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Resource Partitioning During Reproduction in the Norway Rat

Abstract. *Rat pups nursed by pregnant dams grow as fast as pups reared by dams that are not pregnant. Moreover, litters that were in utero during a lactation are as numerous at birth and grow as fast as pups developing in a nonlactating, pregnant mother. These litters continue to grow as fast as pups born to nonlactating dams whether or not the first litter remains after the birth of the second litter. When pregnant and lactating dams have a restricted food supply, some dams are capable of extending the duration of their pregnancies by over 2 weeks past that of nonlactating, pregnant dams. This facultative prolongation of pregnancy apparently allows females to carry normal litters to term.*

Mothers should be expected to partition time and energy between themselves and their offspring in such a way that the number of potential descendants is maximized. In this report we describe the ability of dams to partition their energy resources between themselves and their offspring during a concurrent lactation and pregnancy.

Lactation demands enormous energy from mother rats (*1*) and, since rats can become impregnated during a postpartum estrus (*2*), the demands of a concurrent pregnancy may intensify the strain of lactation. In our study, we determined whether the dams that were both pregnant and lactating would pass less energy, as measured by pup weight, to either the litter they were nursing or to the junior litter in utero than if they were simply pregnant or lactating.

Eight primiparous Wistar rat mothers were impregnated on the evening after the dams gave birth. Each day, maternal body weight, senior litter pup weight, and maternal food intake were recorded between 0900 and 1200 hours. In addition, the duration of the postpartum pregnancy and the number and the daily weight change of the pups born in the junior litters were also recorded. These data were compared, where appropriate, to those obtained in a similar manner from groups of eight mothers that were either pregnant for the first time, lactating for the first time, or lactating for the second time in their lives (*3*).

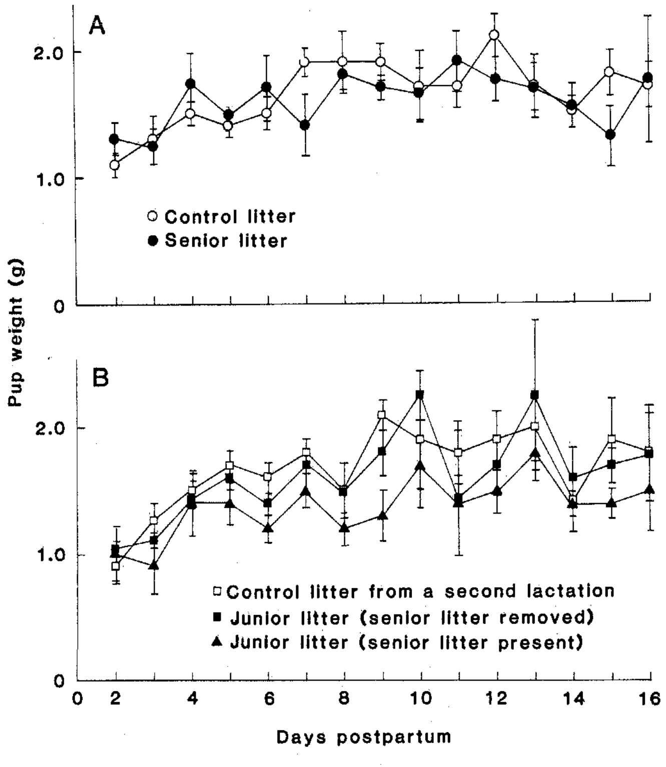

Fig. 1. (A) Mean daily change in individual pup weight of senior litter nursed by a pregnant dam compared to that of pups nursed by a nonpregnant mother (control). (B) Mean daily change in individual pup weight of junior litters nursed by dams with or without the senior litters present compared to dams rearing their second litters that were carried to term while the mothers were not lactating.

Senior litters of eight pups that were nursed by pregnant mothers grew as fast as pups reared by nonpregnant dams [$F(1, 18) = 0.57$, $P > .05$] (Fig. 1A). The number of pups born to pregnant and lactating dams were equal in number and weight to those born of nonlactating dams ($U = 31.5$, $P > .05$; $t = 1.04$, $P > .05$). Whether or not the senior litter was allowed to remain with the dam after she gave birth to the junior litter, the junior litter weight gain was not significantly less than pups raised by dams nursing pups in their second lactation (Fig. 1B) [$F(2, 25) = 3.20$, $P > .05$]. Mothers, therefore, can support the simultaneous normal growth of both senior and junior litters.

We considered the possibility that mothers could provide the resources to nurture junior litters with no apparent cost to senior litters by catabolizing their own tissues to supply energy to the young, as the dams do when their food supply is restricted (*4*). The change in body weights of dams that were pregnant and lactating, however, was no different from that of control pregnant females over the course of their pregnancy ($t = 0.54$, $P > .05$) or during the first 3 weeks of lactation without pregnancy ($t = 1.25$, $P > .05$).

Another mechanism that would allow dams to compensate for the additional energy required during a pregnancy accompanied by lactation would be an increase in food intake above that of lactating dams (*5*). Mothers that were pregnant and lactating, however, did not eat any more than mothers that were only lactating [$F(1, 18) = 0.91$; $P > .05$], at least during the first 16 days postpartum, which includes the period of peak milk production (*6*).

A third mechanism may postpone the investment of energy in the in utero litter until the lactational investment has peaked; resources previously directed to milk production could then be transferred to support the pregnancy. In our study, the time between impregnation and parturition was extended by about a week (Fig. 2). Previous studies have shown that rats have a delay in uterine implantation in a postpartum pregnancy and that this may be proportional to the size of the senior litter (*7*). While a delay in implantation of the junior litter delays the investment of energy to those pups, the milk output to the senior litter does not peak until after another week (6). During this week dams, without increasing their food intake or catabolizing their tissue, can nurture the litter in utero and nurse the senior litter normally. Dams may be using their food with increased efficiency. In fact, the elevated progesterone in mother rats (8) increases the efficiency of diet utilization (9).

While mother rats can compensate for the separate strains either of food restriction (4) or of concurrent pregnancy and lactation, it seemed unlikely that they could deal adequately with both simultaneously. It seemed more likely that either the senior litters would suffer from a decreased milk supply, or that the junior litters would be resorbed in utero, or both. In the next experiment, we determined the effect of food restriction on pregnant, lactating mothers and on their litters.

Sixteen mother rats were impregnated during their postpartum estrus. Eight dams were given free access to Purina Lab Chow (10) while the other eight were restricted to 25 g of the diet each day, an amount slightly more than virgin females normally eat. After 15 days postpartum, the restricted group was allowed to eat freely. Senior litters of eight pups were switched each day between a restricted and an unrestricted dam to ensure the equality of pup stimuli for these two groups of mothers. These litters were weaned at 25 days of age. Junior litters were not switched.

Diet restriction in pregnant, lactating dams proved to be a great strain. Although food-restricted dams lost a mean of 41.25 g during the first 15 days postpartum, compared to a gain of 44.29 g by unrestricted dams (t = 12.46; $P < .005$), the senior litters consistently gained less weight with the restricted dams ($\bar{X}$ gain per day per pup = 0.48 g) than pups with dams unrestricted in diet [$\bar{X}$ gain per day per pup = 1.61 g, $F(1, 14) = 16.64$; $P < .01$]. Moreover, 50 percent of the junior litters were resorbed before parturition, while all of the control dams gave birth. The 50 percent of food-restricted dams that did give birth had pups that weighed as much as those of unrestricted dams ($t = 0.68$, $P > .05$), and the number of live pups born to restricted dams ($\bar{X} = 10.5$) was no different from the number born to unrestricted dams ($\bar{X} = 12.5$; $U = 11$, $P > .05$).

For those mothers that succeeded in delivering normal offspring, the length of time between impregnation and parturition was prolonged ($\bar{X} = 37.0 \pm 0.4$ days) relative to pregnancies of nonlactating dams ($\bar{X} = 22.75 \pm 0.16$ days) or pregnant, lactating dams unrestricted in food ($\bar{X} = 27.0 \pm 0.76$ days; $U < 0$; $P < .01$) (Fig. 2).

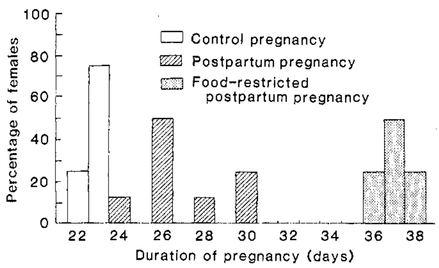

Fig. 2. The percentage of mothers giving birth at different times after conception.

Milk production, as we have noted, peaks on day 15 postpartum (7), and it was by just that period that the postpartum pregnancy was extended under conditions of food restriction, although in our experiment this period also coincided with the period of food deprivation.

It appears that rat dams may be using one of two mechanisms in this situation (i) The rate of growth of the litter in utero may be reduced, thus presumably necessitating less investment of limited resources in these offspring. (ii) Alternatively, implantation may be delayed in the food-restricted dams until after either the period of food deprivation ends or the period of peak milk production has passed. In either case, maximal competition for extremely limited energy resources between the dam and her two litters would be avoided.

The Norway rat, therefore, can use various mechanisms to ensure the success of reproduction: (i) an increase in food intake in response to increased suckling, (ii) the catabolism of maternal body tissue to increase available resources for milk production, (iii) possible increased efficiency in the use of food, and (iv) the facultative prolongation of postpartum pregnancies.

BARBARA WOODSIDE*
RUTH WILSON
PHYLLIS CHEE
MICHAEL LEON†

*Department of Psychology,
McMaster University,
Hamilton, Ontario, Canada L8S 4K1*

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* Present address: Department of Psychology, Concordia University, Montreal H4B 1R6.

† Present address: Department of Psychobiology, University of California, Irvine 92717.

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A Metric for Thought: A Comparison of P300 Latency and Reaction Time

Abstract. *We confirm that the latency of the P300 component of the human event-related potential is determined by processes involved in stimulus evaluation and categorization and is relatively independent of response selection and execution. Stimulus discriminability and stimulus-response compatibility were manipulated independently in an "additive-factors" design. Choice reaction time and P300 latency were obtained simultaneously for each trial. Although reaction time was affected by both discriminability and stimulus-response compatibility, P300 latency was affected only by stimulus discriminability.*

In his autobiography, Charles Darwin described his fall from the parapet of an old fortification: ". . . the height was only seven or eight feet. Nevertheless the number of thoughts which passed through my mind during this very short, but sudden and wholly unexpected fall, was astonishing, and seem hardly compatible with *what physiologists have, I believe, proved about each thought requiring quite an appreciable amount of time* . . ." [italics added] (1). Darwin was presumably referring to the work of his "friend and contemporary" (2), the Dutch physiologist F. C. Donders who, in 1868, described a technique he used to demonstrate that mental acts have measurable durations. Donders' method was based "on the idea that the time between stimulus and response is occupied by a