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The Maternal Behaviour Cycle in Golden Hamsters (*Mesocricetus auratus*)

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With 11 figures

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Maternal behaviour in golden hamsters has been the subject of several studies (ROWELL 1960, 1961 a, 1961 b; LOTT 1962; NOIROT & RICHARDS 1966; RICHARDS 1966 a, 1966 b). Most of these have investigated the response to the presentation of pups placed outside the nest by the experimenter, analysing the functional relations between test behaviour and such variables as reproductive stage, hormonal state, age of test pups, and experiential variables.

DIETERLEN (1959) and ROWELL (1961 b) have described maternal behaviour in the absence of such tests, but little quantitative information has been published. ROWELL (1960) presented data for undisturbed mothers on a single measure, the time spent out of the nest. RICHARDS (1966 c) time-sampled behaviour during the oestrous cycle, pregnancy and pseudo-pregnancy, but not after parturition. In an unpublished investigation, SCOTT (1970) extended such time-sampling over the reproductive cycle. The present paper is primarily intended as a quantitative account of the changes in the mother's behaviour over the course of the entire reproductive cycle, in the absence of retrieval tests. While standardized pup retrieval tests have proved a valuable research method, they have necessarily failed to provide a complete picture of the successive stages of maternal activity and mother-pup interactions.

A further matter of interest is how maternal behaviour is influenced by conditions of laboratory maintenance. This problem has been approached in this study by comparing behaviour in cages to that in boxes providing the opportunity to burrow.

Methods

All animals were maintained in a single colony room under a reversed 12-12 light-dark cycle, and were housed in burrow boxes or cages. Burrow boxes consisted of two sheets of glass 5 cm apart enclosing a space 48 cm deep and 76 cm long, a wooden 'run' 76 cm × 13 cm × 13 cm at the surface, and a hinged mesh lid. The space between the glass was filled with an irregular mixture of topsoil, clay, peat moss and sand, which was tamped down hard before an animal was introduced, and which was moistened daily. The glass was covered with heavy opaque construction paper except during observations. Cages were of wire mesh, 23 cm × 46 cm × 38 cm, with sliding metal tray floors which were covered with sawdust.

All subjects were provided with shredded paper toweling as nest paper. The diet was ad lib Purina lab chow pellets with daily supplements of carrots, fresh greens and skim milk powder. Throughout pregnancy and lactation, these supplements were also provided in ad lib quantities.

Experimental animals were descended from the golden hamster breeding colony maintained by the Department of Zoology, University of Toronto. Ten litters were born and reared in the two experimental environments, five in cages and five in burrow boxes. Typically one cage mother and one burrow mother were rearing litters simultaneously. Four ♀♀ were observed in both conditions. In the fifth case, corresponding mothers in the two groups were littermates. In each group two of the five mothers were primiparous.

Observation

Behaviour recording was performed by an observer with a keyboard panel of 20 keys connected to programming equipment. The basic datum was the number of seconds in a recording interval during which the behaviour pattern in question was being performed.

All mothers were introduced into their home cage or burrow box at least 6 days before conception, and were observed for one 15 min trial each day for at least 4 days before mating and throughout pregnancy with the exception below. After parturition each mother was observed with her pups during two 15 min trials each day for 27 days. One trial preceded and one followed (by at least 1 hr) her daily removal from the home, at which time she remained in a holding cage while the pups were observed; she was then weighed and returned home with the day's food allotment.

On the 28th day post-partum, the pups were removed, and the mother was again observed alone for one 15 min trial daily from day 28 to day 32, with the following exception: one mother in each group (the first two run) was not observed before pregnancy or after weaning.

All observations were conducted during the first 5 hrs of darkness under the illumination of a 25 W red light bulb. The golden hamster is primarily nocturnal, and, unlike other common laboratory rodents, shows only a single peak in the activity cycle, early in the dark period (ASCHOFF and MEYER-LOHMANN 1954).

The behavioural categories scored were the following: lactation posture, nursing (defined by pup behaviour), rearing (both forefeet lifted from substrate), climbing (all feet clear of substrate), time in nest, sleeping, below ground, retrieving pups, digging, eating, licking pups, greeting and play-fighting with pups, urinating, defecating, yawning and stretching, grooming, nest-building, drinking, gnawing, and food-piling and hoarding.

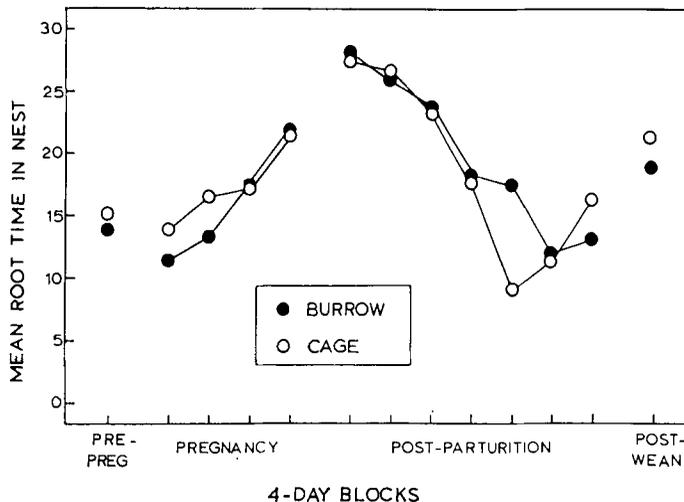


Fig. 1: Time in the nest

Results

Figs. 1 to 9 show the amount of time in which the mothers engaged in each of several activities. The data are grouped into 4-day blocks to damp out variability associated with the 4-day oestrous cycle and make trends more conspicuous. (Conveniently, the gestation period is a multiple of 4, namely 16 days.) As the distribution of scores for any pattern was typically positively skewed, a square root transformation was performed to render the distributions more nearly normal, and reduce the influence of atypical extreme scores. The maximum possible score is 30 which corresponds to a full trial of 900 sec. The data represent the mothers' behaviour during their most active hours.

As one mother in each group was not observed before pregnancy or after weaning, these data points represent only four animals each, whereas the others represent five. All data points for rearing and climbing (Fig. 7), pup-licking, and greeting and play-fighting (Fig. 9) represent four animals, because these activities were each combined with others for recording purposes in observing the first mother in each group, and only differentiated thereafter.

Fig. 10 presents a record of body weights, which were measured daily in all subjects and averaged over 4-day blocks.

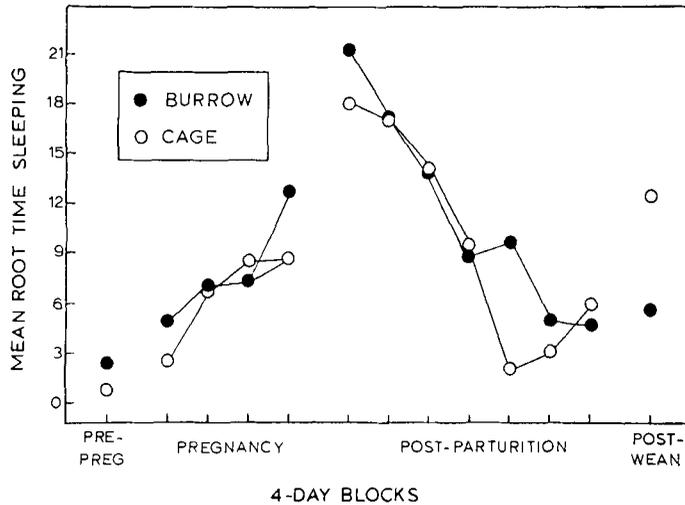


Fig. 2: Time sleeping

The significance of behavioural changes at impregnation, parturition, and weaning were assessed by comparing 4-day blocks before and after each of these events with F- and t-tests for correlated observations.

Upon impregnation, behaviour away from the nest changes. Similar sharp increases are evident in the gnawing of cage dwellers (Fig. 4) ($t = 3.23$, 3 df, $p < .05$), and the digging of burrow-dwellers (Fig. 3) ($t = 1.84$, 3 df, $p < .10$). The failure of this latter comparison to achieve significance deserves comment. The four ♀♀ for whom the comparison was possible were introduced into the burrow boxes 6, 9, 17 and 17 days before conception respectively. For the first two, digging scores were high both before and after mating, while in the others, digging declined before mating, and rose again the day after. Regular sketches

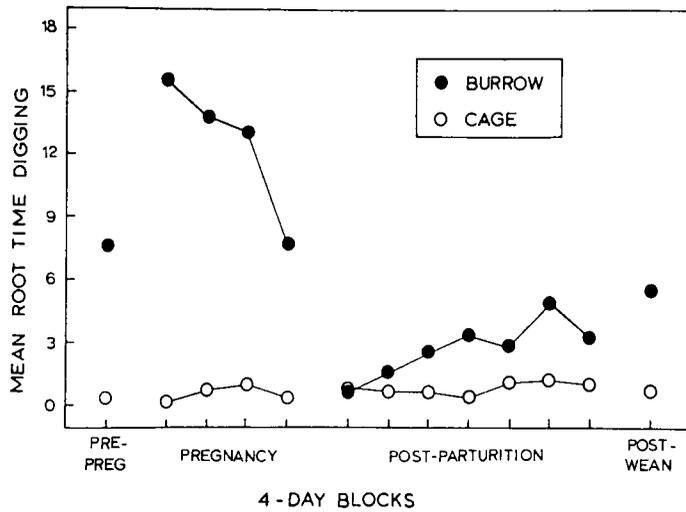


Fig. 3: Time digging

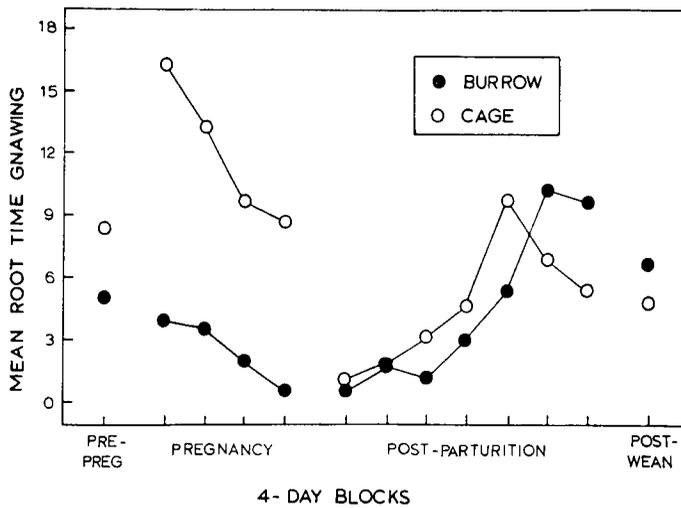


Fig. 4: Time gnawing

were made of the burrows. The records for these latter two ♀♀, the fifth ♀ in the experiment (for whom pre-pregnancy time-sampling data were not collected), and a pilot animal all clearly showed that modifications in burrow structure almost ceased after a few days in the box, but in every case resumed immediately upon conception, several completely new burrows being dug daily for at least the first few days.

Nest-building behaviour (Fig. 8) exhibits an abrupt increase near delivery (comparing the final two 4-day blocks in pregnancy, $F = 8.69$, 1,4 df, $p < .05$).

Post-parturition

Changes in behaviour at parturition are mostly continuous with changes over pregnancy. That is, trends observed through gestation continue into the

early post-partum period, except for a drop in grooming ($F = 8.25, 1,4 \text{ df}, p < .05$).

Changes in pup retrieval are presented in Fig. 11. Unsuccessful retrievals comprise both attempts thwarted by resistance from the pups, and intention movements which were arrested without such resistance. (A separate plotting of these two categories yields similar functions.) Intention retrieval is an ambivalent action which may involve two or three wavering little approaches and withdrawals, the mother opening her mouth just above the back of an oblivious pup, before she turns away. One mother regularly hopped toward the nest after incomplete and intention retrievals, with a movement similar to that used in actual carrying.

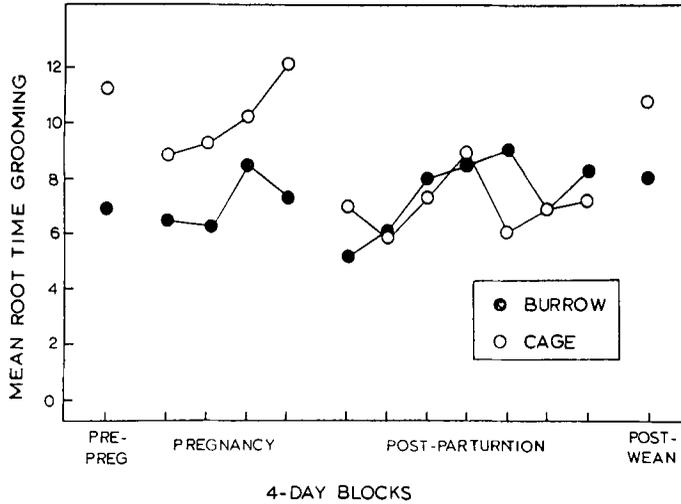


Fig. 5: Time grooming

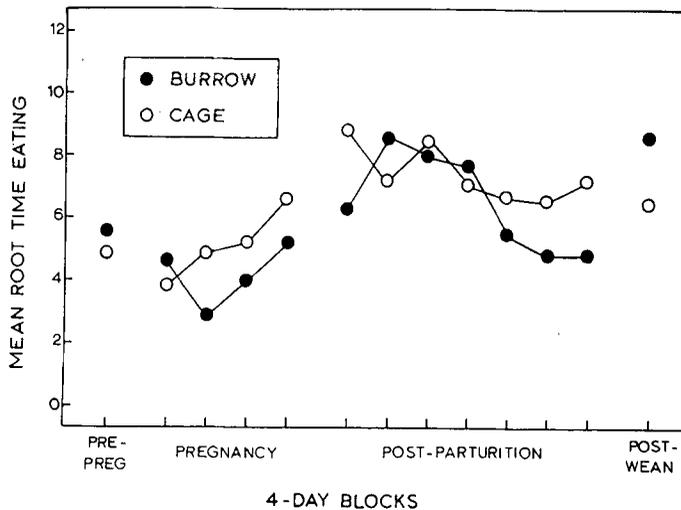


Fig. 6: Time eating

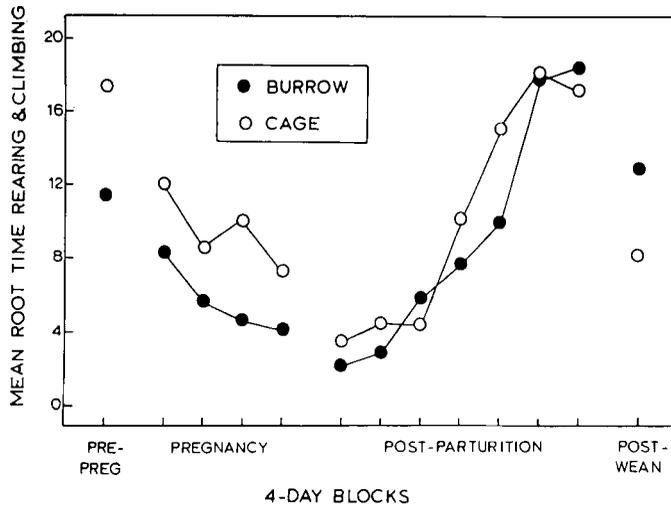


Fig. 7: Time rearing and climbing

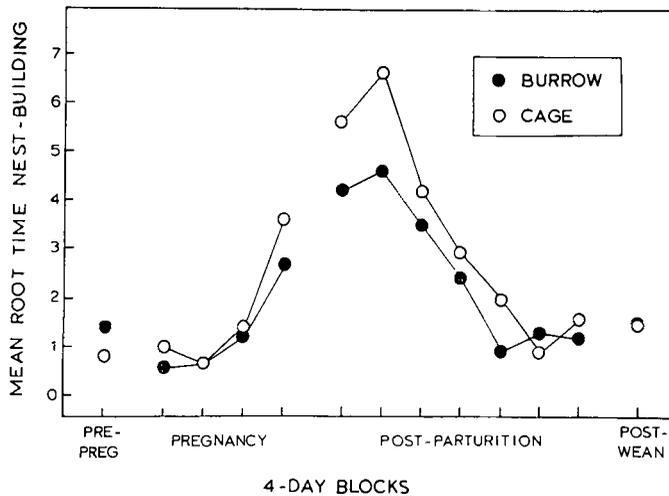


Fig. 8: Time nest-building

Retrieval may also be redirected to food objects. One ♀ habitually hoarded all food except greens, which she left scattered about the cage. On three occasions, this mother was observed to make an intention movement of retrieval over an unresisting pup, then, in a continuous motion, to scoop up a piece of spinach and carry it to the nest. After incomplete and intention retrievals, all mothers occasionally ran directly to the nest and embarked on a bout of food-piling.

Effects of environment

Of the behaviours measured, only digging showed a significant effect of experimental environment before pregnancy ($t = 3.19, 3 \text{ df}, p < .05$).

Fig. 9: Interactions with pups

During pregnancy, the most conspicuous differential effects were the above-noted changes in digging and gnawing. In addition, the caged group groomed more than the burrow-dwellers during gestation ($t = 4.18, 4 \text{ df}, p < .05$).

The weight gain during pregnancy was greater in the cage group ($t = 2.66, 4 \text{ df}, p < .05$). However, caged mothers maintained slightly higher ad lib weights before pregnancy (Fig. 10), and the difference is not significant when the gain is expressed as a percentage of body weight at conception.

The gradual shift after parturition from maternal activities to other behaviour is very similar in the two conditions, except for the data points representing days 17 to 20. Mothers spent considerably more time in the nest (Fig. 1) in the burrow condition than in the cages during this 4-day block ($t = 17.74, 4 \text{ df}, p < .001$). Effects of similar magnitude and significance are evident in sleeping and nursing (Figs. 2 and 9), but not in nest-building or pup-licking (Figs. 8 and 9).

Pup retrieval is strongly related to housing condition (Fig. 11). In the total observation of mothers with pups (67.5 hrs in each condition), 133 completed

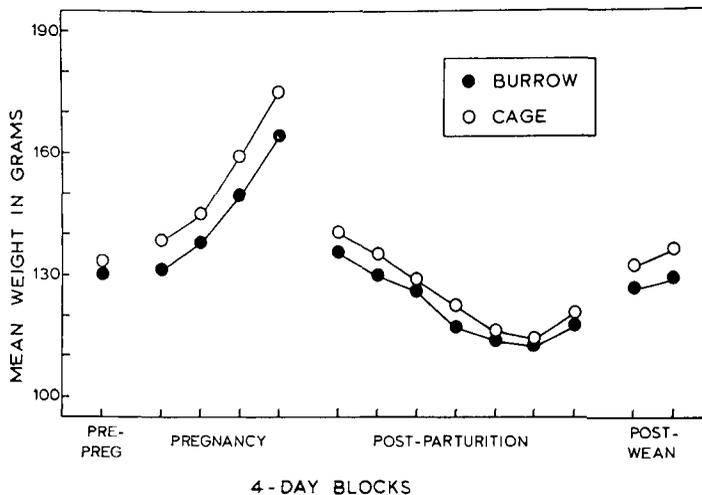
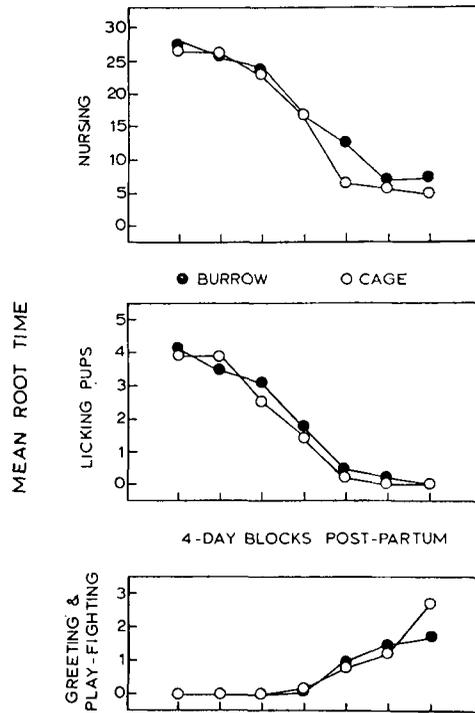


Fig. 10: Maternal body weights

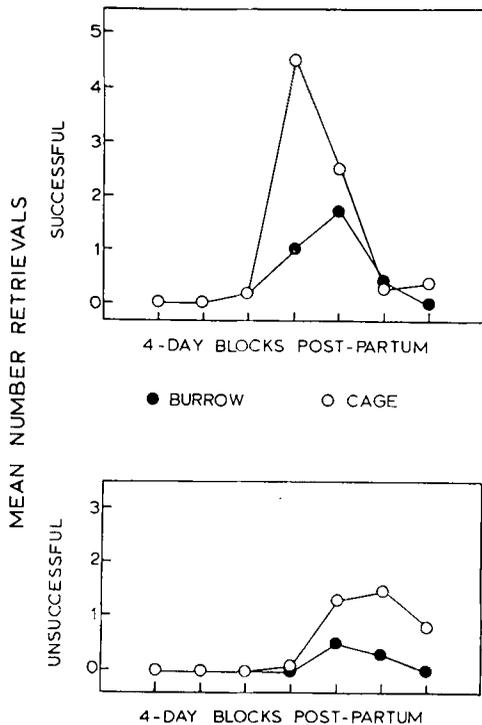


Fig. 11: Pup retrieval

retrievals were observed in burrow boxes and 299 in cages. Incomplete retrievals totalled 14 in burrows and 80 in cages; intention retrievals 19 in burrows and 53 in cages. In individual comparisons, successful and incomplete retrievals were more numerous in the cage for all mothers, and intention retrievals for four of five.

Discussion

Effects of pregnancy

The increase in gnawing by caged ♀♀ upon conception presumably reflects the same change in motivational state as does the renewed burrowing behaviour of the other group. Gnawing and digging are closely associated temporally;

chipping with the teeth is an integral part of digging in hard soil, and brief bouts of these two behaviours may be seen in regular alternation even in bare metal cages. FELLNER (1956) similarly interpreted a seasonal change in gnawing as indicative of burrowing inclination. RICHARDS (1966c) found that gnawing dropped between oestrous and the first day of pregnancy in his cage-dwelling hamsters, but rose to a maximum (some 45% of all observations) by the fourth day of pregnancy. SCOTT (1970), by contrast, found an immediate permanent decrease in gnawing upon conception, and a very rapid change to nest-based sedentariness.

The change observed here cannot be characterized as an increase in arousal or general activity. Rearing and climbing (Fig. 7) in fact showed a decline at conception; RICHARDS (1966c) similarly found that wheel running drops immediately after mating and continues to decline until parturition. The change is thus in the specific nature of the mother's activity. In all likelihood, pregnancy in nature triggers the excavation of a more extensive burrow in which to raise the young. (Wild rats are known to respond to pregnancy by burrowing, CALHOUN 1962.) It is of interest that this increased burrowing is a phenomenon distinct from the increase in nest-building which occurs later in pregnancy and can be explained by hormonal mechanisms (RICHARDS 1969).

RICHARDS (1966c) compared the first 8 days of pregnancy to the last 8 for several of these same behaviours. In general, his animals spent somewhat more time in their nests and in nest-related activities than the present subjects, but trends over pregnancy were similar, with the single exception that RICHARDS observed a small but significant decline in grooming over the gestation period. SCOTT (1970), by contrast, observed a steady increase in grooming during pregnancy, but the level throughout the gestation period was much lower than that before conception. The reasons for the discrepancies between studies remain obscure.

Effects of environment

The burrow vs. cage manipulation was only partially successful in that 'burrow mothers' did not typically rear their litters from birth below ground. Overzealous digging by certain ♀♀ resulted, in these confined circumstances, in repeated destruction of the burrows they dug. Furthermore, several ♀♀ were reluctant to move their nests below ground. (Hamsters maintained in terraria often establish nests on the surface, dig burrows later, and move below ground only after some days if at all, ROPARTZ 1963.) Four of five litters were born in surface nests. One of these was moved to a subterranean nest at 6 days post-partum. The other three all moved below ground about days 15 to 17. This move was at the initiative of the pups, whose eyes have just opened at this age, and was resisted by each mother for about a day.

Two striking effects of environment were evident in maternal behaviour: the much greater retrieval behaviour exhibited by cage mothers (Fig. 11), and their earlier cessation of brooding and nursing (Figs. 1 and 9) as indicated by the large difference at days 17 to 20.

The retrieval effect does not reflect any difference in the frequency with which pups left the nest. Animals in both cage and burrow show an increasing tendency to depart, beginning about day 11 when occasional sojourns to urinate are first seen. By about day 21, entire observation sessions may elapse in which the whole brood is never once assembled in the nest.

However, the burrow pups do not actually climb to the surface so early. In the sole instance where pups were reared from birth below ground, none was observed to reach the surface until day 18, nor were any retrievals observed before this. In a pilot experiment in which a single pup was reared in a burrow, he was first seen to attain the surface on day 21. This is at first clearly a matter of the young's capacity to climb away from the nest. The return is all downhill, without even an elevated nest edge to be surmounted, and self-return after a short excursion is usual.

The situation is quite the opposite in a cage. Here all the available material is piled up in a mound, with the nest depression scooped out of the top. Once a pup passes the lip of the nest wall, it is all downhill, whereas returning to the nest is difficult or even impossible for a young pup, who thus may wander about until retrieved.

The continuing strenuous efforts to retrieve older resisting pups by the cage mothers suggest that a major excitatory factor for retrieval is that the pup be 'exposed'. This is evident in the change over days of the circumstances under which the reaction is released. Whereas the cage mothers at first retrieved any pup who was detected out of the nest, soon pups remained unmolested as long as they stayed in the back of the cage near the solid metal rear wall. (All other walls were wire mesh.) This 'safe area' expanded until finally, in the last few days before the hamsters were separated, retrieval was initiated only when pups climbed the mesh walls, and they were ignored elsewhere.

The comparison of the two maternal environments suggests that retrieval is an emergency reaction, which is subject to an extreme unnatural overelicitation in the usual laboratory setting. Even the burrow scores are almost certainly inflated, since in those two cases where the nest was established below ground before the pups were walking, retrieval was far less frequent still.

The second major effect of environment, that the cage mothers virtually stop nursing and avoid the nest somewhat sooner than the burrow mothers,

may depend on any or all of the following factors. First, maternal care may be more taxing for the cage mothers, who alone showed a significant increase in sleeping after the young were removed. (Cage litters were non-significantly larger at 8.2 pups per litter vs. 6.8 in the burrows, and cage mothers lost non-significantly more weight during lactation.) Considering these data in conjunction with retrieval differences, one may hypothesize that maternity in the cage places exaggerated demands on the mother. Second, cage-reared pups may develop somewhat more rapidly since they were heavier at weaning. However, no such difference was evident at the time when maternal behaviour diverged in the two conditions, nor was there any evidence of a differential rate of behavioural development by pups (see DALY 1971 for details). Finally, the overelicitation of retrieval in the cage may inhibit the brooding activities characteristic of the previous stage; frequent agonistic interactions between mother and pup may accelerate the development of anti-social reactions in mother, young or both.

Summary

The maternal behaviour cycle of five golden hamsters was observed in standard laboratory cages, and in boxes where mothers could burrow. Time-sampling data were collected from before conception until after weaning in observation sessions in which the mothers and young were not disturbed.

Changes in the specific nature of the mothers' activity were evident at conception, as burrowing behaviour increased immediately. Nest-maintenance activity increased sharply shortly before delivery.

Mothers ceased nursing a few days earlier in the cages than in the burrows, and pup retrieval was much more frequent in the cages. Consideration of the circumstances releasing such retrieval led to the conclusion that this behaviour is excessively elicited in typical laboratory settings.

Zusammenfassung

Der mütterliche Verhaltenszyklus von je fünf Goldhamstern in normalen Laboratoriumskäfigen und in Terrarien, wo die Mütter Bauten graben konnten, wurde beobachtet, und zwar von der Zeit vor der Empfängnis bis nach der Entwöhnung und ohne Mütter und Jungen zu stören.

Das Verhalten verändert sich bei der Empfängnis; das Baugraben erhöht sich sofort. Der Nestbau nimmt kurz vor dem Wurf plötzlich zu.

In den Käfigen hörten die Mütter einige Tage früher als in den Bauten auf zu säugen. Eintragen der Jungen war in den Käfigen viel häufiger, weil es in den üblichen Laboratoriumssituationen übermäßig oft ausgelöst wird.

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