier age, and for females the relationship was significant (see Fig. 4). Kit weight did not, however, predict the length of this growth pause, and individual kits in litters with growth pauses were no heavier than those in litters without.

Sex differences

Male kits grew faster than females; comparing the mean weight of siblings showed that the growth rates of males per day were significantly greater than those of females (paired $t = 12.42$, $d.f. = 29$, $P < 0.0001$), as were their weights at weaning (paired $t = 4.34$, $d.f. = 28$, $P < 0.0001$; mean male weight = 192.4 ± 37.3 g, and mean female weight = 171.9 ± 33.1 g).

The sexes did not differ significantly in the age at which they temporarily ceased growing. However, male pauses tended to last longer. The female growth pause typically lasted 2.7 days (± 2.4 ; $n = 11$), while that of the male typically lasted 3.8 ± 2.2 days ($n = 14$). The difference in

length of this pause approached significance: $Z = -1.82$, $P = 0.067$. There was no significant sex difference in weaning age (paired $t = 0.34$, $P > 0.10$, $d.f. = 28$).

Male kits, but not female, tended to be older at weaning if they had previously had a growth pause (no. with growth pause = 14, no. without = 16; $U = 67.5$, $P = 0.058$). The presence of a growth pause also influenced the weight at weaning for male, but again not female, kits; those that had a period of arrested growth were lighter. This was shown when the influence of litter size on weight was corrected for by categorizing kits according to whether they were from small (4-6; $n = 14$) or large (7-8; $n = 16$) litters (2-factor ANOVA; weight difference according to presence of growth pause: $F_{1,26} = 5.29$, $P < 0.05$; for females, $F_{1,25} = 0.81$, $P > 0.10$).

Maternal age

Maternal age predicted whether or not the litter's growth was arrested pre-weaning. Eleven of the 15 multiparous females had a pause in the growth of their male kits, compared with only three of the 16 primiparous females ($\chi^2 = 9.31$, $d.f. = 1$, $P < 0.01$); and nine of the 15 multipares also had a pause in the growth of their female kits, compared to only two of the 16 primipares ($\chi^2 = 7.63$, $d.f. = 1$, $P < 0.05$).

As enteritis tended to coincide with having a period of arrested growth, the six litters that suffered from enteritis had older mothers than healthy litters ($U = 38.5$, $P < 0.05$; G-test to compare primipares with multipares: $G = 3.88$, $d.f. = 1$, $P < 0.05$).

Females who were regularly difficult to persuade out of the nestbox away from their litters ($n = 24$) tended to be younger than the females for whom this was not the case ($n = 7$) ($U = 48$, $P = 0.061$). This trend stands if I removed from the analysis the two females who vocalized and so may have stayed in the nestbox out of fear of me rather than out of maternal protectiveness.

Maternal age did not predict weight at weaning, even when the data were corrected for litter size (2-factor ANOVA). Maternal age did have a significant effect on age at weaning, however, for male kits (but not female). Males with primiparous mothers ($n = 16$) were weaned on average 1.3 days earlier than males with multiparous mothers ($n = 14$, $U = 58.5$, $P < 0.05$), at 31.6 days, compared to 32.9. Their offspring were not born significantly later, so this was not a birthdate effect. (It was not possible to disentangle the relative influences of maternal age and the presence or absence of a growth pause as ANOVA cells were too small to reach significance.)

Discussion

Weaning of mink kits

The age at which mink kits in litters of three or more are weaned in captivity, 32.2 days, is comparable to that of the cat (29.7 days—Bateson & Young, 1981; 31.6 days—Deag *et al.*, 1987, 1988), and coincides with a time of enzymatic change in the intestine (Elnif *et al.*, 1988; Oleinik & Svetchkina, 1992). Weaning of course marks only a stage in the development of independence. Mink kits are not completely nutritionally independent until eight (Rice, 1967) or even ten (Macdonald, 1984: 117) weeks old, and at ten weeks of age they still make distress calls if separated from their mothers (Houbak & Jøppeson, 1987; Jeppesen, 1988). In the wild (Macdonald, 1984: 117), or in large enclosures (Jonasen, 1987), the young do not begin to disperse from the natal territory until 12-16 weeks old, or even older (Mitchell, 1961; Gerell, 1970).

Kits from big litters were lighter when weaned, indicating that the amount of milk a female mink

can produce is limited, and only partially adjusted to litter size. This result resembles that found for cats (Deag *et al.*, 1988) and house mice (Fuchs, 1982; König & Markl, 1987), but differs from that in ground squirrels (Kenagy *et al.*, 1990).

That the timing of weaning is predicted by birthdate does not appear to have been found in any other species. The age at which mink kits were weaned was predicted neither by litter size, nor total litter weight, nor kit weight, unlike the species reviewed in the Introduction. However, litters born later in the season were significantly younger when weaned. This could be because mink are strictly seasonal breeders (Enders, 1952; Eagle & Whitman, 1987; Elofson *et al.*, 1989). They only mate during a period of a few weeks in the year, and furthermore, litters conceived late in the season have relatively short gestation periods (e.g. Enders, 1952) so that they are not born correspondingly late in the summer. This strict seasonal breeding probably indicates that in the wild there is only a narrow window in which it is optimal to rear young (e.g. Bronson, 1988). It is therefore perhaps unsurprising that offspring born late in the season reach or are encouraged to reach nutritional independence at an earlier age. Seasonal effects on weaning have been observed in bighorn sheep, where weaning is completed before times of rapidly declining food availability (Berger, 1979). It seems highly unlikely that anything directly comparable is happening in mink, as the young are weaned in June, when food is not in short supply. However, there might be selection pressures on the kits to be big, strong and independent by the winter, and on the mother to have recovered from lactation by this time. Seasonal effects on the rate of early development also occur in other species. In elephant seals, birthdate does not affect weaning age, but it does affect the age at which the young leave the rookery. Young born late in the season leave at a relatively young age, with the result that, although pups are born over an eight-week period, they all leave over the three-week period during which food is most abundant (Reiter *et al.*, 1978). Seasonal effects are also seen in microtine rodents, with young born early in the season growing and maturing particularly fast so that they can themselves breed that same year (reviewed Negus & Berger, 1988; see also Lee & Zucker, 1988). However, the seasonal nature of mink breeding rules out this possibility in this species. Likewise, the absence of post-partum oestrus means that the females are not hastening the independence of one litter in order to produce a second.

A final point raised by these results is that the pause in the growth of many mink litters brings into question the idea that the upturn in growth signals the time at which the mother is reducing her investment most rapidly. In litters where a pause occurs, disinvestment by the mother is presumably occurring when nursing is so reduced that the growth of the young is compromised. It might therefore be more appropriate to consider the first discontinuity in growth as the age of weaning, in these litters. However, the upturn in growth remains the time at which the young switch to relying on solid food.

Cessation of growth pre-weaning

A growth pause occurred prior to the change to solid food in approximately half the litters. It would be interesting to know how this pause was mediated; whether the females' milk dried up (see, e.g. Krackow, 1989), or they avoided their young, or they blocked attempts to suckle. For example, during the growth pause phase in the mouse, mothers spend less time with their litters (König & Markl, 1987), and in the pre-weaning period in the cat, mothers block access to their nipples (Martin, 1986).

The lack of significant effect of biomass of the litter suggests that the halt in growth is not simply the product of the mother's milk supply being over-stretched: litters with a high total demand were

no more likely to have growth pauses. If overall demand on the milk supply was not the important factor, one possibility is that whether there is a growth pause depended on some attribute of the mother, rather than of the litter as a whole. For one thing, maternal age was a reliable predictor of the occurrence of such a growth pause. However, in those litters in which the pause occurred, individual kit weight did then play a role. Why should heavy kits cease growing at an earlier age? It is possible that kits at a certain stage of development, in particular litters only, are voluntarily abstaining from suckling. However, although the young of some species do often wean themselves voluntarily (e.g. Thiels, Cramer & Alberts, 1988), it would seem unlikely in this case as the kits are evidently not compensating by eating enough solid food to grow. A second possibility is that mothers of a certain predisposition deny milk to their kits when they reach a certain stage of development.

The frequent coincidence of the growth pause with illness indicates that it may represent a time of vulnerability, perhaps to pathogens due to the immuno-suppressive effect of stress (e.g. Martin, 1989), or because the young are attempting to take solid food before their gut physiology is sufficiently developed to cope with it. That the pause is not itself the result of illness is suggested by the fact that growth cessation usually preceded signs of enteritis, and that in some cases there was a growth pause but no illness. If the pause in growth is imposed on the kits by the behaviour of their mothers, this raises the possibility that there is a conflict of interests between mother and young (Trivers, 1974) out of which the young do not always do well, the cost to them being an increased risk of disease, and, if male, a reduced body weight at weaning.

Sex differences

Like kittens (Deag *et al.*, 1987, 1988), male and female mink kits did not differ in their age at weaning. However, they did differ in weight. The sex difference in the kits' early development reflects their sexual dimorphism in adult size.³ Adult females are usually less than two-thirds the weight of males (Birks & Dunstone, 1985; Eagle & Whitman, 1987). The weight of a male kit while dependent on his mother predicts his weight as an adult, but the same is not true of females (Mason, 1992). If this is true in free-living mink, it suggests that parental investment probably has a greater effect on the fitness of sons than of daughters (cf., e.g. red deer; see Clutton-Brock, 1991), especially as the variance in the reproductive success of males is often greater than that of females (Trivers, 1972; Maynard-Smith, 1980; Clutton-Brock, 1991), and in mink themselves large males gain more mates than small ones (Macdonald, 1984: 117). It therefore makes sense for the female mink to supply her sons with adequate milk early in life.

The greater growth of males presumably results in a sex difference in milk demand, as is seen in many other species (e.g. Clutton-Brock, 1991). There are two possible reasons why the greater energy need of males may explain their greater tendency to have longer periods of arrested growth. One possibility is that some mothers selectively deny milk to their most demanding kits. However, there is little evidence from other mammals that mothers actively treat their sons and their daughters differently (Clutton-Brock, 1991), and, indeed, it is difficult to envisage how a mink could selectively suckle only part of her litter. The more likely reason is that the males' growth is more severely affected by reduced nutrition. To illustrate, although male juvenile woodrats

³ It is interesting that in some species sexual dimorphism in size emerges during the pre-weaning period, whereas in others it is deferred. The minks' sex difference in weight at this young age resembles that of, e.g. bighorn sheep (Hogg, Hass & Jenni, 1992), and contrasts with the situation in, e.g. mice (e.g. Krackow, 1989) and also cats (Deag *et al.*, 1987, 1988; although sex differences pre-weaning in this species have been reported elsewhere; Martin, 1986).

typically grow faster than females, male nestlings stop growing at a certain body mass if food-restricted, while the females are able to continue growing and become the heavier sex (Clutton-Brock, 1991, citing McClure, 1981). And for the male mink kit, as discussed above, this growth pause results in him being both significantly older and lighter at weaning than if he had not experienced this pause.

Maternal age

In the mink, the presence of the pause in kit growth distinguished primiparous from multiparous mothers, i.e. primiparous females seemed to supply milk more freely as the time of weaning approached. They also seemed more protective to their offspring, being less willing to leave them when disturbed. This finding does not meet the predictions of Trivers (1974). However, such findings may make functional sense if the primipares are unable to wean early without detriment to the young (Nicolson, 1987), for instance if their own body size already limits their milk production. An alternative, mechanistic, explanation is that primipares lactate for longer simply because they are less effective at weaning their young (Duncan *et al.*, 1984). The offspring of primiparous female mink also began relying on solid food earlier, but at the same weight, as multiparous females, i.e. their development was faster.

Summary

To summarize the most interesting findings, in the mink some litters experience a pause in growth before the transition to reliance on solid food. The evidence suggests that some mothers may deny milk to their young once they reach a certain stage of development, and that it is older mothers that are most likely to do this. The age differences in mothering-style found in mink are difficult to explain in terms of parent-offspring conflict theory. The accelerated development of the litters born latest in the season suggests that mink are breeding in a narrow optimum time window, but it is not clear what factors constrain their reproduction thus. The occurrence of the growth pause raises the difficulty of defining weaning in an empirically useful way, as in these litters the time at which the rate of parental investment falls most rapidly would seem to occur a few days before the kits' transition to a reliance on solid food.

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