BRIEF REPORT

Non-Nurturent Functions of Mother-Young Interaction in the Agouti (*Dasyprocta punctata*)

BENNETT G. GALEF, JR.¹

Department of Psychology, McMaster University, Hamilton, Ontario, Canada

and

MERTICE M. CLARK

Department of Psychology, University of Toronto, Toronto, Ontario, Canada

Field observation of the interaction of the precocial young of the agouti (Dasyprocta punctata, a Neotropical rodent) with their dam suggests a number of adaptive functions of mother-young interaction not readily observed in either the species or situations normally employed in laboratory studies of maternal behavior. The presence of the agouti mother in the vicinity of the nest site provides protection for her young from predators and decreases the probability that the young will follow unrelated adult conspecifics away from the nest area. Trips taken together by mother and young during the first 2 weeks of pup life both define the area in which pups explore alone during the third and fourth weeks postpartum and provide the young with information concerning safe refuges in the vicinity of the nest. The similarity in state of development between neonatal agouti and the weanling young of altricial rodents suggests that the dams of altricial young may serve functions with respect to their offspring at weaning similar to those which agouti mothers serve with respect to their precocial young in the weeks immediately following parturition.

Psychological research on the maternal behavior of rodents has been concentrated on the interaction of altricial young and their dams in laboratory settings. Such research has been concerned, for the most part, with the

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description and analysis of the proximate causation (Lack, 1954) of maternal behaviors such as nursing, huddling, nest-building, and retrieval in which the dam serves obvious nurturent functions with respect to her offspring. Other aspects of maternal behavior, frequently described by field biologists, (see, for example, Eisenberg and Gould (1970) or Altman (1965)) in which the parturient female's actions do not serve evident nurturent functions with respect to her young, have received relatively little study. It seems probable that this difference in the relative attention paid by laboratory and field workers to the various facets of maternal behavior is not purely fortuitous. Because the neonates of altricial species are so clearly dependent on their dams for the provision of food, warmth, and shelter, attention of observers may have been directed to aspects of maternal behavior serving these functions rather than less prominent non-nurturent facets of mother-young interaction. Similarly, the study of maternal behavior in simplified laboratory settings, from which many of the selection pressures and complexities of the natural environment are excluded, may have made difficult the discovery and observation of non-nurturent functions of maternal behavior.

The present field study of the maternal behavior of the agouti (*Dasyprocta punctata*, a Neotropical, hystricomorph rodent) was undertaken to extend the range of environments and rodent species in which maternal behavior has been quantitatively described. Agoutis engage in maternal behavior under conditions particularly suitable for field observation. Their activity is largely diurnal (Smythe, 1970) and the interaction of agouti mother and young sometimes occurs exclusively on the surface and in plain view (Enders, 1935; Smythe, 1970). Although there are already available in the literature discussions of agouti maternal behavior (Crandall, 1964; Enders, 1931, 1935; Lemon and Weir, 1968; Roth-Kolar, 1957; Rowlands and Weir, 1974; Smythe, 1970; Weir, 1967), these are either purely descriptive, very fragmented, or based in large measure on the behavior of captive animals and, thus, do not provide a very strong data base for evaluation of hypothesized functions of the behaviors observed.

The present study was conducted on Barro Colorado Island, Canal Zone from June 24 to August 8, 1974 in the Allee Creek ravine immediately adjacent to the Smithsonian Tropical Research Institute field station.

The female, whose maternal behavior was observed, was the focal animal in a 7 month study of agouti behavior (Clark and Galef, in press). She was thoroughly habituated to the presence of humans in her vicinity.

Systematic observations were undertaken, conditions permitting, from 8 to 12 AM and from 1 to 6 PM, 6 days a week within the known home range of the mother (see Fig. 1). During the $6\frac{1}{2}$ weeks of the present study an observer was in contact with the focal animal's offspring for 172 hr. No observations were made during the fifth week of life of the pups.

Most observations were made from a distance of 6-10 m using 8X



Fig. 1. Study area. The heavy line indicates the southern boundary of the home range of the focal animal. The heavy dotted line surrounds the area of exploration by pups with their mother and the stippled area is that explored by the pups alone. The light dotted line in the northeast of the figure indicates the path of a single trip by mother and young outside the area in which all other joint trips occurred.

binoculars, though it was sometimes possible to approach to within 1 m of mother and young without disturbing a nursing bout or other ongoing activity.

The behavioral interaction of the dam and her young changed systematically with the maturation of the pups and, for purposes of exposition, has been described below in four phases. No mention is made of interaction of the young with male individuals or of maternal contact vocalizations because none were observed, though both have been reported by previous investigators (Roth-Kolar, 1957; Smythe, 1970).

Phase 1 (birth-2 weeks). We failed to observe delivery of the young. However, the mother-to-be had been observed alone for 3 hr on the day prior to our first sighting of her pups, and we, therefore, assumed they were born the preceding night. On the morning of June 24 we discovered a newly excavated hole in the face of a small rise atop which was located (at a distance of about 1 m from the hole) the mother's most frequently previously employed daytime rest-spot. The hole (10 cm in diameter, 0.5 m long, opening to a larger cavity at its distal end) was considerably too small for an adult agouti to enter or have constructed. During the first day postpartum, the pups were observed to nurse, groom, search in leaf litter (presumably for food), eat bits of solid food in the vicinity of the nest site, carry dead leaves into the nest cavity, and explore in the area of the nest site. This extreme precocity of the young agouti apparently precludes the need for parturient females to GALEF AND CLARK

engage in a variety of nurturent maternal behaviors (nest-building, transport, huddling over the young) obligatory in altricial species.

As can be seen in Fig. 2, during the first 2 weeks postpartum the female spent much of the day (59%) in the immediate vicinity of her pups and a relatively small proportion of this time (13%) nursing them. Pups spent much of the day in their nest cavity (45%) and most of the time they spent on the surface (91%) was during the time their mother was in their vicinity (see Fig. 3). As can be seen in Fig. 5, nest-building by pups, and play with the mother and the sibling (mother and pup centered activity) were most common during



Figs. 2-5. Frequency of observed patterns of behavior as a function of age of pups. The histograms indicate daily observations during the first week and the points weekly means: Fig. 2. Frequency of interaction of mother and pups and of nursing; Fig. 3. Frequency of pup visibility on the surface alone and with their mother; Fig. 4. Frequency of pup exploration alone and with mother; Fig. 5. Frequency of miscellaneous activities.

this period. Exploration by pups to distances greater than 2 m from the nest entrance were begun on Day 1 and were almost exclusively carried out in the presence of the mother (see Fig. 4). Such trips occupied 27% of the pups' time on the surface during the first 2 weeks of life. During these trips the pups would chirp (Eisenberg, 1974) constantly, frisky-hopping (Kleiman, 1974) about their sedately moving mother. If the mother encountered a hole in a tree or the ground she would sometimes stick her nose into it for a few seconds and the pups would typically enter the hole shortly thereafter. On three occasions the adult left the pups in such holes for an hour or more, while foraging alone, before returning with them to the nest site. Pups were not observed to enter the nest site after their mother stuck her nose into its entrance, as she did on four occasions.

During trips with her pups, the dam would occasionally stop to eat a piece of fruit she discovered. In 24 of the 25 occasions on which she did so, the pups attempted to snatch the food from her mouth, and in seven of these 24 cases the pups were clearly observed to ingest samples of the food. The adult rarely brought food to the nest site (17 occasions) and on only one occasion did a pup try to acquire it directly from her.

Phase 2 (Weeks 2-4). As can be seen in Fig. 2, there was a gradual decline in the amount of time the adult female spent with her pups, corresponding to the decreased time she spent resting in the vicinity of the nest-site (Fig. 5). The pups began to appear alone on the surface in the vicinity of the nest-site (Fig. 3) but still did not undertake exploration away from the nest site in the absence of their mother. Nest-building ceased, play was markedly reduced (see Fig. 5), and the chirp vocalization began to be replaced by a gentle "purr" which the pups emitted both when in contact with their dam and with each other. During the middle of the third week, the adult female escorted her pups to a new nest-site (n.s.₂, Fig. 1) 3 m from her second most frequently previously utilized daytime rest spot. This new nest was located on the surface under a clump of fallen bamboo. Neither mother nor young was observed to bring nesting material to the site.

Phase 3 (Week 6). The mother's attendance on the pups continued to decline (Fig. 5) while nursing remained at its previous frequency (Fig. 2) and thus consumed a steadily increasing proportion of the time mother and pups spent in contact. Trips away from the nest-site by the dam with her pups ceased as did her allogrooming of the young (Roth-Kolar, 1957), while the pups began to undertake extended explorations on their own (Fig. 4).

Phase 4 (Week 7). Mother-young interaction continued at a low level. The adult female began to attack her pups (five observations) when she encountered them exploring independently at a feeding site, but continued to nurse them and behave amicably toward them during brief periods of interaction elsewhere. The pups in turn, began actively to avoid their mother at feeding locations (three observations), leaving a feeding site as their mother

approached it. In the middle of the 8th week the pups disappeared from the home range of their mother and were seen only twice, still together, in the following 5 months.

As is clear from inspection of Figs. 2 and 5, the parturient female spent more than 50% of the daylight hours in the immediate vicinity of her pups and less than 10% of this time nursing and allogrooming them. The question of particular interest to us concerns the possible functions of the mother's attendance on her pups during the extensive periods of time she spent in contact with them during the first weeks postpartum, but during which she did not engage in any obvious nurturent activities.

The fact that the 1 and 2 week old pups seldom emerged from their nest site in the absence of their mother suggests that she provided security on the surface for her neonatal young. Our observations indicated that this security was of two kinds. First, the mother's presence provided the young with a degree of protection from predators. On two occasions she was observed to drive tayra (Eira barbara), large weasel-like animals, from the vicinity of the nest-site. Similarly, Smythe (1970) has reported that recently parturient agouti drive predatory coati (Nasna narica) from the vicinity of their young. Second, during the time the maternal adult was present in the vicinity of the nest-site other adult agouti kept at a distance. In her absence these strangers would occasionally walk close by the nest entrance and when the pups were three or more weeks of age and active alone on the surface, they showed a strong tendency to follow these strangers off into the brush for distances up to 30 or 40 m. It seems likely that the mother's presence at the nest-site, in conjunction with the reluctance of the pups to emerge in her absence, served to decrease the probability that the pups would be lost as a result of following disinterested conspecifics from the nest area at a time when the young did not know the route back to the nest-site. Kleiman (1972) has suggested a similar function for maternal presence in the closely related acouchi (Mvoprocta pratti).

The observation that the pups did not explore away from the nest-site on their own during the first month of life and that during this period they spent considerable time (710 min) traveling with their mother suggests that these trips may have served to familarize the pups with the area in which they were living. As can be seen in Fig. 1, the area in which pups explored on their own (226 min in Weeks 6-7) was completely contained within the area they had been observed to travel with their dam. Thus the experience of traveling with the dam had a marked effect on independent exploration by the pups, restricting their activity to specific portions of the environment. The experience of the pups in entering holes pointed to by their dam, similarly, affected their independent behavior. This phenomenon was particularly striking in the case of a piece of pipe lodged at a 15° angle in the ground, the accesible end of which was 20 cm from ground level. The dam introduced the pups to this opening in the usual way and, after a considerable struggle, the larger pup entered it; the smaller pup attempted to do so several times but failed. Two days later, while exploring with its mother, the larger pup entered the pipe directly after being chased briefly by a strange adult agouti. Thus, pups appeared to learn of the existence of safe hiding spots as a result of interaction with their dam.

It has been previously suggested that the food snatching by agouti pups from their dam, in addition to providing the pups with food, serves to familiarize them with edible substances available within the area in which they live (Roth-Kolar, 1957). We, however, saw no evidence that ingestion of mother-introduced foodstuffs had any particular influence on the direct acquisition of food by the pups. To the contrary, we observed pups ingesting substances not ingested by their dam (roots and bark) from the first day of life.

In summary, our observations suggested that the major functions of the time spent by the focal adult female with her young were to provide them with increased security while above ground and to familiarize them with the area about the nest-site. The consequence of exploration by the pups with their dam was to restrict their movement, during the second month of life, to the area they visited with her during the first month and to make known to the pups places of safety near the nest-site.

Although observations of the interaction of a single agouti female and her young are obviously not sufficient to provide strong evidence of nonnurturent functions of mother-young interaction, we would suggest that they may provide a useful heuristic for the identification of phenomena to be investigated in greater depth under controlled circumstances. In particular, the fact that newborn agouti are of a comparable stage of development to weanling altricial rodents suggests that the functions served by agouti dams with respect to their neonates may be similar to those served by the dams of altricial young at the time of weaning of their offspring. For example, the tendency of young wild rats to follow their mothers on initial explorations away from the nest-site (Calhoun, 1962) and to restrict their movement to the home range of their clan (Telle, 1966; Galef and Heiber, in press) may represent the results of processes similar to those reported here in agouti.

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