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# A Behavioral Taxonomy[1] for *Macaca nemestrina* and *Macaca radiata*: Based on Longitudinal Observation of Family Groups in the Laboratory

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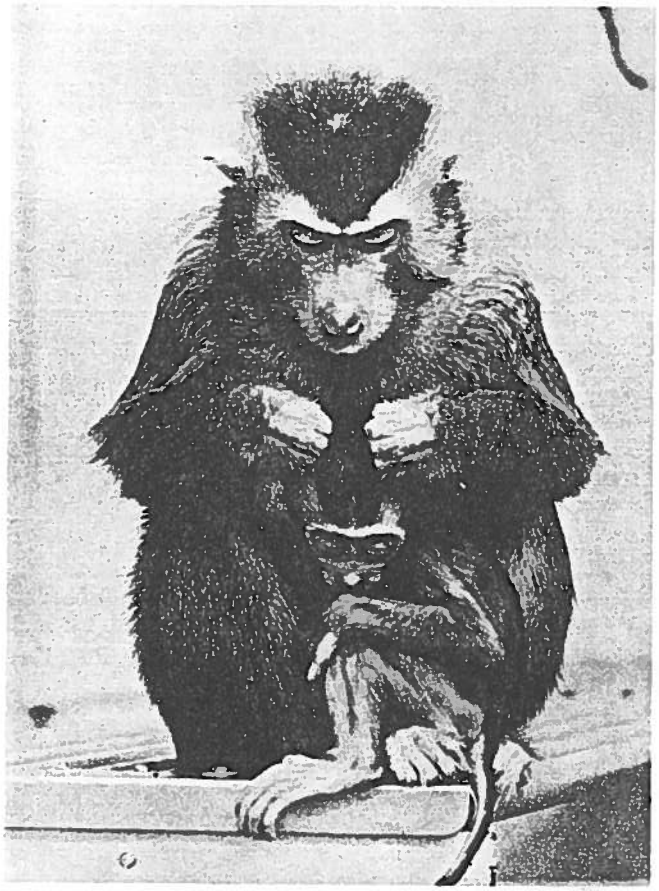


*Social grooming* of a young infant by a pigtail mother. The infant is showing a *Passive response-to-grooming*.

## INTRODUCTION

In order to formulate theories for ordering behavior into motivational or functional schemata it is first necessary to describe empirically the units of behavior themselves and the contexts in which they arise. Indeed, the elemental processes of description and subsequent classification in the field of behavioral analysis should of necessity parallel similar courses followed in the physical sciences and other branches of the life sciences, such as anatomy and physiology. Even though the ultimate goals of the researcher in behavioral science may be the experimental manipulation and subsequent understanding of behavior at varying degrees of abstraction, for such conceptualizations and hypotheses to provide broadly meaningful conclusions they inevitably must be founded upon the measurement of behavior at far lower levels of abstraction and at minimal levels of interpretive ambiguity. The present paper is an initial attempt to provide this sort of description of the population of social and nonsocial behaviors observed in two species of macaque, pigtails (*Macaca nemestrina*) and bonnets (*Macaca radiata*), under specifiable laboratory conditions.

### Background

In conjunction with a broad program of study of social behavior and its development in nonhuman primates during the past three and a half years, nearly fifteen hundred hours of systematic observations of groups of pigtail and bonnet monkeys have taken place in our laboratory. Since the study of the young and their development was among our primary concerns, we sought to maximize the breeding potentials of our groups by composing them originally (1961) of one adult male, four adult females, and one male and one female adolescent. This basic seven member group was roughly in keeping with sex ratios described for feral rhesus macaques. Each was placed in a pen approximately $8' \times 12'$ and $7'$ high to provide ample room for locomotion and heterogeneous social interactions. All observations were made through large one-way vision screens set into the front wall to minimize external distractions and the subtle effects of the presence of human observers, which may influence behavioral expression even after long periods of observation. To add the important analytic tool provided by a comparative approach, and to gain some understanding of the stability and generality of patterns within the genus, as well as their stability in different groups within the same species, two such basic groups were formed for each of the two species.

With a view towards ultimately determining the influences of controlled intervention on the course of normal development, e.g., by experimental separation of mother and young, we became impressed with the need for an inventory of definable elements of behavior which could be observed in a laboratory situation such as ours, in a form suitable for accurate and reliable notation. A catalogue of this sort

was needed since it was anticipated that the interweaving of specific circumscribed elements of the animal's behavior would provide the fabric of normative development, against which the effects of subsequent experimental manipulation, measured in the same structured terms, could be evaluated.

Unfortunately, no catalogue was available for either the bonnet or pigtail. In the early development of this catalogue in 1961 we were guided by the previous experience of one of us (ROSENBLUM 1961) in taxonomic formulations of the behavior of a related species, the rhesus, as well as by the prior rhesus catalogue of CHANCE (1956). (Since that time several other rhesus catalogues have appeared. See Index.) Naturally we were also guided by the many separate descriptions of particular behaviors of various primates reported by numerous observers. These various sources provided our earliest catalogue of behaviors to observe. As we noticed new behaviors these were added. Often behaviors were subdivided or combined as categories were defined. We made an effort to retain previously described terms unless they seemed not quite exact or appropriate enough, or could not be rendered into the nominative form we chose, traditionally used by dictionaries. We tried to provide an exact description of each behavior and a title that would embody the description. In this effort we are indebted to all previous reporters even if we did not always retain their descriptive titles.

The structure of our taxonomic scheme was also affected by our research goals and by the system of observation and notation which we decided to utilize in order to achieve them. Since we were embarked upon an area in which experimental procedures could have a variety of diverse and perhaps subtle effects, it appeared necessary to establish our norms for behavior and its development in as multidimensional a fashion as was possible. Inasmuch as behavioral events occur with a certain repetitiveness, last for varying intervals at each occurrence, seem to be sequentially ordered, and are directed at the self or other objects of the physical or social environment, and since our experimental procedures might produce effects reflected in any one or more of these measures, we selected a system which could provide the frequency, duration and object of each behavior, as well as the sequence of behaviors for a given animal and, to a limited extent, the interaction between animals. The system we chose was to observe in succession each animal in the group for a specified period of time, while simultaneously and continuously dictating onto tape the beginning and end of every observed behavior, as well as the object(s) of each behavior.[2] This system of dictation, in addition to providing unambiguous quantitative data, also provided the necessary immediate flexibility for expansion of the behavioral catalogue as new behaviors appeared in the course of development.

## Purpose

It is intended that the current work present a detailed blueprint of the structure of behavior in two congeneric species of monkey. It is hoped that the descriptions

and illustrations will serve as a useful guide to investigators interested in carrying out research on the behavior of these and related species by providing them with an initial focus on behaviors of significance, their discriminable elements, and the relevant contexts in which they fall.[3] Similarly, it is hoped that the careful delineation of these varied patterns may also be helpful in the selection of appropriate behaviors as dependent variables whose changes would indicate the effects of diverse experimental interventions.

In addition to simply providing a descriptive listing of the behavioral items which we have observed, we have also attempted a tentative grouping of behaviors under a series of headings. We would have preferred a categorization based on a single aspect of behavior, e.g., motivation, but in our present state of knowledge such an attainment is still beyond our grasp. Rather, the groupings were established through the use of several criteria which are often intersecting. In some cases, for example, the categorization was based on functional characteristics, as in "BEHAVIORS CONCERNED WITH BODY FUNCTION AND CARE"; in others it was based on the identity of the actor, as in "MATERNAL BEHAVIORS." Similarly, within each broad heading[4] an attempt has been made to place the behaviors into what seemed to be coordinate sub-groups, again by means of several organizing criteria. For example, "HIERARCHICAL BEHAVIORS" was subdivided into "Manifestations of Dominance, Subordinance and Ambivalence," whereas "SEXUAL BEHAVIORS" was subdivided into "Autosexual, Heterosexual and Homosexual." As a result of this multidimensional and intersecting classification scheme it will be noted that some behaviors appear under several different headings of relevance, e.g., maternal protective behaviors appear in the "MATERNAL BEHAVIORS" category and also in the "HIERARCHICAL BEHAVIORS" grouping. Where this occurs the definition appears in the category of putative primary relevance.

One additional purpose which the current paper should serve is to provide a structure and some initial substance for the comparison of the behavioral repertoires of these two species with each other and with other well-observed species. It is our belief that only through detailed study of a variety of forms, under closely comparable and carefully described conditions, can some insight be gained into the problems of phylogenetic comparisons of behavior. If we are to generate hypotheses at one phylogenetic level which will be meaningful to adapt and test at other markedly disparate levels, we must gain some understanding of the degree of generality of behavioral patterning between closely related forms, as well, of course, as of the differences. For example, whereas adult "ASSOCIATIVE BEHAVIORS" may take somewhat different forms in the two species we have studied, other patterns, such as those of maternal support, are quite similar in the two. The causes and functions of these similarities and differences must be studied further. Such comparisons will not only underline the inadvisability of indis-

criminate cross phylum generalizations, but equally importantly, point to areas of essential stability of patterning in particular segments of behavior.

## Special Features

The point must be made that the current work represents a start rather than a finished attempt at formulating a behavioral taxonomy for these species. Growing out of a special research setting, the current work has a number of particular limitations. As was alluded to above, our special concern with the development of the young and in particular the interaction of mother and infant, led to a considerably greater discreteness of categorization of behaviors within those areas. Those interested in sexual or exploratory behavior, for example, may find that though a number of categories covering these areas have been included, they are too gross to serve beyond the role of initial guidelines. Similarly, those investigators who are becoming increasingly concerned with the importance of the inclusion and variation of the discrete elements in certain larger gestures, such as the variability of ear or lip movements during expression of the *Threat* pattern, may feel that our need to directly observe and continuously record a very wide variety of ongoing behaviors has left the taxonomy wanting in regard of this detailed precision. Despite the deficiencies of the current catalogue in this matter, we recognize that the delineation of these fractional components and the conditions which regulate their presence is essential to the ultimate understanding of behavior in any species, and that the inclusion of such elements will be necessary for what we trust will be the increasingly precise taxonomies of the future. It is likely that the increased use of film and video tape recording techniques will, through their potential altering of time axes, allow for the detailed description of these components and their ultimate use in general behavior observations. In the same manner, it is undoubtedly of importance to replace eventually the crude onomatopoeic devices used to differentiate vocalization patterns by detailed recording and spectrographic analysis. An additional deficiency of this taxonomy clearly derives from the fact that many behaviors which are a normal part of the behavioral repertoire of these species are undoubtedly absent from the present taxonomy because the specific conditions of captivity did not allow for their appearance. Behaviors relating to inter-group confrontations and foraging behavior, to name several conspicuous examples, are types of behavior not elicited in our laboratory and thus lost to the present catalogue. It is hoped that as field studies of the behavior of these species appear, an elaboration of the present catalogue will be made both in terms of the behaviors described and their widened significance in the feral state.

Finally, in an attempt to place the current taxonomy into some perspective regarding similar efforts of this kind by others, which are based primarily on rhesus (*Macaca mulatta*) behavior, we have included in the index cross references for each behavior we describe to these other extensive primate behavior catalogues. The

utilization of this index will enable the reader to determine the corresponding names for similar and related behaviors used by the authors of these other catalogues, as well as the category groupings and differentiations which they have employed. We restricted our efforts at cross referencing to other relatively comprehensive catalogues.

*Notes:*

1. The research upon which this taxonomy was based was supported by USPHS Grant #MH04670. The authors wish to thank A.J. Stynes, W.I. Barnett and Dr. T.S. Nathan for their invaluable assistance and suggestions in this work.

2. The behaviors which serve as the actual units of our observational system appear in italics in the accompanying taxonomy. For dictation purposes each such behavior has a code name and each animal has a number. Thus, "2-1 socex" means that animal 2 performs the behavior *Social exploration* to animal 1; "2-1 socex stop" means that animal 2 stops the behavior *Social exploration* to animal 1. Since the tape runs continuously in parallel with an electric clock, when the tape is played back with the clock the start and stop of each behavior is marked to the second. This allows each desired dimension of behavior to be included in the data transcript. When this data is punched on cards for computation purposes each behavior is otherwise coded, in a 3 letter system. For a more detailed description of the system, as well as an example of the data obtained, see ROSENBLUM, KAUFMAN & STYNES (1964) or ROSENBLUM, KAUFMAN & STYNES (1965).
3. Information concerning behavioral contexts, sex and species differences have been appended to each definition in the taxonomy whenever adequate data was available.
4. The major headings and many of the subheadings in the taxonomy are essentially generic in nature and are included for heuristic purposes. Since these do not identify discrete observable behaviors they are not italicized.

## TAXONOMY

## HIERARCHICAL BEHAVIORS

### I. Dominance Manifestation

(This category includes those activities directed against another animal which cause physical insult, effect withdrawal, or otherwise intimidate the other, thereby securing immediate and/or facilitating subsequent advantage, i.e., establishing and stabilizing dominance relations.)

A. *Attack*

(Any act which causes physical insult to another animal.)

1. *Bite*

Common usage.

(This behavior is involved in high intensity aggressive encounters.)

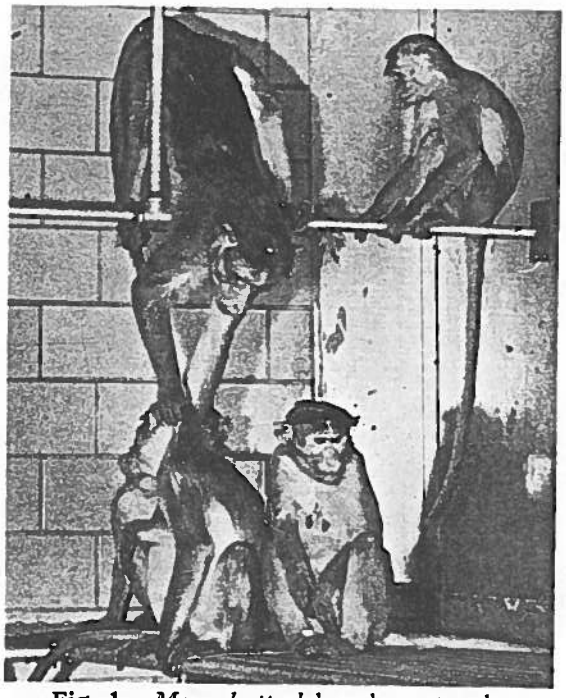


**Fig. 1.** *Manual attack* by a bonnet male.

2. *Manual attack* (See Fig. 1)
   The use of one or both hands for grabbing and pulling the fur, striking, pushing, and/or restraining the motion of another animal, rarely causing serious injury.
   (*Manual attack* appears both contextually and consequentially to reflect a lower attack tendency than *Bite*.)

B. *Pursuit*
   Vigorous chasing of another animal while showing repeated *Threat(s)* (see below) and invariable attacks of the opponent upon capture. *Pursuit* is sometimes abruptly terminated as soon as the other animal flees.

C. *Intimidation*
   1. *Threat* (See Figs. 2a, 2b)
      A varied communicative pattern which may include opening of the mouth with exposure of the teeth, thrusting the head forward, flattening the ears against the head and retracting the brow; the body is generally held stiff and upright and is thrust forward.
      (When this behavior elicits Subordinance it generally is not followed by Attack.)

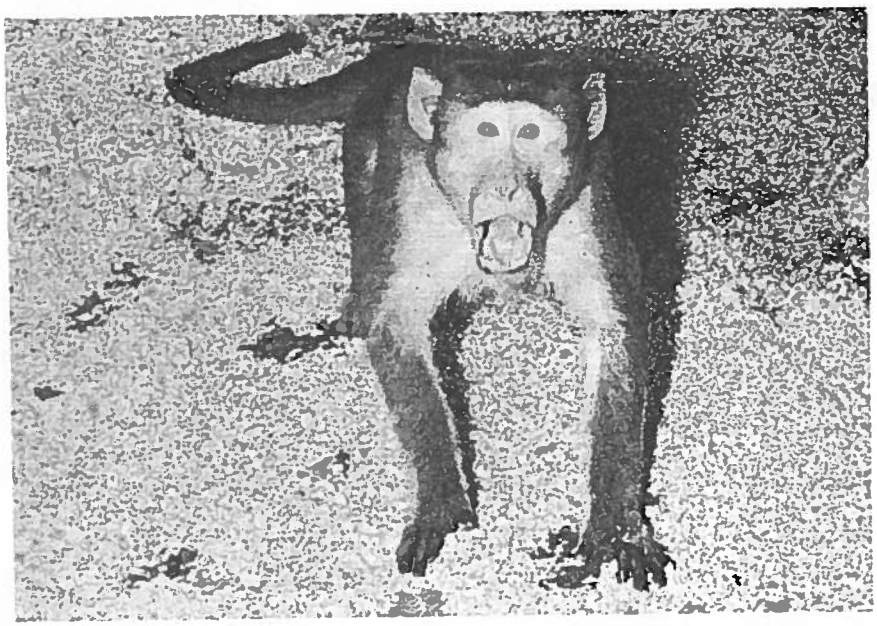


**Fig. 2a.** A *Threat* of relatively high intensity by a bonnet male.

**Fig. 2b.** A low level, hesitant *Threat* by the same male.

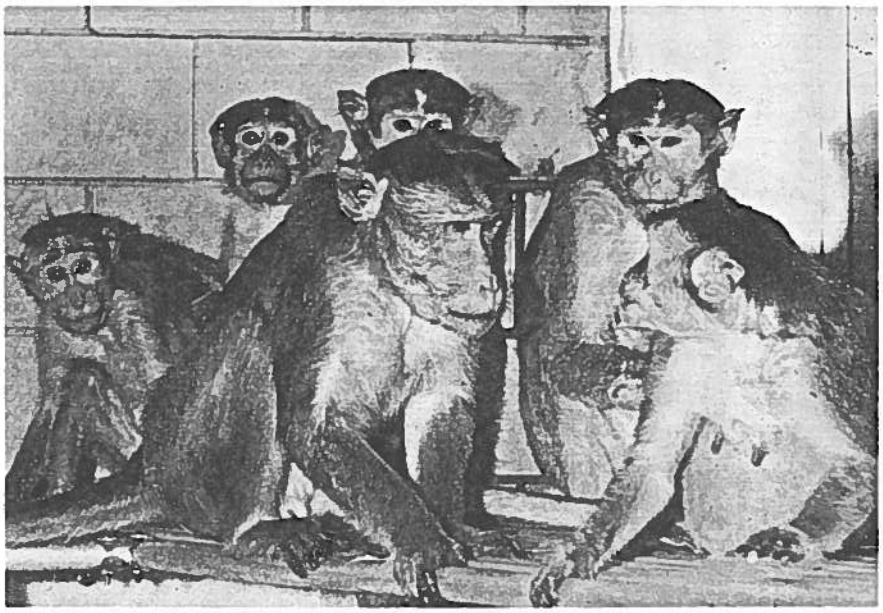


**Fig. 3.** A *Stare* by the same male, resulting in a *Crouch* by a pregnant bonnet female.

2. *Stare* (See Fig. 3)
   Intense visual fixation of another animal, frequently catching its gaze for several seconds. The head is generally held slightly forward and the brow protruded.
   (When this behavior is directed at a subordinate it will usually result in *Withdrawal* or *Grimace* in the latter.)
3. *Brow movement*
   Slow or rapid retraction of the scalp and brow, often with accompanying ear movements.
   (These movements appearing alone seem to represent a low intensity threat. Movements of the scalp, brow, and ears frequently precede and then become part of the *Clonic jaw movement* and *Jaw thrust* or of the full *Threat* pattern.)
4. "*Gugu*"
   A sound similar to *Gugugugu* (see p. 252) but with the forcefulness of the expulsion of air increased, the length of each burst markedly shortened, and with a consequent increase in huskiness.
   (This sound is heard only in adults.)
5. *Threat shake*
   Violent, repetitive shaking of parts of the environment, e.g., the shelves of the room (or the branches of a tree), producing a loud clatter.

(This behavior is generally seen in males and seems to serve a threatening function.)

D. *Assertion*
   1. *Positioning* (See SEXUAL BEHAVIORS)
   2. *Mount* (See SEXUAL BEHAVIORS)
   3. *Take-away*
      a. *Inanimate-object take-away* (See INANIMATE-OBJECT-DIRECTED BEHAVIORS)
      b. *Infant take-away*
         Gentle taking possession of an infant away from his mother, usually not from her ventral surface. (An adult bonnet male has been observed to actively remove infants repeatedly from their mothers, following which he has cradled them or played with them.)
   4. *Approach* (See ASSOCIATIVE BEHAVIORS)

E. *Descending-hierarchical-aggression*
   The continuation of dominance behavior down the hierarchy, i.e., animal A manifests dominance over animal B, who shows little or no direct response to A, but turns on animal C in a similar fashion.

## II. Subordinance Manifestation

(This category includes those behaviors which communicate or demonstrate an acknowledgement or acceptance of another animal's dominance.)

A. *Acute*
   1. *Defensive aggression*
      Hesitant and tentative retaliatory attacks by an animal under attack.
   2. *Rigid response-to-grooming* (See ASSOCIATIVE BEHAVIORS)
   3. *Withdrawal*
      A movement of at least twelve inches, in a deliberate manner, away from a partner in response to the latter's initiation of some social act.
   4. *Flight*
      Rapid and generally undirected withdrawal from another animal.
   5. *Present* (See SEXUAL BEHAVIORS)
   6. "*Eeeh*"
      An exceptionally loud, high pitched and repetitive scream. (It is apparently unique to bonnet males. This behavior was first observed when an adult female was removed from a bonnet group for medical treatment. The adult male lunged forward with considerable piloerection of the fur of the back and neck, emitting this sound repeatedly, We have heard this sound on numerous occasions whenever other animals have been handled within his visual field.)

7. *Grimace* (See BEHAVIORS REFLECTING EMOTIONAL DISTURBANCE)
8. *Lip smacking*
   Rapid opening and closing of the pursed lips, probably accompanied by tongue motions, producing a soft clicking sound, similar to the "tsk-tsk" sound produced by humans. (This behavior is frequently placating or submissive and is generally accompanied by such behaviors as Present, *Crouch*, and *Withdrawal*.)
9. *Crouch* (See BEHAVIORS REFLECTING EMOTIONAL DISTURBANCE)
10. *Communication avoidance*
    The seemingly intentional avoidance of potential visual communication by another animal, e.g., the avoidance of eye contact which might otherwise elicit *Threat* or attack behavior. (Our observations suggest that the failure to receive a communication often obviates the need to respond to it appropriately.)
11. *Raised tail* (See BEHAVIORS REFLECTING EMOTIONAL DISTURBANCE)

B. *Chronic*

1. *Check*
   Visual location of another animal and determination of its activities, by rapid, frequently repeated turning of the head in the direction of the other. (It is performed under a number of circumstances, e.g., by a mother with respect to her separated infant, and by a subordinate animal with respect to a more dominant one.)
2. *Watch*
   Prolonged observation of another animal's location and activity.
3. *Rigidity* (See BEHAVIORS REFLECTING EMOTIONAL DISTURBANCE)
4. *Distance keeping*
   Maintenance of a minimum distance from another animal for prolonged periods. This occurs in the absence of overt behavior by the other animal towards the subject. (This complex behavior is characterized by constant vigilance (See *Check*) and a variety of locomotor techniques. What distinguishes this pattern is not the movements involved per se but the directiveness with which it is organized.)

## III. Ambivalence Manifestation

(This category includes those behaviors in which neither dominance nor subordinance is clearly expressed.)

A. *Competitive inanimate-object interest* (See INANIMATE-OBJECT-DIRECTED BEHAVIORS)

B. *Inanimate-object protection* (See INANIMATE-OBJECT-DIRECTED BEHAVIORS)

C. *Embrace* (See Fig. 26)

A mutual ventral-ventral embrace generally in the sitting position. It is usually accompanied by *Lip smacking* on the part of both partners, and frequently by kneading of the partner's flesh.

(This behavior is generally seen between females and usually appears to reflect a temporary state of dominance equivalence. It generally occurs on occasions when the stability of the dominance hierarchy is jeopardized, e.g., upon the introduction of a stranger to the group. The ambivalent quality of this behavior is suggested by the presence of both apparently dominant and apparently submissive tendencies in the form of ventral orientation and *Lip smacking* respectively.)

D. *Yawn* (See Fig. 4)

Common usage.

(Preliminary evidence suggests that in the drowsy animal exposure of the teeth during a *Yawn* is not too prominent, whereas at other times exposure of the teeth may be very obvious. In non-drowsy animals, particularly in males, the *Yawn* appears repetitively in situations in which the group or individual is threatened, but dominance manifestation is inhibited, as when *E* enters the

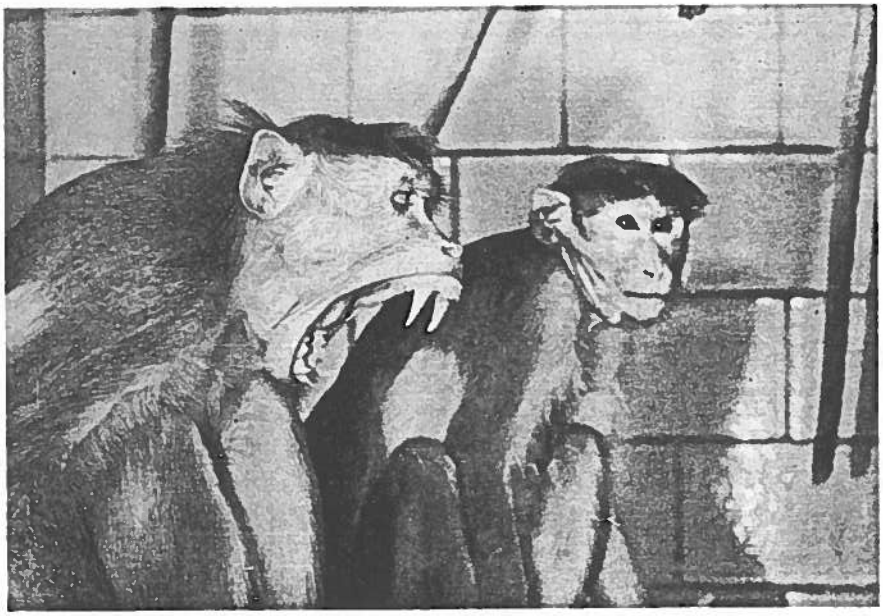


**Fig. 4.** A *Yawn* by a bonnet male in reaction to the presence of *E*.

group area. In a different context we have commonly observed that a short time after copulation, particularly in pigtails, the male yawns once.)

E. *Teeth grinding*
A low intensity sound produced when the teeth are ground together with the lips closed. (It is most frequently heard when adult male pigtails are approached and cornered by *E.*)

### IV. Maternal Behavior

A. *Protective attack-pursuit* (See MATERNAL BEHAVIORS)
B. *Protective threat* (See MATERNAL BEHAVIORS)
C. *Social-danger retrieve* (See MATERNAL BEHAVIORS)
D. *Protective withdrawal* (See MATERNAL BEHAVIORS)
E. *Protective interference* (See MATERNAL BEHAVIORS)
F. *Social-activity restraint* (See MATERNAL BEHAVIORS)

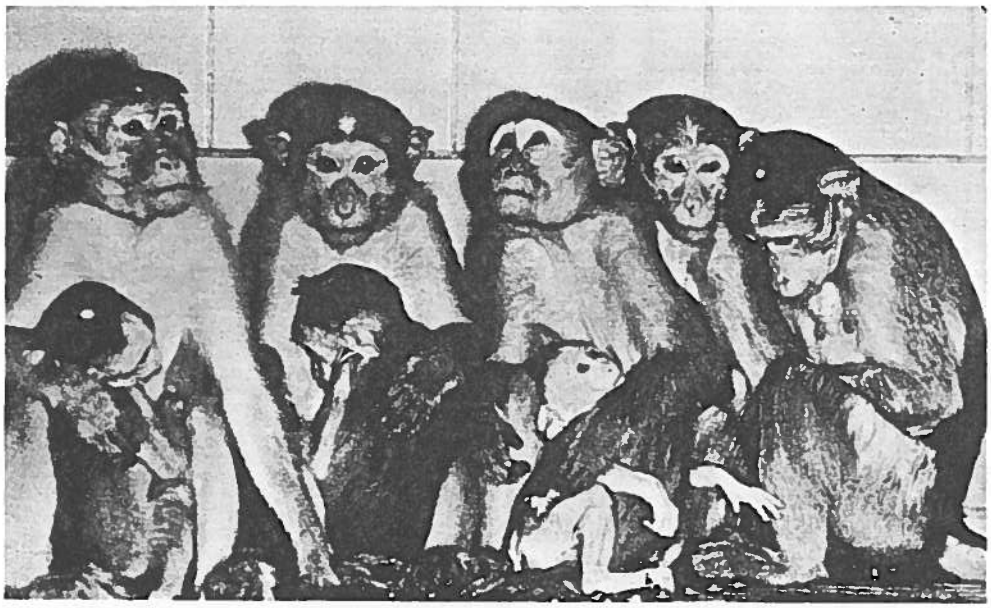
## ASSOCIATIVE BEHAVIORS

### I. Concerning Spatial Relation to Others

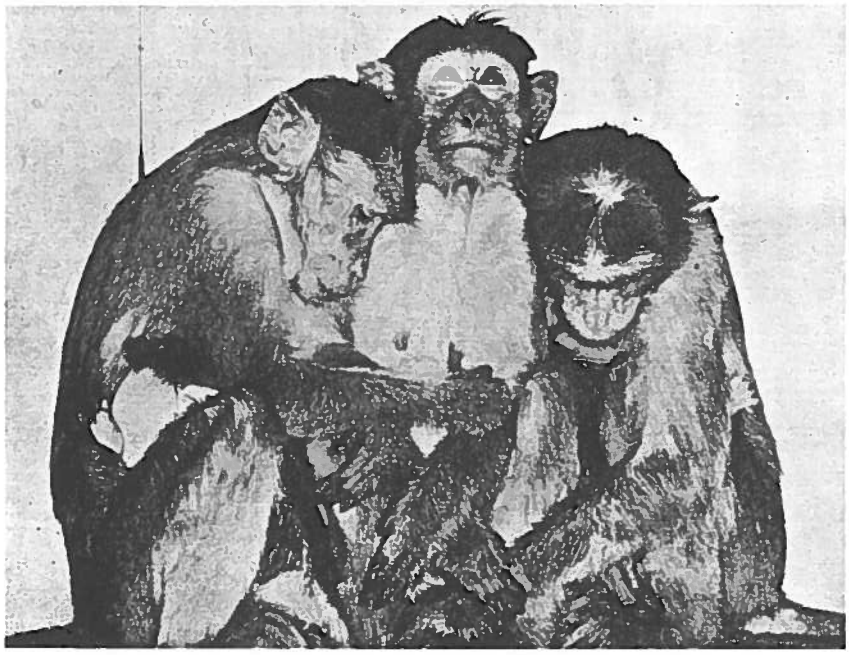
A. *Approach*
1. *Completed approach*
Moving twelve inches or more into the immediate vicinity of another while maintaining orientation to the other.
2. *Incompleted approach*
The same behavior as in "1" except that the animal being approached is not finally reached. The approaching animal either stops or redirects his movement during the approach.
3. *Approach-pass*
The same behavior as in "1" except that the approaching animal walks past the other in a continuous movement.

B. *Proximity* (See Figs. 5a, 5b)
Passive standing or sitting within twelve inches of another animal without making contact or engaging in any additional categorized social behavior. (We include this category because the seeking and acceptance of physical closeness appears to have social significance, e.g., a female in behavioral estrus shows a marked rise in her *Proximity* behavior to the male.)

C. *Contact*
1. *Passive contact* (See Figs. 5a, 5b, 6a, 25a, 25b, 26, 27b)
Remaining in physical contact with another without engaging the other in any additional categorized social behavior. (This pattern, although



a



b

**Fig. 5a & 5b.** *Passive contact*, *Proximity*, and *Clasp* in bonnet females. Note *Enclose* and *Passive support* of infants.

uncommon in pigtails, is the most characteristic social pattern observed in bonnets. In the latter, one frequently observes a physical contiguity of the entire group through this pattern.)

2. *Clasp* (See Figs. 5a, 5b, 26)
   Gentle grasping of the fur or skin of another with the hand or foot, or placing of the arm around the body of another. (Placing the arm around another is rare, more characteristic of bonnets than pigtails, and is frequently interspersed with periods of *Passive contact*.)

D. *Departure*
   Moving away in a deliberate manner twelve inches or more from a partner during the course of an ongoing social interaction.

## II. Grooming and Related Behavior

A. *Grooming solicitation* (See Fig. 6a)
   A sustained presentation of the head, throat, chest, or side to another animal. (Though the subject by this behavior makes himself vulnerable to attack, the most frequent response by the partner is *Social grooming*.)

B. *Social grooming* (See Frontpiece, Figs. 6a, 18c)
   Careful picking through and/or slow brushing aside of the fur with one or both forepaws. The material that is picked out, such as small hairs and flakes of skin, may be placed into the mouth.
   (Grooming is the most frequently observed from of active social interaction in both species. It is primarily engaged in by females and is usually directed towards females. The behavior occasionally takes the form of simultaneous mutual grooming.)

C. *Response to social grooming*
   1. *Passive response-to-grooming* (See Frontpiece)
      Remaining quiet and relaxed in response to *Social grooming*, while generally continuing to sit upright. The subject sometimes slowly moves the body to redirect the groomer to new grooming areas.
      (This behavior is the most common reaction to *Social grooming*.)
   2. *Reverie response-to-grooming* (See Fig. 6b)
      Sitting or more generally lying on either side or back, the body relaxed, with eyes either fully or half closed, in response to *Social grooming*.
      (This behavior generally eventuates from an initial *Passive response-to-grooming*.)
   3. *Rigid response-to-grooming* (See Fig. 6c)
      Tautness, inflexibility, and immobility of the body in response to *Social grooming*.

D. *Social exploration* (See Fig. 13b)

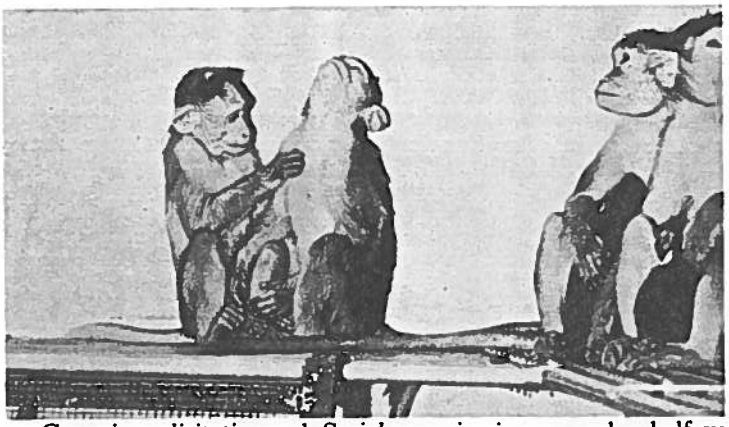


**Fig. 6a.** *Grooming solicitation* and *Social grooming* in one and a half year old bonnet infants. Nearby are their mothers in *Passive contact*, showing *Cradle* and *Enclose* of their younger infants.

**Fig. 6b.** A *Reverie response-to-grooming* in a bonnet female.

**Fig. 6c.** A *Rigid response-to-grooming* in a pigtail female. Note the hunched shouders and fixation of the eyes away from the groomer, who was the dominant female in the group. Note also the *Cradle* of infant who is showing *Nipple hold*.

Close visual, oral or olfactory inspection and/or tentative manipulation of the body of another animal.

### III. Concerning Inanimate Objects

A. *Mutual inanimate-object interest* (See INANIMATE-OBJECT-DIRECTED BEHAVIORS)

## SEXUAL BEHAVIORS

### I. Autosexual

A. *Genital self-stimulation*
Manipulation of the animal's own genitalia, accompanied by evidence of sexual excitement, e.g., erection in the male during manipulation of the penis, or pelvic thrusting in the female when the tail is rubbed against the labia by repetitively pulling it between the legs.

### II. Homosexual

A. *Reciprocated anogenital contact*
A *Proper Present* in response to the *Proper Present* of a partner, the two subjects backing towards one another until the anogenital regions make contact. They then reach back through their legs and manipulate the genitalia of the partner. (This behavior has only been observed in bonnets. It has always been homosexual, more often between males, and usually initiated by the subordinate partner.)

### III. Heterosexual

A. *Pre-copulatory*
1. *Male*
a. *Summoning and related behavior*
1. *Brow movement* (See HIERARCHICAL BEHAVIORS)
2. *Head rock*
Rocking of the head and shoulders backward and forward through a short arc. (The behavior is often followed by the full *Clonic jaw movement* in bonnets and by the *Jaw thrust* in pigtails.)
(This very obvious movement pattern apparently serves to attract the attention of the recipient and to increase the likelihood of the communication of the *Jaw thrust* or *Clonic jaw movement* which follows it. The

*Head rock* is primarily a male behavior and is more pronounced in bonnets.)

3. *Clonic jaw movement* (See Fig. 8a)
   A complex behavior involving the following: rhythmic to-and-fro movements of the head and shoulders: rhythmic contractions of the brow and scalp; retraction of the lips and exposure of the teeth while the jaws rapidly and rhythmically open and close, producing an audible clicking sound.
   (This behavior only occurs in bonnets. It occurs most often in adult males and usually leads to copulation, during which it invariably occurs. If the other animal does not respond sexually to the summoning, it generally flees.)
4. *Jaw thrust* (See Figs. 7a, 7b)
   Thrusting of the lower jaw forward and upward, with the lips pursed, the brow and ears retracted, and the head moved forward. This pattern often gains emphasis from adduction and flexion of one of the arms to the chest. The pattern varies in length from a fraction of a second to perhaps three seconds in length, and is frequently repeated a number of times.
   (This behavior has been seen only in pigtails. The *Jaw thrust* appears in a number of other contexts in both males and females in addition to the sexual, e.g., maternal behaviors; cf., *Crouch jaw-thrust*. In some ways it appears analogous, if not homologous, to the *Clonic jaw movement* seen in bonnets.)

b. *Anogenital exploration* (See Figs. 8a, 8b, 8c)
   Sniffing at, engaging in close visual inspection of, or making tentative manual or oral contact with the genital region of the partner.
   (This pattern is most frequently a part of the precopulatory behavior of adult males, more often in pigtails than in bonnets. It is seen in another context, in maternal exploration of the infant (cf., *Inspection*).

c. *Positioning* (See Fig. 28)
   Manual orientation and/or raising of the hindquarters of the partner to a position suitable for mounting.
   (When this behavior is directed by a male towards a female, it is generally followed immediately by mounting. In the case of all other pairings, when dominance relations seem paramount, mounting follows less frequently.)

2. *Female*

a. *Summoning and related behavior*

1. *Clonic jaw movement* (See above)
2. *Jaw thrust* (See above)
3. *Lip smacking* (See HIERARCHICAL BEHAVIORS)

b. *Present*

1. *Proper present* (See Figs. 8b, 8c, 10a)
   Assumption of a posture in which the hindquarters are raised and oriented

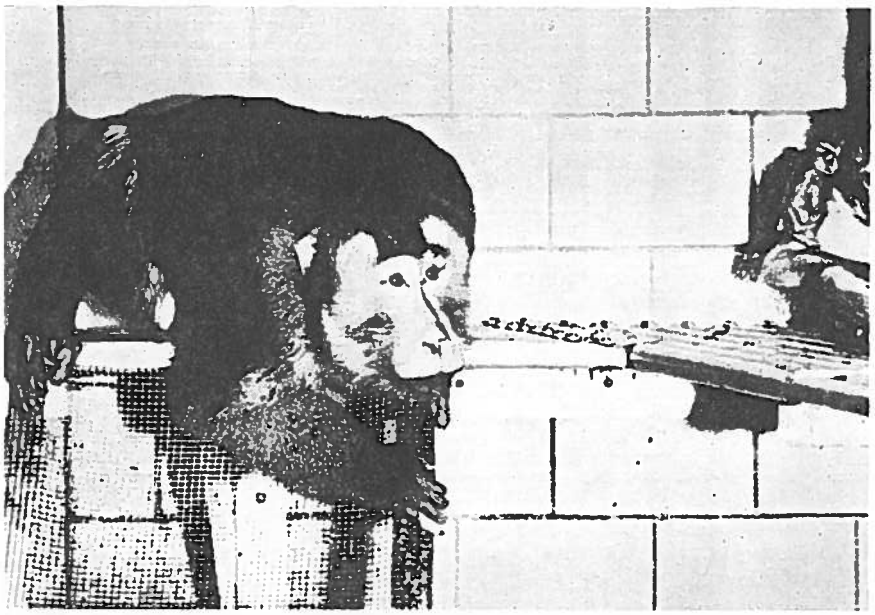


**Fig. 7a.** A summoning *Jaw thrust* by a pigtail male.

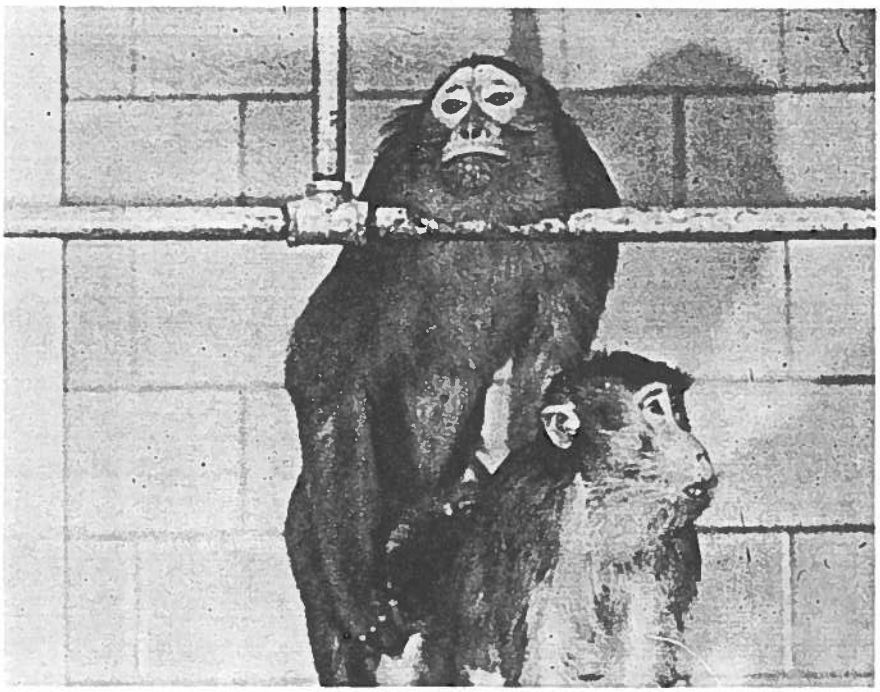
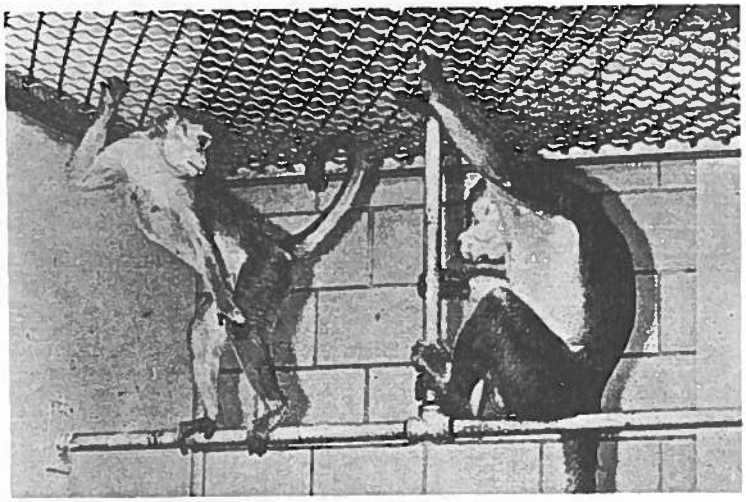
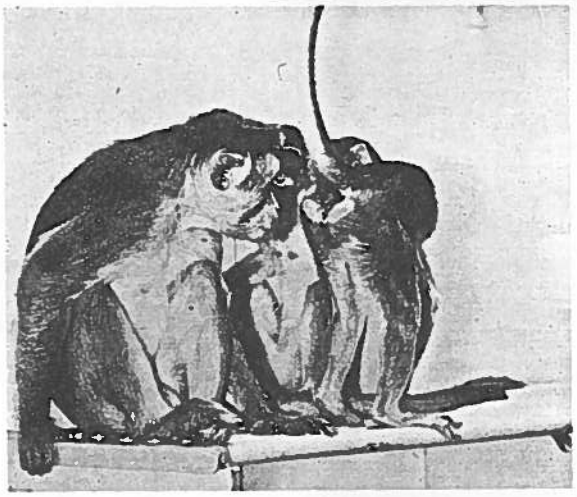


**Fig. 7b.** A *Jaw thrust* by a pigtail male during copulation.



↑

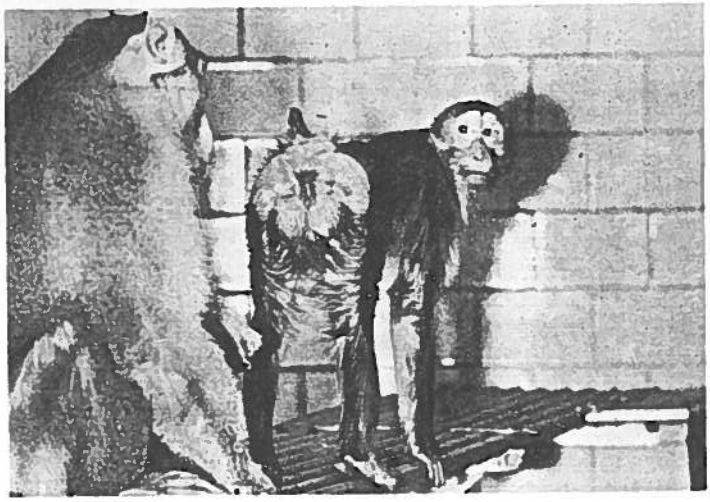
**Fig. 8a.** A sudden present posture by a bonnet female in response to a *Clonic jaw movement* by the male. The male is seen showing *Anogenital exploration.*



←**Fig. 8b.** *Anogenital exploration* by a bonnet male in response to a *Proper present* initiated by the female.

**Fig. 8c.** A *Proper present* by an estrus pigtail female with *Anogenital exploration* by the male.

↓



towards the partner, and the front legs are generally rigid or only slightly flexed, though occasionally the forelegs may be completely bent and the chest pressed to the floor.

(This pattern is typically seen in females during behavioral estrus at which time mounting by the male generally follows, after one or several repetitions of the behavior. When the male has made a sexual initiation, such as a *Jaw thrust*, variations of the above components may appear prior to a mount. These same postures appear in animals of both sexes as apparent demonstrations of Subordinance towards partners of either sex (cf., Assertion).

2. *Disoriented present*

A present which is not appropriately directed to the partner.

3. *Inadequate present*

A properly oriented present posture in which the hindquarters are not raised and the hind legs are not properly extended to allow proper mounting by the partner. (*Disoriented present* and *Inadequate present* are generally seen in immature animals. In animals receiving ample social experience it appears to be a brief transition stage to the adult *Proper present*.)

B. *Copulatory*

1. *Male*

a. *Mount*

1. *Proper mount* (See Figs. 9a, 9b, 9c, 10a)

Climbing upon the partner with feet clasping the calves and hands grasping the loins, and with pelvic thrusting beginning as the position is attained. (This pattern does not include intromission. It is performed by either sex on either sex. Although an invariable part of copulation, it more frequently occurs alone in other contexts in which it appears to be a demonstration of Dominance, e.g., when female mounts female during periods of aggressive activity.) (See HIERARCHICAL BEHAVIORS)

2. *Disoriented mount*

Mounting without the proper ventral-dorsal orientation.

3. *Inadequate mount* (See Fig. 25d)

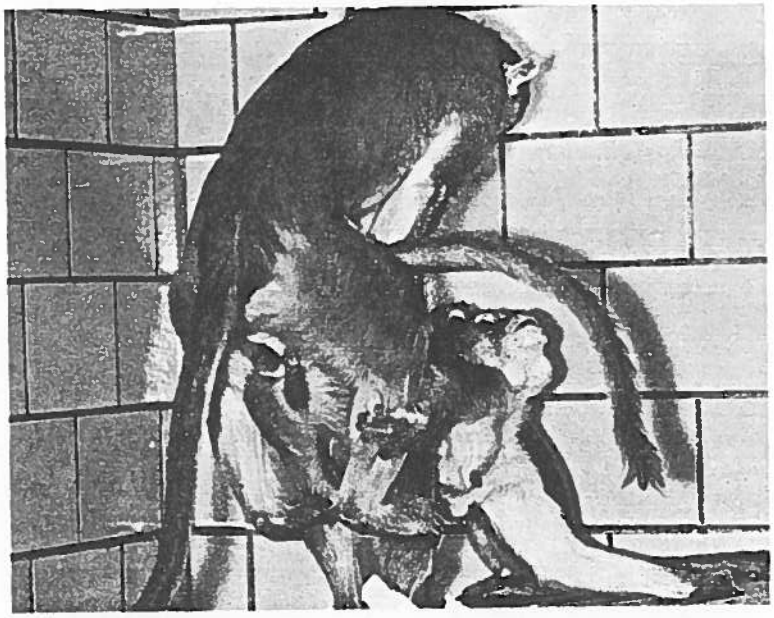
Mounting with appropriate orientation but with position not suited to accomplish intromission, e.g., without calf clasping.

b. *Intromission* (See Figs. 9a, 9b, 9c, 10b)

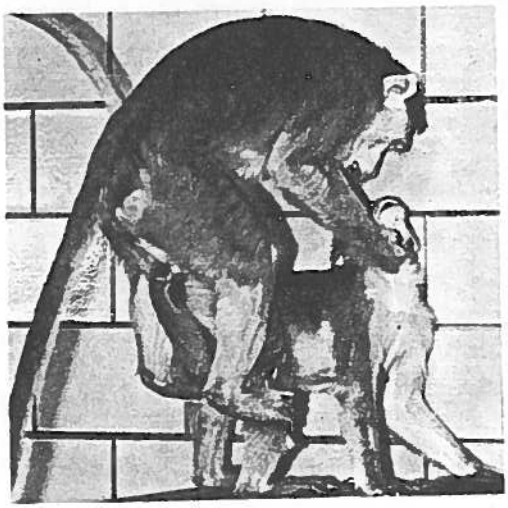
Common usage.

c. *Ejaculation*

Common usage; generally indicated by a pause in rhythmic thrusting followed by stacatto thrusts and body stiffening. (In our experience *Intromission* without *Ejaculation* rarely has been observed in bonnets. In pigtails



a



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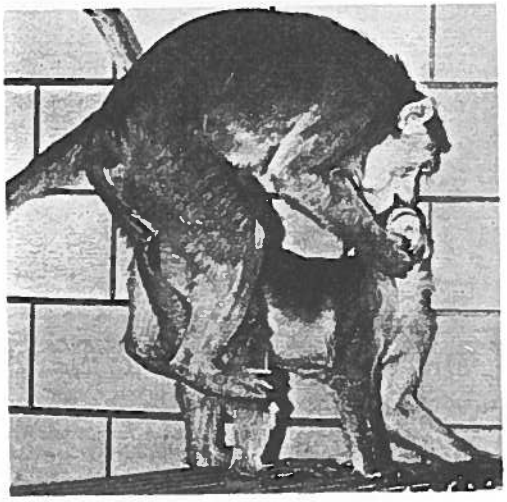
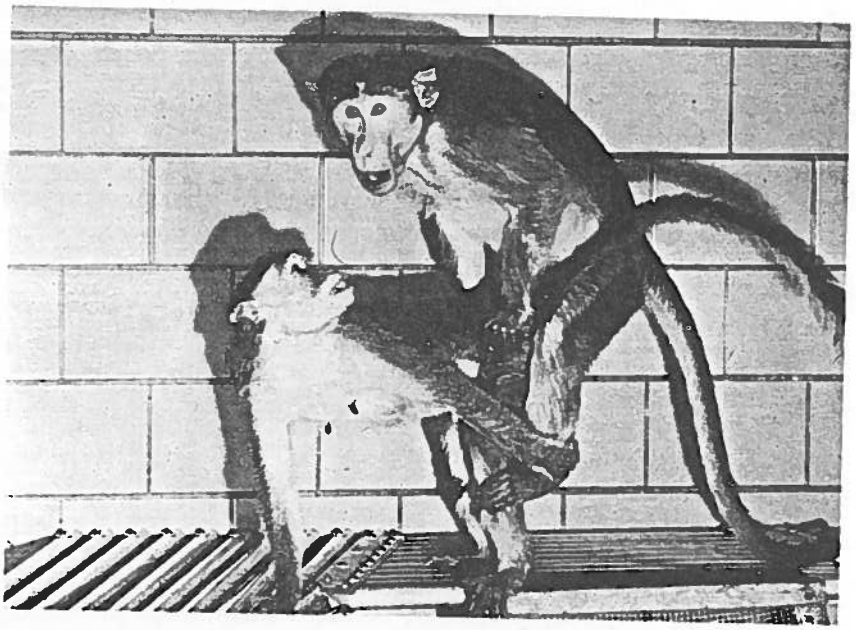
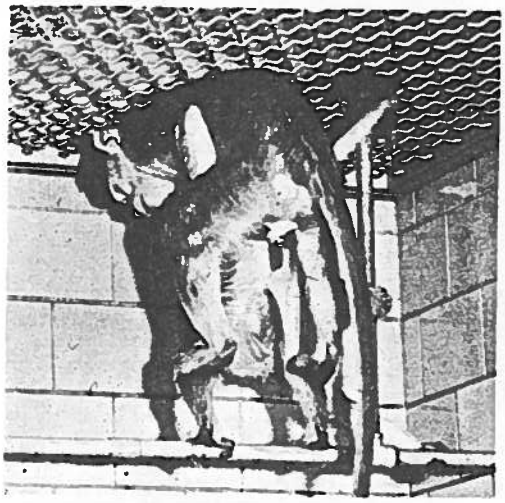


c

**Figs. 9a, 9b, & 9c.** A copulatory sequence in bonnets showing *Proper mount* and *Intromission* by the male and *Nongenital reach* by the female in 9a. The grasping and mouthing of the face of the female, though not a common variant of the copulatory pattern, appears in a number of forms in the bonnets as an apparent manifestation of their unusually high degree of excitability during copulation.



a



b

c

**Fig. 10a.** Copulation in bonnets showing *Proper present*, *Proper mount*, and *Nongenital reach* as well as facial gestures by both male and female. A variant of the copulatory position showing *Intromission* in a bonnet pair.
*Genital-secretion ingestion* by a bonnet male following copulation.

Figures 10a, 10b & 10c should be reversed

*t* and *Intromis-*
e in 9a. The
gh not a com-
mber of forms
unusually high

however, *Ejaculation* generally has been preceded by a varying series of *Proper mounts* and *Intromissions*.)

d. *Facial gestures*

1. *Jaw thrust* (See above)
2. *Clonic jaw movement* (See above)

2. *Female*

a. *Reaching back to partner*

1. *Nongenital reach* (See Figs. 9a, 10a)
   Reaching back with one forepaw, generally to grasp or pull the hind leg of the mounting animal. Occasionally the upper part of the mounter's body, including the face and shoulders, is also grasped or pulled. (This latter behavior is more characteristic of bonnets.)
2. *Genital reach*
   Reaching at and grasping of the genitals of the mounting animal.

b. 1. *Jaw thrust* (See above)
2. *Lip smacking* (See HIERARCHICAL BEHAVIORS)
3. *Clonic jaw movement* (See above)

C. *Post-copulatory*

1. *Male*

a. *Genital-secretion ingestion* (See Fig. 10c)
   Eating of the genital secretions, i.e., the ejaculate by the male and the contents of the vagina by the female.
   (Immediately following copulation, the male commonly eats the ejaculate remaining on the penis. The estrus female who is intermittently copulating frequently eats both her own secretions and male ejaculate drawn from the vagina.)

2. *Female*

a. "*Chu-chu*"
   A deep repetitive grunt produced by adult females just prior to or just following the conclusion of copulation.
b. *Social grooming* (See ASSOCIATIVE BEHAVIORS)
c. *Withdrawal* (See HIERARCHICAL BEHAVIORS)
d. *Genital-secretion ingestion* (See above)

## MATERNAL BEHAVIORS

### I. Parturient & Post-parturient Behavior

A. *Squat* (See Fig. 11a)
   Common usage.
B. *Bearing down* (See Fig. 11a)

Common usage.

C. *Vaginal probing* (See Figs. 11b, 11c)
Manual exploration of the vagina during labor, followed by smelling and licking the secretions adhering to the hands. (This behavior is repeated intermittently throughout labor especially after rupture of the membrane and partial emergence of the infant's head. It is actively continued until after the placenta has appeared and then rapidly diminishes as the secretions disappear and attention is turned to the placenta and infant.)

D. *Infant cleaning*
Licking and grooming of the newborn which serves to remove the amniotic fluids and blood adhering to the fur.
(As with grooming in general, there appears to be some variation in the intensity and exactness with which this behavior is performed.)

E. *Self-cleaning* (See Fig. 11b)
Licking and grooming of her own body after parturition which serves to remove the amniotic fluids and blood adhering to her fur.

F. *Placenta ingestion* (See Fig. 12)
Rapid eating of the placenta up to and somewhat into the umbilical cord.

## II. Body Care of Infant

A. *Nurse*
Common usage

B. *Social exploration* (See ASSOCIATIVE BEHAVIORS)

C. *Inspection* (See Figs. 13a, 13b)
Active examination of the infant through somewhat vigorous handling that includes pulling the limbs of the infant, raising the infant and turning the infant over.
(This maternal behavior frequently appears to serve the function of exposing the genital region of the infant to inspection and is directed towards male infants almost exclusively. Other females, including adolescents, show the same interest in the genitalia of male infants.)

D. *Social grooming* (See ASSOCIATIVE BEHAVIORS)

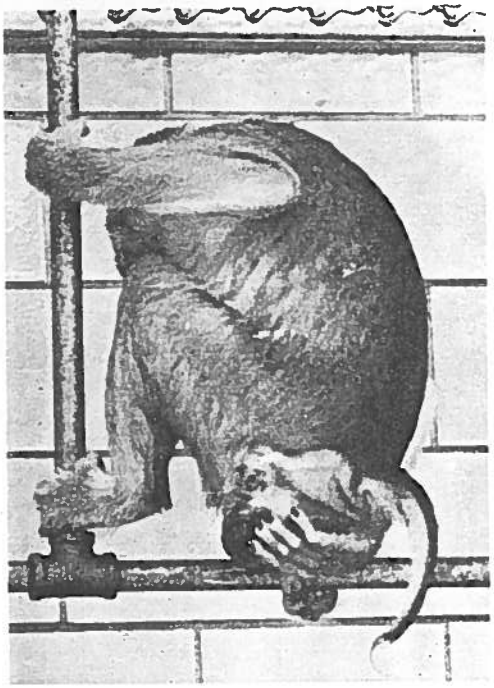
## III. Support of Infant

A. *Sitting*

1. *Cradle* (See Figs. 6a, 6c, 12, 14a)
While seated, grasping and pressing of the infant to the ventral surface of her body through the active use of her hands. The orientation is almost invariably ventral-ventral.

a

b



c

**Fig. 11a.** *Squat* and *Bearing down* in a pigtail female two hours prior to parturition.

**b.** *Self-cleaning* by the same female in the midst of a period of *Vaginal probing*.

**c.** *Vaginal probing* by the same female just prior to delivery of the young; the head of the infant has just appeared.

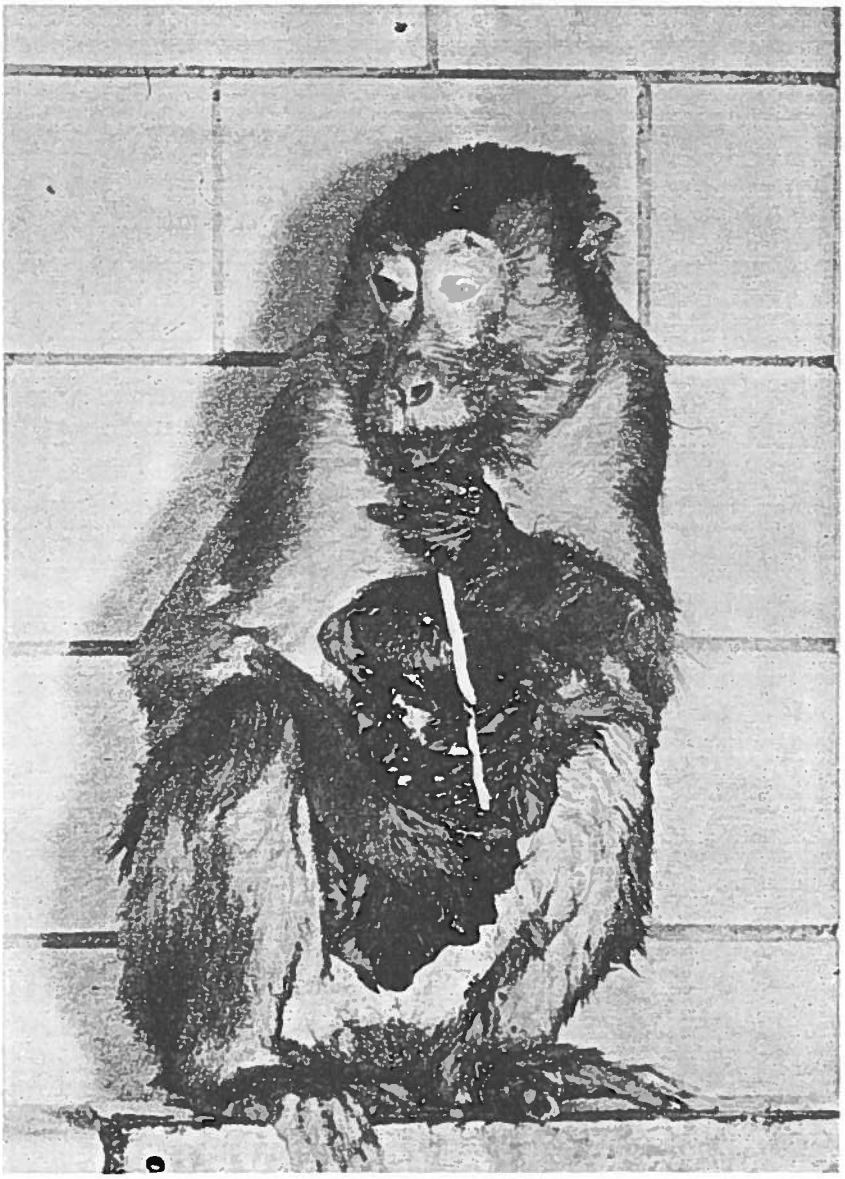


**Fig. 12.** *Placenta ingestion* by a pigtail female. Note *Cradle* of infant.

2. *Enclose* (See Figs. 5a, 5b, 6a, 14b)
   While seated, more or less tight surrounding of the clasping infant with the flexed forearms and/or flexed hind limbs. What characterizes the behavior is the lack of palmer contact with the infant. The orientation is generally ventral-ventral but occasionally may be ventral-lateral.
3. *Passive support* (See Figs. 5a, 5b, 14c)

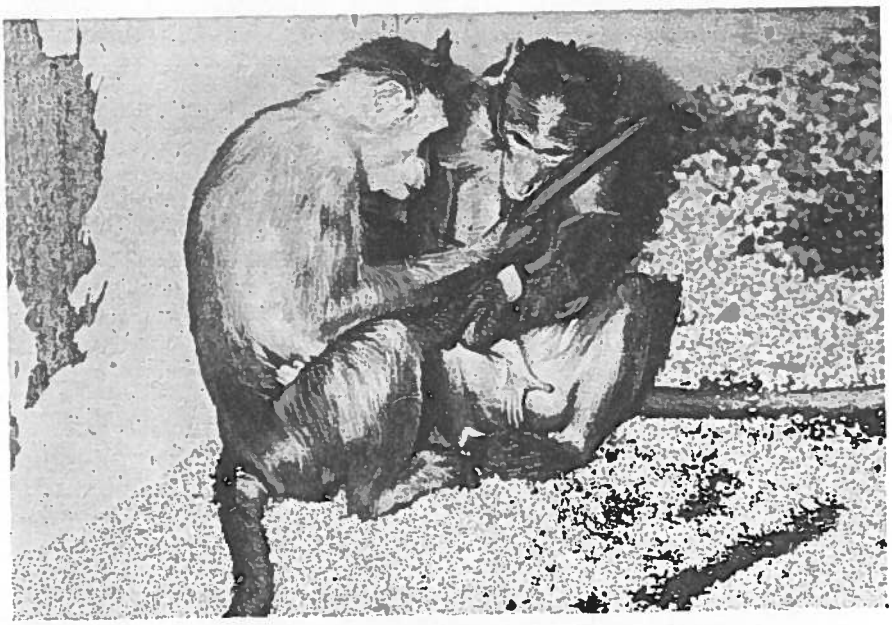


**Fig. 13a.** *Inspection* of a neonate by bonnet mother and another female.

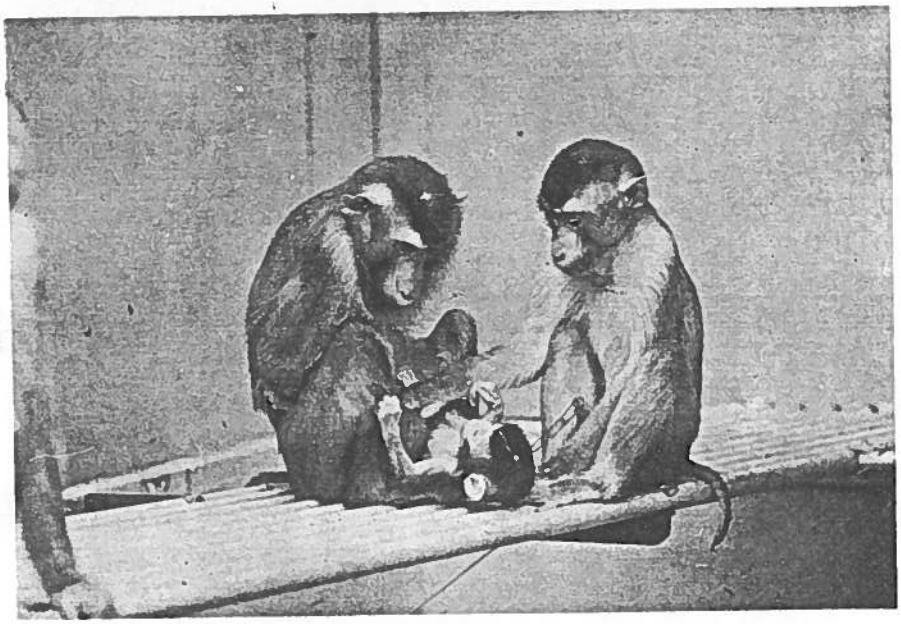
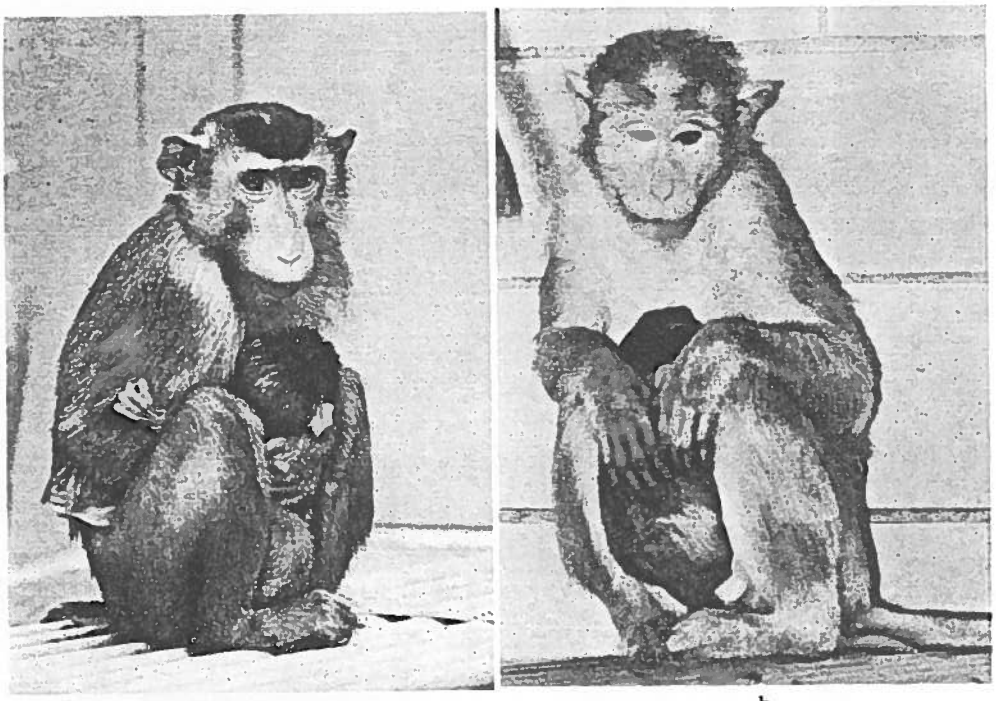


**Fig. 13b.** *Social exploration* and *Inspection* of a male infant by an adolescent female pigtail under mother's watchful gaze.



a b

c

**Fig. 14a.** *Cradle* of her newborn infant by a pigtail mother.
**b.** *Enclose* by a bonnet mother.
**c.** *Passive support* of an older infant by a pigtail mother.

Sitting with the infant resting or supporting himself at her ventral surface without a *Cradle* or *Enclose* by her.

(With the neonate both the *Enclose* and *Cradle* are common behaviors, with *Passive support* appearing somewhat later. As the infant matures, *Enclose* and *Passive support* are most common, with the *Cradle* increasingly observed only during conditions of social and environmental stress.)

4. *Clasp* (See ASSOCIATIVE BEHAVIORS)

B. *Standing*

1. *Cradle stand*
   Erect stance without locomotion while manually supporting the infant clinging to her ventral surface.
2. *Passive-support stand*
   Erect stance without locomotion while offering no support to the infant clinging to her ventral surface.

C. *Moving*

1. *Cradle carriage* (See Fig. 15a)
   Locomotion with manual holding and support of the infant at her ventral surface.
2. *Passive-support carriage*
   Locomotion with the infant supporting himself at her ventral surface, without her holding or bracing him.
3. *Dorsal-ventral carriage* (See Fig. 15b)
   Locomotion with the infant supporting himself on her back, usually close to her tail.

   (The *Passive-support carriage* is the most frequently observed carrying pattern. The *Cradle carriage* is primarily seen only with young infants, whereas *Dorsal-ventral carriage* is seen only with older infants, when coordination and greater strength have been achieved.)

## IV. Protection of Infant

A. Without direct social referents

1. *Guard* (See Figs. 16a, 16b)
   Maintenance of *Passive contact* of one or both hands with the free infant, or moving along next to (within one foot) or above the locomoting infant.
2. *Follow*
   Following after the infant outside of *Proximity* distance.
3. *Watch* (See HIERARCHICAL BEHAVIORS)
4. *Check* (See HIERARCHICAL BEHAVIORS)
5. *Physical-danger retrieve* (See Fig. 24b)
   Grasping and rapid cradling of the free infant who is in a precarious

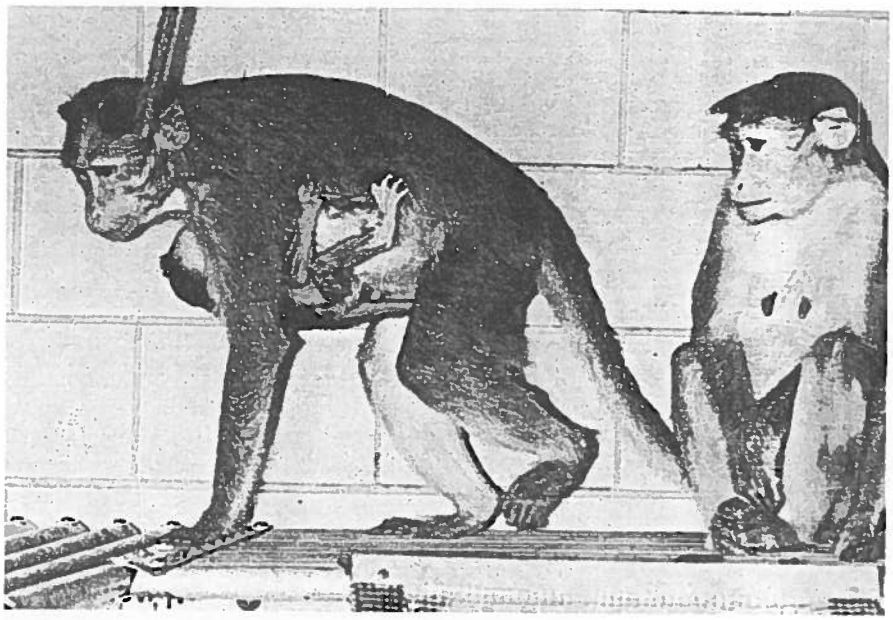


**Fig. 15a.** *Cradle* carriage of a neonate by a bonnet mother. Note *Ventral-ventral* cling by infant.

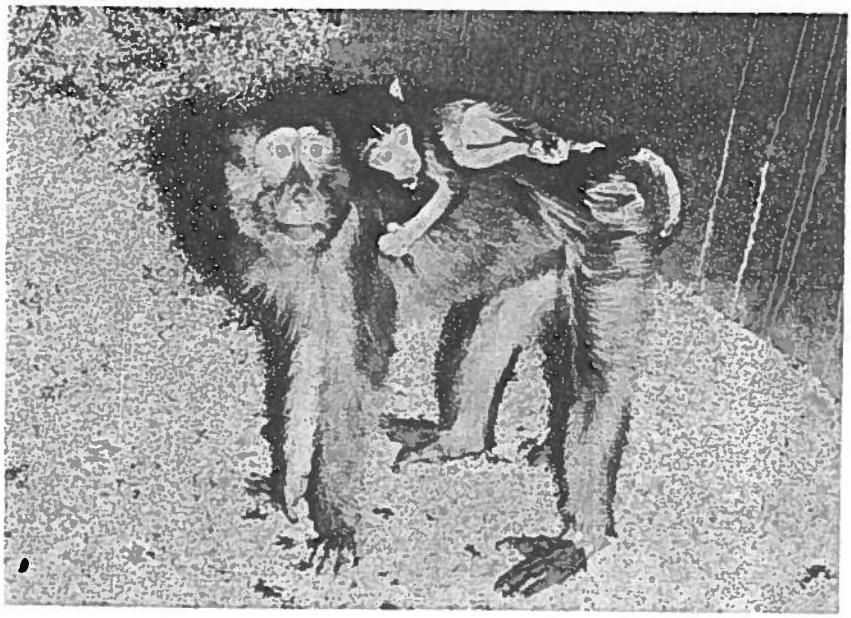
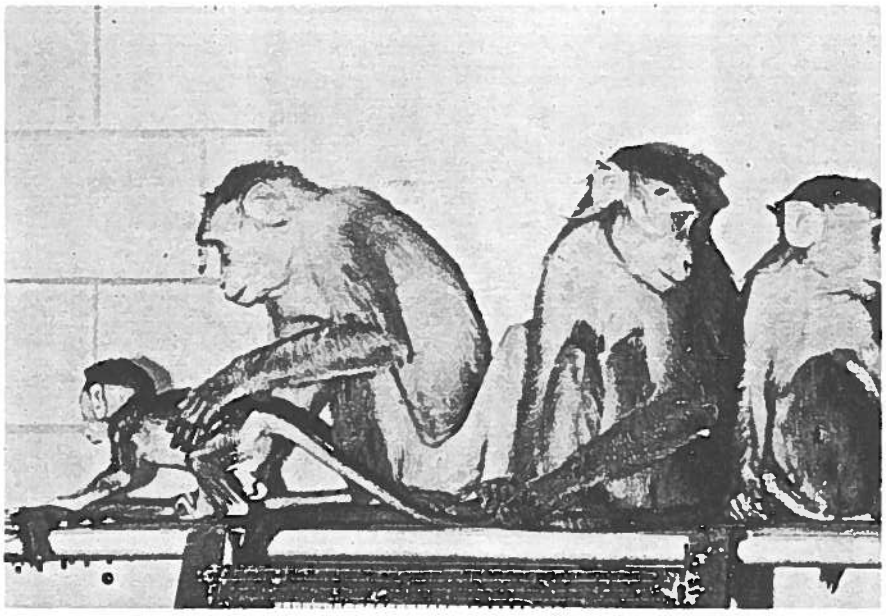


**Fig. 15b.** *Dorsal-ventral* carriage by a pigtail mother of an older infant.

a



b

**Figs. 16a & 16b.** Two forms of *Guard* of young bonnet infants by mothers.

position, or who has just fallen or suffered some other mishap.

B. With social referents

1. *Protective withdrawal*
   Withdrawing with the infant in reaction to an activity directed towards her infant by another animal.
2. *Protective threat*
   Threatening of an animal who is directing an activity towards her infant. e.g., *Social exploration.*
3. *Protective attack-pursuit* (See Fig. 17a)
   Attack and/or pursuit of an animal who is directing an activity towards her infant.
4. *Protective interference* (See Fig. 17b)
   Termination or prevention of an activity directed towards her infant by another animal without attack, pursuit, intimidation or widthdrawal; e.g., she removes the hand of another animal from her infant or turns her back to another animal that is directing an activity towards her infant.
5. *Social-danger retrieve*
   Grasping and rapid *Cradle* of the free infant in reaction to an activity directed towards the infant by another member of the group.

## V. Facilitation of Filial Behavior

A. *Suckling facilitation*
With her infant in the ventral-ventral orientation moving of her body or of her infant's head so as to bring the nipple close to or into the infant's mouth.

B. *Crouch jaw-thrust*
*Jaw thrust* to the free infant with the chest pressed close to the ground and usually with adduction and flexion of the hand to the chest. (This behavior appears to serve the function of summoning the infant back to the mother.)

## VI. Restriction of Filial Abdyadic Behavior

A. *Restraint*

1. *Departure restraint* (See Figs. 18b, 18c)
   Prevention of the infant from breaking contact with her or leaving her immediate vicinity. This is generally accomplished by tightly grasping the infant's limb or body, and is frequently associated with pressing the infant to the ground. She may at times do this while simultaneously otherwise occupied.
2. *Nonsocial-activity restraint*
   Prevention of the infant from engaging in a nonsocially oriented activity,

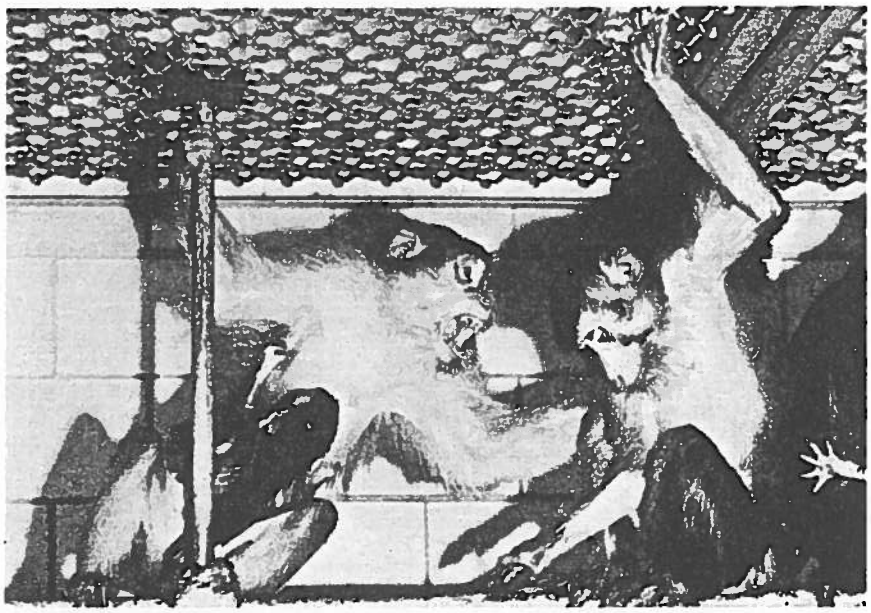


**Fig. 17a.** A pigtail mother of a young infant beginning a *Protective attack-pursuit*. Note that the young infant, in *Ventral-ventral cling* position, is fully able to support itself at the mother's ventral surface.

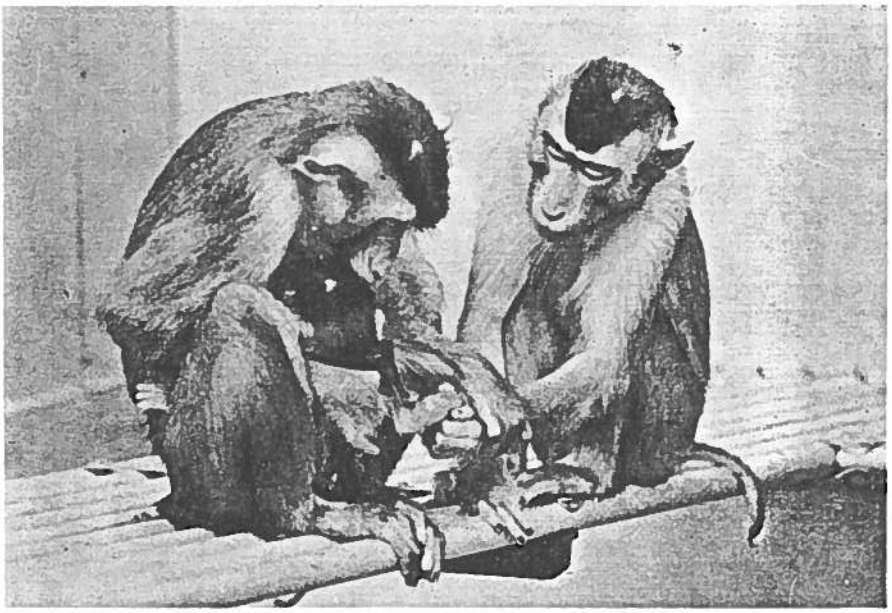
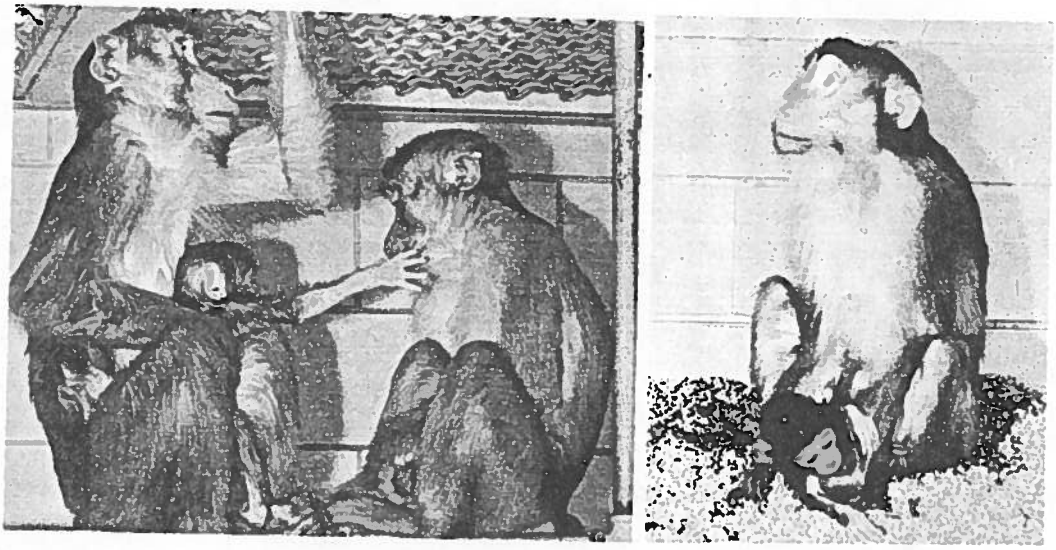


**Fig. 17b.** *Protective interference* by a mother directed at an adolescent pigtail female.



a b

**Fig. 18a.** *Social-activity restraint* by a pigtail mother.
**Fig. 18b.** *Departure restraint* by a pigtail mother.

c

**Fig. 18c.** *Departure restraint* by the mother of an older pigtail infant accompanied by *Social grooming* of the infant.

e.g., climbing, hanging from the shelf, or approaching some inanimate object, using the same techniques as described in *Departure restraint.*

3. *Social-activity restraint* (See Figs. 18a, 24c)
   Prevention of the infant from engaging in an activity directed towards another animal, using the same technique as described in *Departure restraint.*

B. *Retrieve*
   1. *Physical-danger retrieve* (See above)
   2. *Social-danger retrieve* (See above)

## VII. Abdyadic Behavior

A. *Play-on-mother deterrence*
   Stopping of the infant from vigorous play on, and vigorous explorations of her body.

B. *Contact break*
   Physical separation from the infant while remaining in proximity to it.

C. *Infant removal*
   Active pulling of the limbs of the infant from around her, and pushing of his body away from her, which thereby breaks ventral-ventral contact.

D. *Contact deterrence* (See Figs. 19, 29)
   Prevention of the infant from attaining ventral-ventral contact by holding the infant to the floor or at arm's length.

E. *Nipple withdrawal* (See Figs. 20a, 20b)
   Removal of the nipple from the infant's mouth, e.g., by the lifting of her arms and jerking up and away of her breast, or the manual pushing away of the infant from the breast.
   (Though rarely done to the neonate, this behavior is performed by virtually all mothers by the time their infants reach six months of age.)

F. *Mouth-nipple contact deterrence* (See Fig. 21)
   Prevention of the infant from reaching the nipple with its mouth, e.g., by holding of the infant's head between her arm and the side of her body.
   (This behavior frequently follows upon, and is interspersed with, *Nipple withdrawal.*)

G. *Punitive deterrence* (See Fig. 22)
   Constrained biting of the limbs, shoulders, and head of the infant, or violent shaking of the infant's body.

H. *Teasing withdrawal*
   Slow and intermittent movement away from the approaching infant, thus preventing contact and apparently encouraging increased infant locomotion.

I. *Departure* (See ASSOCIATIVE BEHAVIORS)