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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

MOTHER-INFANT BEHAVIOR AMONG CAPTIVE GROUP-LIVING CHIMPANZEES (*Pan troglodytes*)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

EMILY SUE SAVAGE

Norman, Oklahoma

1975

MOTHER-INFANT BEHAVIOR AMONG CAPTIVE GROUP-LIVING

CHIMPANZEES (*Pan troglodytes*)

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THE CHIMPANZEE COLONY

The following glossary reflects 3 years of observational study of captive chimpanzees who ranged in age from premature infants to 35 years. During this period, more than 40 individuals have been studied, but the bulk of the observations were concentrated upon 8 mothers and their offspring. The animals were housed at the Institute for Primate Studies and were kept either on an ½ acre island or in cages. Caging facilities included both indoor and outdoor enclosures which ranged in size from 7 x 9 feet to 15 x 30 feet. Normally 2 to 4 cages were continually available to each chimpanzee group.

Observations took place daily, 5 to 6 days a week, between the hours of 9:00 a.m. and 5:00 p.m. for 3 to 8 hours per day. The cages were usually hosed clean twice daily, in the morning and late afternoon by the staff. Animals were fed a specially prepared diet prior to both cage cleanings and they received fruit early in the evening. Although quantitative data was not collected during feeding, cleaning, or other maintenance activities, observations often continued during these periods. The author normally handled some chimpanzees each day, in addition to observing.

Observations were largely recorded by hand and a shorthand notation system was developed for those patterns which occurred repeatedly and regularly. Although items such as sitting down, lying down, leaning on the wire, etc. are not delineated as specific items in the glossary, they were recorded during observation sessions. It

did not appear that slight variations in such posture significantly altered interactions, however, some postures were highly characteristic of particular individuals and thus may reflect dominance status as well as personal idiosyncrasies. A study of the variety of postural states typically assumed by chimpanzees is needed, but was outside the scope of the present report.

Written observations were supplemented by still photos taken with a 35mm Pentax and by video tape using a portable Song videocorder. The tapes and photos were later carefully viewed in order to determine the detailed expressions and movements involved in behavior patterns chosen for the glossary.

PART I

GLOSSARY OF BEHAVIOR PATTERNS FOR CAPTIVE, GROUP-LIVING MOTHER, JUVENILE AND INFANT CHIMPANZEES (*Pan troglodytes*)

INTRODUCTION

Attempts to categorize behavior into describable, repeatable and objectifiable units has been a cornerstone of the ethological approach. The purpose of such a classificatory system is to permit the objective study of natural ongoing behavioral sequences by looking at what the individual does rather than the "implicit motivation" or the "desired consequences" of the behavior. Once a classification system has been evolved, discrete behaviors become susceptible to quantitative analysis. Frequencies of a given pattern, combinations of patterns and the sequencing of patterns can be looked at statistically (Van Hooff, 1973; McGrew, 1972). Basically, the ethological approach retains the objectivity of the experimental psychologist, but attempts to study all facets of behavior in a natural ongoing setting. It further emphasizes the importance of the evolutionary nature of behaviorally patterned sequences. Thus, before a detailed study of any species can be undertaken, a catalogue of sorts, which describes and delineates the various behavior patterns of the species, must be developed.

The present glossary of chimpanzee behavior was developed in rough form in 1973. At that time, Van Hooff's (1971) glossary and Van Lawick-Goodall's (1968) monograph were available but Van Lawick-Goodall's unpublished glossary was not. Van Hooff's (1971) glossary included no mother-infant interactions or interactions typical of infants since the Holloman group was composed only of older juveniles and adults. I thus began to compile my own repertoire. Shortly

after I had completed a rough catalogue of patterns, I received a copy of Van Lawick-Goodall's unpublished glossary. This glossary is quite extensive and covers all aspects of chimpanzee behavior among all age-sex groupings. Numerous patterns defined by Van Lawick-Goodall were identical, or nearly so, to patterns I had also classified for the captive mother-infant-juvenile group. In the interest of avoiding duplication of terms, I revised my glossary using Van Lawick-Goodall's terminology wherever I was reasonably certain that we were describing similar units of behavior. In this presentation of this glossary I have noted, in the initial alphabetical listing of patterns, whether or not Van Lawick-Goodall (unpublished glossary) or Van Hooff (1971) included this pattern in their glossaries. Many patterns in the present glossary are not included in either Van Lawick-Goodall's (unpublished glossary) or Van Hooff's (1971) catalogue. It is not assumed that Van Lawick-Goodall or Van Hooff did not observe these patterns. In many cases, they have mentioned similar patterns, but do not separate them from others or do not choose to put them in the glossary. There are however, some patterns which are, perhaps, specific to the Oklahoma colony.

Glossaries, by their very nature, involve an artificial and arbitrary splitting and lumping of the ongoing flow of behavior. Although a concerted effort was made to look for "natural units" of behavior as described by Altmann (1967), I do not feel that success in that endeavor was attained. The chimpanzee behavioral repertoire is extraordinarily complex and units of facile expression, posture and movement are broken apart and recombined in what seems to be infinite variety. After thousands of hours of observing chimpanzees, it is apparent that there are "rules" of sorts governing this process, but as

yet they have eluded us. This repertoire exists only as a starting point, an elementary and initial attempt to point out at least the grosser units of the chimpanzee's behavioral repertoire, and to place them in some sort of meaningful context.

Often, in working through Van Hooff's or Van Lawick-Goodall's glossary, I was uncertain as to whether their verbal description of a pattern corresponded with my visual image of a similar behavior seen in the Oklahoma group. When a picture or drawing of the pattern was available, however, I had much less trouble determining whether or not the pattern corresponded with one which I had observed. Hence, this glossary is accompanied by photos or drawings wherever possible in hopes that they will add to the clarity of each pattern's definition.

Although numerous behavioral patterns appear to be unique to the Oklahoma colony, it is difficult to ascertain whether they definitely have not been observed elsewhere, or whether other authors simply decided not to include them in their glossaries. For this reason, speculations as to why the Oklahoma group perform patterns apparently not observed in other colonies, have been avoided. Adequate assessment of cultural differences between groups must await the work of a single researcher studying several different chimpanzee groups in detail.

GLOSSARY

LOCOMOTOR PATTERNS

1. Bipedal Locomotion (Fig. 1)	Van Lawick-Goodall, Van Hooff
2. Brachiate (Fig. 2)	Van Lawick-Goodall
3. Climb	
4. Charge	Van Lawick-Goodall, Van Hooff
5. Crutch (Fig. 7)	Van Lawick-Goodall
6. Footstamp (Figs. 3 and 4)	Van Lawick-Goodall, Van Hooff
7. Freefall (Fig. 5)	
8. Gallop (Fig. 6)	Van Lawick-Goodall, Van Hooff
9. Jump (Fig. 9)	
10. Knuckle slide	
11. Playwalk	Van Lawick-Goodall
12. Pirouette	Van Lawick-Goodall
13. Quadrupedal Locomotion (Fig. 8)	Van Hooff
14. Rock	Van Lawick-Goodall
15. Somersault	Van Lawick-Goodall, Van Hooff
16. Swagger (Fig. 55)	Van Lawick-Goodall, Van Hooff
17. Tripedal Locomotion (Fig. 10)	

FACIAL EXPRESSIONS and VOCALIZATIONS

18. «Uhh grunt», «Ehh squeak»	Van Lawick-Goodall, Van Hooff
19. «Low grunt»	
20. «Pant grunt»	Van Lawick-Goodall, Van Hooff
21. «!Ouggh bark» (Fig. 12)	
22. «!Aggh bark»	
23. «!Ugh bark» (Fig. 11)	Van Lawick-Goodall
24. Bite threat	
25. Cheek or lip-suck	Van Lawick-Goodall
26. Closed-teeth-face	

27. Full-closed-grin (Fig. 86) Van Lawick-Goodall, Van Hooff
28. Glare Van Lawick-Goodall, Van Hooff
29. Grin face (Fig. 7)
30. Hoo call Van Lawick-Goodall
31. Hoo whimper (Fig. 20) Van Lawick-Goodall, Van Hooff
32. <<Iieow scream>>
33. Laugh Van Lawick-Goodall, Van Hooff
34. Lip bulge (Figs.13 & 72a) Van Lawick-Goodall, Van Hooff
35. Lip buzz Van Hooff
36. Lip flip Van Lawick-Goodall
37. Look at (Fig. 15) Van Lawick-Goodall
38. Low-closed-mouth-bared-teeth Van Lawick-Goodall, Van Hooff
39. Normal face (Fig. 19) Van Lawick-Goodall
40. Pant Van Lawick-Goodall, Van Hooff
41. Pant hoot (Figs. 14 and 37) Van Lawick-Goodall, Van Hooff
42. Pant scream Van Lawick-Goodall, Van Hooff
43. Play face(full and half) (Fig. 16) Van Lawick-Goodall, Van Hooff
44. Open-mouth-bared-teeth
45. Open-mouth-bared-teeth-and-gums (Fig. 17) Van Lawick-Goodall, Van Hooff
46. Raucous scream (Fig. 18) Van Hooff
47. Rising hoo whimper Van Lawick-Goodall, Van Hooff
48. Silent pout face (Fig. 20a) Van Lawick-Goodall
    a) hoo whimper (Fig. 20)
    b) horizontal pant face
    c) rising hoo whimper
    d) open-mouth-bared-teeth-and-gums
    e) squeal
49. Tonal scream
50. <<Waa bark>> Van Lawick-Goodall, Van Hooff
51. Wide eyes face (Fig. 21)

INTERACTIVE PATTERNS

52. Arm-around-back (Fig. 22) Van Lawick-Goodall, Van Hooff
53. Arm-around-embrace (Fig. 23)

54. Ano-genital inspection (Fig. 24)	Van Lawick-Goodall, Van Hooff
55. Backhand thump (Fig. 26)	
56. Bite	Van Lawick-Goodall, Van Hooff
57. Bodyfling	
58. Chase (Fig. 25)	Van Lawick-Goodall
59. Finger tickle (Fig. 27)	Van Lawick-Goodall
60. Follow	
61. Groom (Figs. 28 & 28a)	Van Lawick-Goodall, Van Hooff
62. Hairhold (Fig. 29)	
63. Hairtug	Van Hooff
64. Handclap (Fig. 42)	
65. Hand or finger-in-mouth (Fig. 30)	Van Lawick-Goodall
66. Head nod	
67. Head touch (Figs. 31 and 31a)	
68. Hold seat against (Fig. 32)	
69. Ignore	
70. Leg shake (Fig. 53)	
71. Lip beg (Fig. 33)	Van Lawick-Goodall
72. Lip-tongue-kiss (Fig. 85)	
73. Mouthcover (Fig. 34)	
74. Open-mouth-kiss (Figs. 37 & 38)	Van Lawick-Goodall
75. Pat (Fig. 36)	Van Lawick-Goodall
76. Peer (Fig. 35)	Van Lawick-Goodall
77. Pinch	Van Lawick-Goodall
78. Pinch bite	
79. Place teeth on	
80. Touch under chin	
81. Playbite (Fig. 40)	
82. Playkick (Fig. 39)	
83. Playslap (Fig. 41)	
84. Poutkiss	Van Lawick-Goodall
85. Present (Fig. 44)	Van Lawick-Goodall, Van Hooff
86. Present back (Figs. 43 & 45)	
87. Present crouch	Van Lawick-Goodall, Van Hooff
88. Pull on (Fig. 46)	

89. Punch	Van Hooff
90. Push	Van Lawick-Goodall, Van Hooff
91. Seat bounce	
92. Sit on (Fig. 47)	
93. Slap (Figs. 58 & 59)	Van Lawick-Goodall, Van Hooff
94. Stretch pull	
95. Thrust (Figs. 48, 49 and 50)	Van Lawick-Goodall, Van Hooff
96. Ventro-dorsal embrace (Fig. 60)	Van Lawick-Goodall, Van Hooff
97. Ventro-ventral embrace (Figs. 61 & 62)	Van Lawick-Goodall, Van Hooff
98. Waist clasp embrace (Fig. 63)	
99. Wrestle (Fig. 51)	Van Hooff

POSTURES AND GESTURES

100. Arm headcover (Fig. 64)	
101. Bend away (Fig. 65)	Van Lawick-Goodall
102. Clitoral rubbing	Van Hooff
103. Dangle (Fig. 67)	Van Lawick-Goodall
104. Extend hand (Figs. 68 & 69)	Van Lawick-Goodall, Van Hooff
105. Head down (Fig. 70)	
106. Hold out hand (Fig. 71)	Van Lawick-Goodall
107. Hunch (Figs. 72 & 72a)	Van Lawick-Goodall
108. Hurry shake (Fig. 73)	
109. Lie on back (Fig. 74)	
110. Penile rubbing	
111. Rigid tantrum (Fig. 56)	
112. Touch behind head	
113. Raised palm (Fig. 53)	
114. Temper tantrum	Van Lawick-Goodall
115. Wristbend	Van Lawick-Goodall

MOTHER-INFANT PATTERNS

116. Chest expose (Fig. 80)	
117. Cling (Figs. 75 & 77)	
118. Dorsal carriage (Fig. 8)	Van Lawick-Goodall

119. Gather ventral (Fig. 79) Van Lawick-Goodall
120. Hand dangle (Fig. 83)
121. Hand-to-object
122. Hold hand behind (Fig. 82)
123. Lateral carriage
124. Lean out
125. Leg or arm cling
126. Palm or forearm carry (Fig. 54)
127. Place in front (Fig. 52)
128 Pull up (Fig. 81)
129. Side sitting cling
130. Tail tuft touch (Fig. 84)
131. Ventral carriage (Fig. 78) Van Lawick-Goodall

LOCOMOTOR PATTERNS

Bipedal locomotion (Fig. 1)

Although the chimpanzee is principally a quadruped, most observers report that bipedalism (locomoter movement using only the hind limbs) occurs regularly as a means of seeing over tall grass, carrying food, movement when grass is very wet, and as a ritualized pattern during threat, greeting, and courtship (Van Lawick-Goodall, 1968; Van Hooff, 1971).

In the Oklahoma colony it was noted that bipedal locomotion was especially prevelant among infants of 1½ to 3 years of age. At this age "bipedal locomotion" appeared to be practiced just as were "falling" and "somersaulting." Infants often walked around the cage bipedally for 2 to 3 minutes at a time for no apparent reason. Bipedalism was also observed when mothers moved about with young infants who did not cling tightly.

Brachiate (Fig. 2)

When "brachiating," the chimpanzee moves along under an overhead support by means of alternate hand-arm grasping motions. Typically, one hand clings to the overhead support while the other is extended forward to grasp. Initially, the body is propelled by leaping or pushing against a support with the feet, the momentum is then maintained by rotating the trunk axis through a half turn with each overhand grasping motion. "Brachiation" patterns among captive chimpanzees differed little from those depicted for wild chimpanzees. Infants began "brachi-

ating" between 1 and 1½ years. The pattern usually followed the normal adult movements during its first appearance, though execution was slow and hesitant for several months.

Climb

Chimpanzees live in a three-dimensional environment and the ability to climb rapidly and in agile fashion is important to their survival in the wild. In captivity agile climbing skills are necessary for keeping up with peers, both in playing and aggressive interactions. Chimpanzee infants climb up the wire, sideways along the wire, and down the wire for 1 to 2 months before they begin to move about "quadrupedally" on the floor. When "climbing" on the wire, infants employed the same alternating arm-foot movements used during "quadrupedal locomotion." Up to approximately 1½ years, infants appeared to be more coordinated while "climbing" than while walking and they were less hesitant to break contact with their mother if she stayed near the wire than if she moved to the center of the cage where there was nothing to "climb" on.

Charge (brusque rush)

The locomoter component of this pattern is the same as that of typical quadrupedal locomotion but the limbs are moved much faster and consequently are brought high off the ground. "Charges" were invariably rapid in the Oklahoma colony and differed from normal running in that the head was tucked far down into the shoulders and eye contact with the recipient of the charge was specifically avoided. The angle of the back also appears to be more horizontal during a "charge" than during normal running, presumably because the legs are straightened more fully during "charging." All limbs are placed on the ground with considerable force during a "charge," giving it a thundering quality

that typical running lacks. Hair may be sleek or pilo erect during a "charge," though it was almost always pilo erect during "charges" by males. "Charges" were not always directed toward other chimps, sometimes they were, in fact, directed away from another individual and served to initiate a vigorous chase bout.

Crutch (Fig. 7)

This is a relatively infrequent method of locomotion in which the chimpanzee propells himself forward by first moving his arms forward, as a unit, then swinging his legs (again as a unit) between his arms. "Crutching" often occurred when chimps were seated and they wished to move only a few steps, when they stepped on thorns, and during play. This form of locomotion was rarely used for distances greater than 5 to 10 yards.

Footstamp (stamping) (Figs. 3 and 4)

The "footstamp" involves an upward raising of the leg with the knee flexed. The foot is then brought down almost vertically by a powerful and rapid extension at the hip and knee. The "footstamp" was either directed toward the ground or toward the back of a crouched individual. Infants were only seen to direct "footstamps" toward the ground. Frequently, the "footstamp" involves a double beat in which both feet perform the pattern, one foot stamping slightly before the other with the second stamp being noticeably louder than the first. Developmentally, the single "footstamp" appears first, between 8 and 10 months, followed by the double "footstamp" about a month or two later. Infants displayed the "footstamp" with "pilo erection" during arousal situations. When they emitted the "footstamp" during playbouts, their hair remained sleek. "Footstamps" which occurred during play were used either to get the at-

tention of another infant who was reluctant to play or to keep another infant from breaking off a playbout and moving away.

Freefall (Fig. 5)

In this pattern, the chimpanzee typically leapt outward from a support and fell, landing on all fours or in a rolling "somersault." Male infants began to perform the "freefall" between 12 and 18 months of age while females began about 6 months later. The first "freefalls" were executed from a distance of only a few inches, but infants gradually worked up to 3 to 5 foot "freefalls" by 2½ years and older juveniles sometimes "freefell" distances of 20 to 25 feet into grassy terrain. Although female infants began the "freefall" pattern later than males, by the juvenile stage they were as proficient as males, and in some cases more so.

Gallop (Fig. 6)

In this pattern the hind and fore limbs are lifted off the ground more or less simultaneously though one fore limb actually preceeds the other briefly, both as it is lifted and placed down, and likewise one hind limb slightly preceeds the other. "Galloping" typically occurs during play.

Jump (Fig. 9)

In this pattern the chimpanzee flexes its knees, and, if standing quadrupedally, its elbows, and pushes upward, straightening the flexed joints rapidly so its body is lifted off the ground. Bipedal jumping, as well as quadrupedal jumping was seen, with bipedal standing jumps producing the greatest lift distances. In some instances, chimpanzees stood bipedally and jumped at least 2½ feet from the ground.

Quadrupedal "jumping" appeared shortly after infants became able to locomote independently. Initially, the infant did not "jump" off the ground, but bounced up and down by bending his arms and knees. Older infants similarly bent their arms and knees but with enough force to hop a short distance off the ground. "Jumping" appeared in most playbouts, but was also seen when new individuals were introduced into the mother-infant group and sometimes during general excitement. "Jumping" differs from "bobbing" in that the chest is not lowered to the ground, and a "bipedal" stance is not assumed between jumps.

Knuckle slide

When exposed to wet or smooth surfaces, chimpanzees of all ages, but especially juveniles and infants, may place their knuckles on the ground slightly in front of their head and shoulders and push themselves along with their feet. The knuckles are not raised, they simply slide over the slick surface as the arms are held stiffly in front of the individuals with the elbows locked into the fully extended position.

Playwalk

This is a rather stiff, stilted gait, with very short bouncy steps, which may be assumed during play. In its most exaggerated form, the individual may actually bounce an inch or so off the floor. The head is tucked back into the shoulders and slightly lowered but the face looks directly forward. It differs from the "jump" in that the bouncing component is obtained not by elbow and knee flexation but by ankle and trunk movement.

Pirouette

In this pattern, the chimpanzee spins round and round by alternately balancing on his knuckles and then his feet. It appears during indi-

vidual locomotor play and may be repeated numerous times until the infant is quite dizzy. The knuckles are placed on the ground, one slightly before the other, and the feet are lifted off the ground and the body is rotated so that the feet land, one slightly before the other, ahead of and at right angles to the knuckles. The knuckles are then lifted off the ground and the anterior portion of the body is rotated so that the knuckles are placed in front of, and at right angles to, the feet. It is the quadrupedal equivalent of "spinning round" exhibited by human children. Occasionally, chimpanzees may also assume a bipedal stance and spin around. One chimpanzee has even been observed to "spin" using only one foot.

Quadrupedal locomotion (Fig. 8)

During typical "quadrupedal locomotion" chimpanzees jointly move the fore and hind limbs on opposite sides of their bodies. The foot may be placed either laterally or medially with reference to the hand of the same side and the lateral or medial placement may be altered in midgait. Chimpanzees generally walk on the soles of their feet and on their knuckles, however, they may occasionally be seen placing the palms of the hands, the backs of their hands, or their fists upon the ground. "Quadrupedal locomotion" may be performed at any speed, from a slow walk to a fast run.

Rock

This pattern consists of stereotypic short swaying movements which may be from front to back, from side to side, or circular. The entire body may "rock" or the movement may be limited to the shoulders or head. Chimpanzees usually "rocked" if confined to one room of their multi-roomed cages, when hosing was done close to them, when strangers entered the laboratory, or when waiting for the handler to arrive at their cage

with food. They also "rocked" during aggressive interactions between chimpanzees in adjacent cages. Infants reared by chimpanzee mothers were not seen to "rock" until near 4 years of age while some human reared chimpanzee infants displayed "rocking" patterns before the end of the first year. Most chimpanzees appeared to adopt their own particular form of repetitive movement, but a few were never observed to "rock." Such individuals typically displayed repetitive pacing or "bobbing" motions if frustrated.

When "rocking," chimpanzees periodically stared straight ahead as though fixated upon an invisible point in space. They were, however, quite aware of everything going on within their field of vision. Once a particular form of "rocking" behavior appeared, it was not observed to undergo developmental alteration.

Somersault

This pattern is almost identical to the human play pattern of the same name and may be performed frontward, backward, or sideways. The back of the head or shoulders is rapidly lowered toward the ground while the back is bowed. As the head or shoulders touch the ground, the legs push off the ground and are then tucked inward toward the chest and the individual is propelled through a 360 degree arc.

In the Oklahoma colony this pattern began to appear at about 18 months of age and was properly executed upon the first observed appearance.

Infants used the pattern in both locomotor and social play. When "somersaults" occurred during individual locomotor play, they tended to be repeated many times, but when the "somersault" appeared during social play, it was less likely to be immediately repeated and was typ-

ically oriented toward another chimpanzee. The performer often used the "somersault" to initiate a playbout by flipping himself over and landing on his back in the recipient's chest.

Swagger (bipedal swagger, sway-walk) (Fig. 55)

When "swaggering" the chimpanzee typically, though not invariably, assumes a bipedal stance. He then begins to sway rhythmically from side-to-side, moving his trunk, shoulders, and arms. The feet may be alternatingly lifted and replaced upon the ground and the chimpanzee may "swagger" in one spot or he may move bipedally while "swaggering." This pattern is one of the most dramatic of the chimpanzee and is employed, with subtle variations, in a wide variety of contexts. Common components in the variations of this pattern include "pilo erection," "hunched shoulders" and a rotation of the arms forward and out from the body. The movement component of a "swagger" may be mild or vigorous and may include the whole body or only the shoulders and arms. (Movement may be entirely absent, in which case the behavior is described in terms of its other components, i.e. "pilo erection," "hunched shoulders," "bipedal" movement, etc.) The "swagger" is displayed by both males and females and begins to appear in play between 1 and 2 years of age. Some degree of "pilo erection" is usually associated with early displays of the "swagger," but the shoulders may be only slightly hunched. "Swaggers" which appear during play often are accompanied by a "footstamp" or other pattern not characteristic of "swaggers" which appear in other contexts. "Swaggers" are typically directed toward a particular recipient by direct, but fleeting and intermittent, eye contact. If "swaggers" are not responded to by the recipient, they may be escalated into a "display" or "charge." If a "swaggering" individual is approached, an

"embrace" of some form frequently ensues. In this context it is interesting to note that mothers occasionally "swagger" toward infants who are temporarily reluctant to cling ventrally when the mother wishes. After "swaggering," the mother then offers her venter, and in all observed cases, infants have climbed immediately into the ventral position.

Tripedal locomotion (Fig. 10)

"Tripedal locomotion" differs from "quadrupedal locomotion" in that the limbs on opposing sides of the body typically do not move jointly. Instead, both the right hand and right foot (or left hand and left foot, as the case may be) are moved forward together while the chimpanzee balances on the remaining foot. That foot is then moved forward and the sequence is repeated.

FACIAL EXPRESSIONS and VOCALIZATIONS

Barks

The range and variability of "grunts" and "barks" is extremely large. Presently it is possible to identify and connect them with 4 general types of social situations, greeting-reunion, approaching and eating food, contact and travel, and agonistic or aggressive interactions. It is not known whether or not "grunts" or "barks" which sound different in a given setting actually convey different, but specific, messages or whether the sounds simply reflect a rise or fall of emotional arousal. All such sounds are made very low in the throat, they are delivered intermittently, and receive little or not modification from the upper vocal tract.

<<Uhh grunt>> <<eeeh squeaks>>

This vocalization is specifically associated with food and is probably innate since young infants reared in species isolation come to pro-

duce the sound spontaneously when presented with food. This vocalization probably falls in Van Lawick-Goodall's (unpublished glossary) category of "grunts" which is characterized as calls "given during feeding, by relaxed individuals during resting, grooming, and traveling, and so forth." Van Hooff (1971) also places this vocalization in a general category of "grunts and grunt barks."

The "≪uhh grunt≫" is usually delivered in a series of repetitive intermittent sounds, which range from 3 or 4 to 30 consecutive sounds in a given exhalation. The sounds rise and fall in pitch and intensity and the vowel sound may change slightly to an "≪eeh≫" like sound. The vocalization is given both during travel toward food when food is not in sight and during eating. It may grade into high "≪eeeh squeaks≫" if a highly preferred food is spotted or eaten. "≪Eeeh squeaks≫" possibly correspond to van Hooff's (1971) "cackles."

≪Low grunt≫

This vocalization is very similar to the "≪uhh grunt≫" except that it is lower in pitch and intensity and is generally delivered in a series of only 1 or 2 intermittent repetitive sounds. It is employed during travel as one individual is ready to move and is given usually just prior to starting off in a particular direction. It also occurs when one traveling individual moves some distance ahead of a companion and then stops and waits. The "≪low grunt≫" is then often given as the companion approaches. "≪Low grunts≫" from one individual during travel may be responded to with similar "≪low grunts≫" from a companion.

≪Pant grunt≫ (Rapid oh oh series)

This vocalization consists of a series of breathy grunt vocalizations made during both inhalations and exhalations. These grunts contain more

variability with regard to the actual phonetic sound which was produced than did "«uhh grunts»" or "low grunts." They ranged from a vocalization identical to that of loud audible "laughter" to vocalizations identical to loud threats. They differed from threats, however, in that they were very repetitive and were interspersed with pants.

«!Ougggh bark» (Fig. 12)

This is an explosive throaty vocalization typically given during agonistic or aggressive situations. It is generally oriented toward an individual who is at least several feet away and reflects displeasure with the actions of that individual. It is not obviously correlated with dominance. It has been given, for example, by a low ranking individual who sees a middle ranking individual getting or eating fruit when the high ranking individual of the group has none. The "«!ougggh bark»" then draws attention to the middle ranking chimp who may be attacked by others, but not necessarily by the chimpanzee giving the original vocalization. On numerous occasions, chimpanzees in one cage caused an individual in an adjacent age to be attacked, or at least threatened by his cagemates, by giving an "«!ouggh bark»." Occasionally, this call was ignored by others in the group, and in such cases no other action followed.

«!Aggh bark» (soft bark, cough threat)

This vocalization is an implosive single syllable threat usually delivered to another individual who is nearby. It indicates a readiness for aggression on the part of the vocalizing individual, as well as displeasure with the presence or action of the recipient of the "«aggh bark»." It is typically directed at lower ranking individuals, though a chimpanzee if sufficiently angered or irritated will orient

the bark to high ranking individuals. The "«!aggh bark»" is not generally followed by aggression since the recipient often moves away and leaves the initiator alone. The "«!aggh bark»" is typically delivered with an upward tip of the head. Situationally, it seems to differ from the "«!ouggh bark»" in that it does not command the attention of other individuals or seek their support.

«!Ugh bark» (soft bark, uh grunt) (Fig. 11)

This vocalization is a low rough single, double or triple syllable bark. It is made directly toward another chimpanzee, usually a subordinate, with a characteristic facial expression in which the lips are slightly parted and the top lip is barely turned upward at the center of the mouth. The lips are held in this position only during the actual vocalization.

The "«ugh bark»" may correspond to van Lawick-Goodall's (unpublished glossary) "soft bark" and as such may simply be a softer version of the "«aggh bark»."

Mothers occasionally used the "«!ugh bark»" to threaten their juvenile offspring if the juvenile became particularly demanding of the mother's food, attention, etc. Infants gave "«!ugh barks»" while clinging ventrally when their mothers were approached by individuals with whom they were unfamiliar. Van Lawick-Goodall (unpublished glossary) classifies the infant vocalization as a separate sound termed the "uh grunt."

Bite threat

This pattern consists of a quick turning of the head toward another individual accompanied by an opening of the mouth and a very rapid upward and outward motion of the center portion of the upper lip. This lip movement is so fast that the observer can often be certain that it occurred

only by watching a slow motion video tape of the episode. This is not because the movement is faster than the eye but rather because the observer's attention is not riveted on this movement or else he is too far away. This threat is used only at very close quarters (lees than 2 feet) and due to the small amount of movement involved and the rapidity of execution, it probably could not be effectively detected at greater distances. This was a very severe threat, superceded only by a more intense form of the same gesture which involved actually placing the teeth upon the opponent's body, after raising the upper lip. The pattern may be parsimoniously interpreted as an inhibited intention to bite. The upper lip is raised to clear the path for the teeth, and the pattern is classified as a "bite threat" only because it is not followed by a true "bite." This pattern was not identified by the author for some time due to its subtlety and quickness. It was, in fact, only after the pattern had been directed toward the author on several occasions, once being followed by a true "bite," that the significance of the expression was finally realized.

Cheek or Lip suck (sucked in cheek face)

In this expression either the sides of the face or the lips are pulled over and between the teeth, probably by creating a slight vacuum in the oral cavity. Van Lawick-Goodall (unpublished glossary) reported that this face may occur during play in particular youngsters. The face was also seen in some youngsters, but not others, in the Oklahoma colony. It was most prevalent in a juvenile who had been reared in a human home since birth and this individual responded to the "cheek face" (made either by a person or a chimpanzee) with play behavior.

Closed-teeth-face

This expression involves partial horizontal retraction of both the upper and lower lip so that the teeth, but not the gums are visible. Morphologically, it is a closer approximation to the human smile than any chimpanzee facial expression. It is not a fleeting expression, nor is it associated with any vocalization. It is often a reaction to strong wind or bright sunlight and does not seem to be employed as a specific social signal.

Full closed grin (closed mouth bared teeth) (Fig. 86)

In this expression the lips were retracted horizontally until both upper and lower teeth and gums were fully visible. The jaws were closed. The "full closed grin" could be reliably interpreted as a submissive signal during aggressive interactions. It was also used by infants to regain bodily contact with one another while brachiating about the cage. In these instances, the infant in the lead would often pause and orient a "full closed grin" toward the following infant who would then approach and both infants would perform a "waistclasp embrace." Further, the "full closed grin" was used by individuals under attack to enlist the support of allies.

Glare

This was a fixed, steady stare directed at another individual. It usually included a setting of the jaw position and a slight furrowing of the browridge. It was further differentiated from "looking" by being directed at the recipient's eyes.

Grin face (Fig. 7)

This facial expression may be regarded either as a low intensity "play face" or a low intensity "closed-teeth-face." It involves a slight

parting of the lips with mild horizontal retraction. The teeth are just barely visible. This expression may be maintained for many minutes while an individual is engaging in solitary locomotor play or object manipulation. It also appears during social play and at times during "thrusting" and "mounting" between youngsters.

Hoo call

This is a medium pitched call, usually given as a single syllable, though it may be repeated several times with a second or so elapsing between repetitions. Van Lawick-Goodall (unpublished glossary) states that the call is made when a chimp suddenly hears or sees a strange sound or object. My observations agree with hers.

Hoo whimper (Fig. 20)

This call is a soft, tonal, repetitive call uttered with both the upper and lower lips pulled toward the center of the face and then turned outward about the rims. Van Lawick-Goodall (1968) reports that among wild chimpanzees the "hoo whimper" serves as a "fairly specific signal in re-establishing mother-infant contact." The "hoo whimper" was used in a similar fashion in the Oklahoma colony but it was further employed to initiate contact between infants, between an infant and a juvenile, or between a mother and another infant. Individuals of all ages were heard to emit "hoo whimpers" but infants used this call fourteen times more frequently than all other age groups combined.

When emitted by infants, the pitch of the "hoo whimper" is higher and less resonant than when emitted by adults. While the author maintained daily observation sessions, the "hoo whimpers" of individual infants were distinguishable by ear alone.

«Iieow scream»

This scream has not been previously separated from the other types of screaming which occur during agonistic and aggressive encounters. It is a savage sounding, extremely high pitched, clear tone which rises and falls rapidly in frequency. Individuals giving "raucous screams" suddenly grade into "«iieow screams» " as they actually attack or lunge toward another individual. Other individuals may also join in giving the "«iieow scream» " as the other chimpanzee is attacked. The "«iieow scream»" is typically associated with the "open-mouth-bared-teeth" and the "open-mouth-bared-teeth-and-gums" expressions.

Laugh

The "laugh" is a breathy, slightly audible vocalization made in a panting fashion during play. Both the inhalation and exhalation portions of the vocalization can be heard. "Laugh" occurs most frequently during rough-and-tumble play and is often absent during chase play.

Lip bulge (Figs. 13 and 72a)

In this expression the lips are pressed tightly together and pushed slightly forward creating a "bulge" around the upper and lower lip areas. It is more characteristic of males than females and typically precedes displays.

Lip buzz

This pattern involves pushing the lips tightly together and then forcing short bursts of air through them to make a buzzing noise. Van Hooff (1971) observed "lip buzzing" in the Holloman colony but van Lawick-Goodall (unpublished glossary) does not report its occurrence in the wild. The signal was typically used to gain the attention of either a handler or a chimpanzee in another cage.

Lip flip

The upper or lower lip is turned inside out and held in that position, exposing the inner lining, for 30 or 40 seconds. In both captive and wild chimpanzees the lip flip seems to be an idiosyncratic behavior of some individuals and it is not associated with any particular type of social situation (van Lawick-Goodall, unpublished glossary). In the Oklahoma colony this signal was used mainly to get the attention of visitors though it also appeared during individual play in some infants.

Look at (glance) (Fig. 15)

Chimpanzees typically avoid staring directly at one anothers eyes, but they do "look at" and attain eye contact with one another continually. Eye contact precedes or accompanies the delivery of communicative vocalizations and gestures and serves to direct the communication toward the appropriate recipient. Van Lawick-Goodall (unpublished glossary) defines a "glance" as looking "towards another for less than 2 seconds." It has been my experience, however, that as long as eye contact is avoided, one chimpanzee can "look at" another for long periods of time.

Low-closed-mouth-bared-teeth (cry face, bared teeth yelp face, low closed grin)

This expression involves a retraction of the lower lip which displays the lower teeth and gums. "Low closed grins" were given with ≪ehh squeaks≫ during eating and as a transitory expression between the "hoo whimper" and various screams. The expression was less common than other bared teeth expressions and, apart from the feeding context, seemed to be given on occasions when an individual was attacked, threatened, rejected, etc. without provocation or warning.

Normal face (relaxed face) (Fig. 19)

The chimpanzee face is capable of a myriad of expressions, many of which will not be listed in this glossary as they are not yet fully sorted out and labeled. A "normal face" usually occurred only when a chimpanzee was not interacting with or looking at another chimpanzee because a facial expression of some sort nearly always accompanies such social interaction. In Figure 19 the infant shows a "normal face," but the mother displays a mild tightening of the corners of the lips as she reacts to the camera.

Pant

This is a non-vocal form of rhythmic breathing in which the rapid in and out movements of the diaphragm are clearly visible. The pants are usually performed with the mouth open and the lips slightly parted so as to form a large "O." The teeth are not visible. "Panting" occurred during greeting and sometimes at the beginning of a grooming session following a greeting. Mothers sometimes "panted" to their infants upon regaining ventral contact following a separation that was generally not initiated by the mother. The infant might have, for example, "hitched a ride" outside with another mother, moved away when his own mother approached, or simply have been out of contact with his mother for a long period of time (relative to the amount of time generally spent out of contact with the mother at any given age). Mothers also rushed toward their infants, "embraced" them ventrally and "panted" when about to be fed a highly favored food.

Frequent, periodic, and often spontaneous "panting" was observed in most mothers for periods of as long as 2 to 7 days following the birth of their infants.

Pant hoot (Figs. 14 and 37)

This is a sonorous, rising vocalization made during inhalation and exhalation. It begins in a very soft medium pitched tone, similar to a "hoo whimper" and crescendos into a piercing scream. Among the captive group at Oklahoma, "pant hoots" were given at the arrival and departure of humans who worked with chimps, before feeding and during displays by adult males. During a "pant hoot" chorus, individuals often looked at one another as they began to "pant hoot" then looked away as the "pant hoot" rose in volume.

Pant screams

This scream is usually given with the "open-mouth-bared-teeth-and-gums" facial expression. In the Oklahoma colony the "pant scream" was typically integrated with the "raucous scream." While giving a loud "raucous scream" the raucous exhalation portion of the scream would become so harsh that the vocal component disappeared and only a pant was heard. The inhalation vocalization remained however, thus producing a combination of "pant" and "scream." Chimpanzees produced "pant screams" when badly bitten or hurt and when being soundly attacked by an opponent they did not dare to resist. They were a fairly reliable indicator of submission to an attacker.

Play face (half and full) (Fig. 16)

The "half play face" is characterized by a relaxed dropping of the lower jaw and lip, thereby exposing the lower teeth. In the "full play face" the lower jaw is pulled down even further thus tightening the upper lip slightly and causing it to retract so that the upper teeth are also visible.

In the Oklahoma colony, the "full play face" is generally observed

when a smaller or younger chimpanzee initiates play or plays with a larger or older chimpanzee. During play the more intense form of the "play face" is often displayed by the youngest individual. Mothers spend long periods of time playing with their own and other infants without displaying any sign of a "play face," but infants typically display some form of the "play face" throughout the interaction.

The "full play face" is also seen when a chimpanzee attempts to initiate play with others who are resting, grooming, etc. and hence are unlikely to be responsive to playful approaches.

Both "half" and "full play faces" are observed throughout playful interactions although they may become less noticeable if the play session evolves into a rapid and vigorous chase game. As long as the play remains slow paced and relaxed, "play faces" are apparent during the entire playbout.

Open-mouth-bared-teeth

This facial expression has not been previously separated from the full "open-mouth-bared-teeth-and-gums" display. Instead of fully retracting his lips so that both gums and teeth are visible, the chimpanzee may retract them only far enough to reveal his teeth. This display also occurs during agonistic and aggressive encounters. This facial display often indicates less inhibition to attack than does the "open-mouth-bared-teeth-and-gums." A chimpanzee, after looking round and soliciting support with "screams" and "open-mouth-bared-teeth-and-gums," will suddenly lunge toward his antagonist, changing to a "raucous scream" and "open-mouth-bared-teeth" expression as he does so. The exact position of the lips and tone of the scream vary considerably and rapidly, depending upon who the chimpanzee is looking at during his display (that

is, whether he is looking at an individual who might provide him with reassurance, one who might lend support, one who is attempting to ignore him, or one who is likely to attack him).

Open-mouth-bared-teeth-and-gums (full open grin) (Figs. 17 and 18)

In this facial expression, both the upper and lower lips are retracted extensively so that the teeth and gums are fully bared. Van Hooff (1971) found that the "pulse scream," "double scream" and "pant scream" were associated with the "open-mouth-bared-teeth-and-gums" expression. The characteristic vocalization accompanying the expression in the Oklahoma group was the "raucous scream," however, "pure screams," "squeaks" and "squeals" also accompanied the facial display, and occasionally the expression was given silently. The display was associated with agonistic and aggressive interactions and was given by both dominant and subordinate individuals. In addition to indicating a high degree of excitement or arousal, the facial expression took on more precise meanings when displayed in conjunction with different vocalizations.

Raucous scream (pulse scream, rough scream, rasping scream) (Fig. 18)

The "raucous scream" occurred during agonistic and aggressive encounters and was accompanied by the "open-mouth-bared-teeth-and-gums" or the "open-mouth-bared-teeth" expression. It did not accompany any of the closed mouth expressions. "Raucous screams" were given by both dominant and subordinate individuals. At times 2 individuals would give repeated "raucous screams" at one another, place their teeth on one another while screaming and "glare" at one another, then one would back off and the screaming would stop. The scream seemed to convey a high level of arousal but was not a reliable indicator of submission or fear. Typically, a chimp giving a "raucous scream" desired to attack but was hesitant to do

so without some support from another or sign of weakness or uncertainty on the part of the recipient. If, for example, a chimpanzee was angered by an individual who took fruit from him, but he was hesitant to attack that individual, he would begin giving "raucous screams" and looking round for support. If the individual who was being screamed at acknowledged it or displayed concern by edging away, shaking slightly, etc. that individual was immediately attacked. If the screaming individual received no support and observed no concern on the part of the recipient, the screamer either quieted down or went in a "temper tantrum" and then quieted.

Rising hoowhimper

This call began with a "hoo whimper" then rose and fell in melodious tones. It was accompanied by a specific facial expression in which the center of the upper lip was turned outward (as in the "hoo whimper" expression) while the lower lip was dropped and drawn back.

Infants were the most frequent initiators of "rising hoo whimpers" and they generally used it toward other infants and toward juveniles. Occasionally, "rising hoo whimpers" were oriented toward mothers. "Rising hoo whimpers" occurred most often in pleading contexts, both when the initiator wanted another chimpanzee to let go of him or when he wanted another chimpanzee to approach him.

Silent pout face, hoo whimper, horizontal pout face, rising hoo whimper, open-mouth-bared-teeth-and-gums, squeal (Figs. 20 and 20a)

This sequential display is quite graded, entailing only a slight puckering protrusion of the upper and lower lips in its mildest form. At a slightly higher arousal level, a "hoo whimper" is heard but the facial expression remains unaltered. If arousal increases, the "hoo

whimper" begins to rise and fall (rising hoo whimper) and the lower lip is retracted to reveal the gums and teeth while the top lip remains puckered. At still higher intensities the upper lip is also retracted and pure tone squeals, squeaks or rasping screams may occur. At the highest arousal levels, a temper tantrum may erupt. A display of the entire graded sequence is usually seen only in infants. Although the display is graded, one cannot assume that an individual who has gone from a "silent pout face" to an "open-mouth-bared-teeth-and-gums raucous scream" conveys the same information as an individual who begins the vocalization with an "open-mouth-bared-teeth-and-gums raucous scream."

Tonal scream (double tone scream, high-pitched long drawn out scream)

"Tonal screams" were typically given with the "open-mouth-bared-teeth-and-gums" expressions. Like "raucous screams," "tonal screams" occurred during agonistic or aggressive interactions, but unlike "raucous screams," if directed at an antagonist, they indicated submission or a readiness for conciliation. They were also employed in a rapidly alternating fashion with "raucous screams" to solicit support or reassurance from a third individual. Acoustically, they were readily distinguishable from "raucous screams" because of the high pitch and purer tonal quality. Even within a given series "tonal screams" however, had a wide degree of variability in pitch, intensity, and duration which possibly conveyed quite specific information.

Waa bark

This is a high pitched explosive single syllable call which appeared to function as a signal of alarm. It was given, for example, if one chimpanzee approached a large or dangerous animal, by others who were with him. Most individuals, upon hearing a "waa bark," stopped immedi-

ately and began to look about them or ceased their approach toward an animal or object which had caused the others to give a "waa bark." "Waa barks" were given during aggressive encounters, but here again they appeared to function as an alarm signal for they were usually given by individuals watching a chase as the pursuer was about to catch and bite his victim.

Van Lawick-Goodall (unpublished glossary) regards the "waa bark" as a high intensity threat.

Wide eyes face (Fig. 21)

This facial expression has not been previously separated from the typical or relaxed face. The eyelids of the "normal face" are typically closed over the top portion of the eye. In the "wide eyes face," the lids are fully retracted and the eyes appear much larger. The head is often tucked down slightly toward the chest, while the eyes look upward and the lips may be slightly parted or mildly protruded. Chimpanzees often assumed this facial expression when a more dominant individual "glared" at them, when they wanted to touch an infant, when they were unsure of their actions, etc.

INTERACTIVE PATTERNS

Arm-around-back (Fig. 22)

In the "arm-around-back" pattern, the arm is placed casually over another's back and the hand may or may not cling to the hair on the partner's shoulder. This position may be adopted only for a period of a few seconds or it may last 5 to 10 minutes as individuals walk around together in this fashion. It most frequently appears among infants and juveniles and becomes extremely common when peers are reared together

without mothers. The "arm-around-back" pattern does appear among adults, however, generally being elicited by a sudden alarming occurrence. This pattern is first seen at approximately 5 to 6 months of age or shortly after the infant becomes independently mobile. It is typically oriented toward a slightly larger infant or toward a juvenile. Infants of this age are unsteady on their feet and by holding onto a slightly larger individual they can greatly increase their exploratory range. Older infants and juveniles are very patient when escorting younger individuals about in this manner, carefully taking short, slow steps to enable the infant to keep up. Often they even notice that infants are encountering locomoter problems and approach them and offer their backs to be held.

Arm-around-embrace (Fig. 23)

In this pattern the arm is placed around the body of the recipient and the upper chest and/or face are held against the recipient for a few seconds. Often the pattern is accompanied by a nuzzling playbite delivered to the recipient's shoulder-neck area. Mothers often embraced their infants in this manner.

Ano-genital inspection (Fig. 24)

An "ano-genital inspection" consists of visual orientation toward the genital area, generally followed by sniffing and then touching of the outer genital or anal region, and then insertion of the finger into the female genital area or gentle holding of the male's penis with hand or lips.

Mothers performed frequent "ano-genital inspection" of their infants, and occasionally performed "ano-genital inspections" of other infants. These inspections led to genital grooming if the mother found the slightest particle of fecal matter, or other material, clinging to the infant's

genital region. The penises of male infants were sometimes gently mouthed, as were the genitals of female infants. Such mouthing produced penile erections among male infants and gave the genital area of females a slightly rosey, turgid appearance.

Infants also performed "ano-genital inspections," usually oriented toward their mothers or other adult females, and, more rarely, oriented toward one another. Frequent, repetitive "ano-genital inspections" were invariably performed by all individuals during introduction to new individuals or reintroduction to previously acquainted individuals.

Backhand thump (Fig. 26)

This gesture consists of orienting the palm toward the face with the forearm held in front of the head and the wrist bent slightly inward, toward the head. The back of the hand or wrist is then directed downward toward the recipient, who faces the initiator. The recipient is firmly but gently thumped with the back of the hand or wrist on the face, head, or shoulders, one or more times.

The gesture appears both in playful and in agonistic contexts. When it occurs in agonistic contexts, it appears to be an inhibited form of aggression and may signal the termination of an aggressive encounter.

Bite

This was a vigorous open jawed lunge toward another individual. When contact was made, the jaws were clamped shut rapidly and forcefully. A true "bite" was preceeded by a flashing of the teeth described under "bite threat." It followed the teeth flash instantaneously, was vigorous, savage, and brief, and was followed by a quick withdrawal from the victim. Chimpanzees generally placed their "bites" at very strategic locations, relative to the position of their victims, such that the

victim had little opportunity to "bite" back before the attacker had withdrawn. An animal who will generally not even threaten a more dominant individual, will "bite" back when being "bitten." (This is not true for many of the other forms of attack, e.g., slapping, dragging, etc.) "Bites" were usually held only as long as it took to pierce and tear the skin of the recipient. Longer "bites" were observed when one adult male, after having repeatedly attacked an unfamiliar adult male in the typical fashion, began prolonged tearing "bites" with 2 to 3 tearing jaw movements during each "bite." In this case, the victim was too weakened to show any resistance whatever to his attacker and had they not been separated, he would surely have been killed.

Bodyfling

The "bodyfling" was performed in a variety of ways, the only commonality among them being that the whole body of the performer was propelled onto or toward the body of the recipient. This pattern occurred from a bipedal stance or from a quadrupedal stance and it did not appear to matter which portion of the body was flung toward the recipient or upon what portion of the recipient's body the performer landed. These matters were more a function of the particular posture at the time of execution than of the performer's intent.

This pattern was typically displayed by infants and they generally oriented it toward individuals larger than themselves. It served both as an initiator of play and as a regularly occurring pattern during play.

Chase (Fig. 25)

In the Oklahoma colony this pattern was one of the first to appear in the play repertoire of the infant chimpanzee, generally occurring at about 8 months of age or when the infant became relatively mobile. The

pattern frequently involved role reversal when it occurred among juvenile chimpanzees with the chaser repeatedly becoming the chasee. This was not always true when the pattern occurred among infants, adolescents, or adults. Perhaps this was because juveniles played more frequently and tended not to break off the playbout until both partners were exhausted. Infants, however, often abruptly walked away from a playbout simply to go and sit next to their mothers. Adolescents and adults often terminated playbouts in a similar manner, moving off to join another group of chimps or to explore on their own.

One of the most important aspects of "chase" play was the frequent "looking back" of the chasee, generally accompanied by a "playface," or "grinface." "Looking back" enticed the other chimp to follow and many "chase" episodes were initiated simply by one chimp orienting his rump toward another several feet away and then "looking back." The "looking back" component effectively differentiates this behavior from actual "fleeing." When a chimpanzee "flees" during an aggressive encounter, he does not "look back" until he is a safe distance away and even then "looking back" may cause the opponent to resume his attack, especially if eye contact between them occurs.

The gait adopted during "chase" play also serves to separate this pattern from "fleeing." It involves exaggerated galloping and cavorting movements often accompanied by a large degree of limb flexion. It appears to be important to clearly differentiate these two patterns since the chaser may actually attack the chased if he perceives him to be frightened. Often the smaller of the two chimpanzees will engage in frequent "looking back," "somersaulting" and "laughing" in order to assure the follower that he is actually playing. Younger chimpanzees oc-

casionally went to great extents, playing long after they were obviously winded in order not to give the impression that they were trying to avoid the other individual.

Finger tickle (Fig. 27)

This pattern involves pushing and proding finger movements which are directed toward ticklish portions of the recipient's body. In the Oklahoma colony the "finger tickle" pattern was most often observed between mothers and infants and was one of the earliest play patterns directed toward infants. Mothers initiated the pattern by pulling their non-mobile infants up over their bodies with their feet as they lay on their backs. Then, as they held the infant above them, they made small "finger tickling" movements under chin, in the thighs and armpits, or on the ribs. Older infants sat next to mothers with their shoulders rolled inward, or lay on their backs while mothers "finger tickled." When the mothers paused the infants would often take hold of one of her fingers and pull it to a ticklish spot on his body.

Follow

This pattern involves the deliberate adjustment of ones path of movement to correspond with the movement of another individual. It is typically done simply by moving along behind another individual.

Infants began "following" their mothers as soon as they were mobile (4-5 months) and by about 9-10 months of age they occasionally "followed" other infants, juveniles, and other mothers. "Following" was initiated either by the "follower" or by the chimpanzee being "followed." "Following" differed from "chasing" in two basic ways. It was executed at a much slower rate and the "looking back" pattern was performed differently during "chasing" than during "following." The lead chimpanzee

usually actively participated in the "follow" pattern by pausing every so often to look back at the "follower." If the "follower" was proceeding adequately, the lead chimpanzee moved on. During "following," these backward looks were given with a slight pause in the gait of the lead chimpanzee, and they were not accompanied by a "play face." During "chase" play the lead chimpanzee did not usually pause when "looking back" and his face characteristically assumed the "play face" expression when he did look back.

Groom (Figs. 28 and 28a)

This is the typical primate pattern of picking through the bodily hair. Captive chimpanzees usually employ one hand to part the hair and the other hand and the lips to scratch or remove particles. Mother-infant grooming techniques differed somewhat from adult-adult grooming in that mothers almost always held their infants in their lap while they groomed them. Infants were also repeatedly positioned and repositioned (as opposed to occasional positioning during adult grooming), and often appeared to be placed in rather uncomfortable positions during grooming bouts. The ano-genital region received the most attention, but other orifices, such as the nose and ears were cleaned regularly, along with the general body hair. When an infant attempted to resist grooming it was pinned in the lap by the mother's arm or leg, and grooming continued unless the infant vocalized loudly. Captive mothers sometimes carried infant grooming to extremes by plucking or biting off hairs until large patches of the infant's body were completely denuded. Mothers employed the teeth and lips much more frequently when grooming infants than when grooming older individuals.

Most mothers groomed infants during nursing bouts and though infants

wiggled as though uncomfortable, they tolerated the grooming and continued nursing.

Infants begin making grooming-like motions at 5 to 6 months of age. These initial grooming bouts usually involved only a poking, touching, or scratching with the index fingers, although occasionally the lips might be pressed against the body of the recipient. These early grooming motions were brief, lasting perhaps 1 to 5 seconds. At 1½ to 2 years of age, both hands began to be used during grooming, the fingers of one hand parting the hair, and the index finger of the other hand poking or scratching. Infant grooming bouts were still brief, normally less than 30 seconds, and infrequent. Infant grooming was almost always directed toward a scrape or scratch on the body of the recipient. "Ruffling" of the hair, as described by Van Lawick-Goodall (1968) was not an infant grooming technique, but did occasionally appear during play.

Juveniles employed adult techniques of grooming, but when grooming adults, they often displayed exaggerated grooming behaviors. They lip-smacked loudly, used vigorous hand motions, peered quite intently at the groomed area, and adopted extreme positions to be able to reach their chosen grooming location. Juveniles also groomed one another, but not frequently and their grooming techniques were not exaggerated during such grooming. Juveniles rarely groomed infants.

Hairhold (Fig. 29)

The "hairhold" typically occurred during play and entailed grasping the hair of another chimpanzee with the hand or foot and twisting the hair about between the fingers and the toes. The hair was not pulled "away" from the body of the recipient and "hairholds" did not appear to cause any pain. The recipient of a "hairhold" responded with a "play

face," "laughter" and feigned exaggerated attempts to break loose from the other's grip. The "hairhold," like many other play patterns, involved frequent role reversal when it occurred between individuals of similar size. Although "hairholds" were initiated upon any part of the recipient's body they were generally directed to the shoulders, the back and the outside of the thighs. "Hairholds" appeared between 5 and 6 months of age, simultaneously with "playbites." They were observed among chimpanzees of all ages.

Hairtug

"Hairtug" is an intermediate pattern between "hairholding" and "hair-pulling." It involves grasping the recipient's hair between the fingers and tugging. Like most other semi-aggressive patterns, the "hairtug" is intensified until it reaches the recipient's pain threshold and is then released or held for only a few more seconds. It does not result in hair removal from the recipient's body, although some previously loose hairs may fall out during "hairtugs."

The "hairtug" pattern, in contrast to the "hairhold," typically results in vocal protests and abortive attempts to move away. Such attempts are short-lived as they only serve to increase the pressure of the "hair-tug." During a "hairtug" the hair is actually pulled away from the opponent's body. The "hairtug" appears frequently during juvenile rough play and its function is analogous to that of the "pinch bite." Developmentally, the "hairtug" does not appear until the last half of the second year of life.

Hand clap (Fig. 42)

The hands are held open and the palms are brought rapidly and noisily together. This may be used to get the attention of the handler, but it

has also been observed to be directed toward other chimpanzees and to precede "embraces" and "copulations."

Hand or finger-in-mouth (Fig. 30)

This is a deliberate placing of the hand or finger into the mouth of another individual. The recipient of the gesture typically presses the teeth down gently on the finger or hand. The "hand-in-mouth" gesture has frequently been observed to be directed toward infants who are fussing. In some cases, individuals have also been observed to attempt to comfort screaming infants by repeatedly taking one of the infant's hands and placing it in their own mouth. The "finger-in-mouth" form is more frequent among adults and is often performed in a mutual fashion.

Headnod

In this pattern, the head is bobbed up and down by pivoting the neck and head, as one unit, from the top of the shoulders. In the Oklahoma colony, this pattern functions as an approach signal whose meaning may be modified by combination with other gestures. Van Hooff (1971) describes a morphologically similar pattern for the Holloman chimpanzees but reports that it is a low intensity form of the stereotypic "vertical rocking pattern." In the Oklahoma group, the "headnod" pattern did not intergrade with vertical rocking.

Adult males used the "headnod" to signal females to approach when they wished to copulate. Dominant individuals "headnodded" toward subordinates who were hesitant to approach them after a display or threat and the "headnod" was frequently oriented toward chimpanzees in adjoining cages to get them to approach the wire.

Head touch (Figs. 31 and 31a)

Touching another's head with the hand often preceded other forms of

bodily contact. In tense social situations, where individuals appeared to be uncertain about approaching one another, the "head touch" often preceeded grooming or play patterns. It also seemed to serve as a signal for an "embrace" in some cases.

Hold seat against (Fig. 32)

This form of presenting was seen most frequently in females. It involved approaching, turning and pressing the ano-genital region against the ventral surface of another. The position was held for several seconds. The pattern occurred often among infants, being used to solicit a ventro-dorsal embrace.

Ignore

"Ignore" was scored when no reaction occurred to an action, vocalization, etc., which could not possibly have gone unnoticed (such as "screaming" and "swaggering" directly in front of the "ignorer"). Chimpanzees typically do not ignore the actions or presence of one another and when they do, it is often significant. It may be indicative of a disruptive social situation, and aggression frequently follows. However, low ranking individuals, family members and infants are often "ignored" with little problem.

Leg shake (Fig. 53)

This pattern involved a rapid back and forth flapping movement of the thighs with the knees bent. It was performed by males when infants clung to them ventrally or when they solicited ventral clinging from infants. While exhibiting a "leg shake," the chimpanzee often "dangles" by both hands from an overhead support, but he may also be seated.

Lipbeg (Fig. 33)

"Lipbegging" involved placing the lips, often slightly perused,

against the lips of another chimpanzee. Sometimes the initiator also placed his hand on the shoulder or muzzle of the recipient. When food was plentiful, mothers shared with all infants, infants shared among themselves, and the juvenile shared with the infants. Sharing often appeared to be done for "the fun of it" between infants and juveniles, as even water (which was always available to all individuals) was shared.

Lip-tongue kiss (Fig. 85)

This type of kiss consists of mouth-to-mouth mutual tongue and lip contact, and lasts from 10 to 60 seconds. "Lip-tongue kissing" is typically an infant-infant pattern or a juvenile-infant behavior and is especially frequent at 1 to 2½ years of age. Infants of both sexes display this behavior and it is usually accompanied by an "embrace" or "waist clasp." "Lip-tongue kisses" appear only during relaxed social situations, such as when most of the group members are resting quietly. They may also occur during food sharing when neither infant is particularly interested in ingesting the shared food. Taking food from one anothers lips gradually becomes "lip-tongue kissing" and the food is ignored. These kisses, when they occur, are typically repeated 2 to 4 times.

Mouthcover (Fig. 34)

This pattern involves a wide extension of the lower jaw, performed at normal speed, with both upper and lower lips covering the teeth. The initiator's open mouth is then placed over the recipient's mouth, mouth and nose, or entire face. The recipient is typically considerably smaller than the initiator.

The "mouthcover" was most frequently observed between mothers and their own infants. Mothers generally directed "mouthcovers" toward their

infants when the infants were distressed. The younger the infants, the more frequently they received "mouthcovers." Some mothers administered "mouthcovers" to their newborn infants when the infant made the slightest "hoo face" or even on many occasions when the infant did not appear distressed. Other mothers gave "mouthcovers" only when their infants "screamed." "Mouthcovers" lasted from 5 seconds to a full minute. They were occasionally performed by mothers toward other infants and by juveniles toward infants. Mothers gave "mouthcovers" to other infants who fell and screamed or were frightened or hurt by other chimpanzees. Juveniles were seen to give "mouthcovers" when they kidnapped infants and the infants began to protest vocally in an attempt to rejoin their mothers. The "mouthcover" silenced the infant and often delayed the mother's retrieval.

Open-mouth-kiss (Figs. 37 and 38)

In this pattern, the mouth was open wide, and lips very mildly retracted. The teeth were gently, but firmly pressed against the recipient's body. The "open-mouth-kiss" often followed "panting" and was frequently directed toward infants during periods of social excitement.

Pat (Fig. 36)

This pattern is very similar to the common human pattern of the same name except that chimpanzees perform "patting" by moving the entire forearm up and down instead of the hand backward at the wrist. The movements employed during "patting" are, therefore, very similar to those used during "playslapping." "Patting" is usually much gentler, slower, and the "pats" are repeated several times in sequence. Also, the hand is raised only an inch or two above the recipient's body during "patting" while it is raised much higher during "playslapping."

Infants began "patting" at approximately one year and early "pats" were often difficult to distinguish from "playslaps" since the infants lacked the coordination to raise their hands repetitively only an inch or so from the recipient's body. "Pats" were generally seen between infants or between juveniles and infants and appeared to be gestures of affection which occurred prior to, during, or following play. Mothers also "patted" infants in an affectionate manner but their "patting" was not typically related to play. One young human reared chimpanzee often "patted" his own stomach when slightly distressed.

Peer (face close) (Fig. 35)

This pattern involves close placement of the face to another's face. Typically, the eyes are placed within a few inches of the other's mouth and the "peerer" closely watches all tongue and lip movements. The pattern differs from the lip beg in that the head is held lower so that the lips of the "peerer" are under, or to one side of, the lips of the chimpanzee being watched. "Peerers" seem interested in how the other chimpanzee chews his food, moves it about in his lips, which part is eaten first, which part is discarded, etc. "Peering" is especially prevalent if an unusual food is introduced and only a few chimps in the colony choose to eat it. "Peering" is also often seen by subordinates who frequently, before eating themselves, will approach the dominant animal and "peer" for a few minutes.

Pinch

This is a forceful pressing together of the thumb and index finger against the skin of another individual. It was infrequent, but when observed, was generally directed toward much smaller individuals.

Pinch bite

This pattern is the semi-aggressive counterpart of the "playbite." During the "pinch bite" both the upper and lower lips are curled slightly inward toward the teeth so that the edges of the teeth are often visible but no gum is displayed. The "pinch bite" is delivered slowly and deliberately upon a pinch of skin held between the initiator's teeth. The pressure is increased to the point where the recipient indicates pain and may then be terminated or held for a few more seconds. This pattern frequently occurred during juvenile playbouts with both partners simultaneously administering "pinch bites." The pattern also occurred when a new individual was introduced into a group whose members were uncertain of their ability to manage a successful attack upon him. They then escalated many playful gestures to the level of semi-aggressive gestures.

Place teeth on

This pattern involves an open-jawed placement of the teeth on the recipient's body. Both the upper and lower teeth are placed on the recipient, in biting position and the jaws are partially closed. The lips are retracted so that the teeth are fully visible. The pattern seems to occur in at least 2 similar contexts. It may be a severe threat. In some cases the initiator may scream loudly and place his teeth on the recipient repeatedly, waiting for the recipient to flinch or pull back. If this occurs, the recipient generally is bitten. The pattern is also seen during greeting, and often the teeth are less visible in this context.

Touch under chin

The index finger is curved slightly and placed gently under the recipient's chin with the hand extended and the palm in the vertical plane.

This pattern is often displayed by adults toward infants as the infants pass them in play. It also appears during greetings toward infants.

Playbite (Fig. 40)

The "playbite," in contrast to a true "bite," was typically preceeded or followed by a "full" or "half playface." Furthermore, it lacked the brief initial outward raising of the center portion of the upper lip as described under the patterns "bite" and "bite threat." "Playbiting" often took the form of gentle prolonged mouthing and was administered much less rapidly than a "bite." The initiator of the "playbite" did not withdraw his mouth quickly upon termination of the "playbite," as is generally the case with a "bite." Instead, he merely relaxed his jaw as the play partner pulled his arm or leg away from the point of the "playbite." "Playbiting" first began to appear commonly in the play repertoire of infants at about 5 months of age and remained an important component of the repertoire thereafter. It was administered to any portion of the recipient's body although the shoulders and limbs were "playbitten" more frequently. "Playbiting" between juveniles was often displayed simultaneously by both play partners and if one began to increase the pressure of the "playbite" to an uncomfortable level, the other merely responded likewise and then both "playbites" terminated, but the playbout continued. This method of signaling that the "playbite" was becoming painful generally occurred between chimpanzees of reasonably equal size. If one participant was much larger or stronger than the other, the recipient went limp and did not return any play patterns. When this occurred, the larger individual usually terminated the "playbite" and then the playbout continued.

"Playbiting" was also frequently administered by mothers to infants. These "playbites" were extremely gentle, involving almost no jaw closure

and were often carried out with the lips pulled inward over the teeth. They were typically directed to the infant's stomach, thighs, and sides.

Playkick (Fig. 39)

The "playkick" is the foot variation of the "playslap" and occurs in similar circumstances. Developmentally, it appears slightly later than the "playslap" and seems to require better body coordination than does the "playslap." The leg is raised toward the body and then slightly outward at the hip with the knee bent. The sole of the foot is then brought toward the partner's body as the leg is extended. "Playslapping" and "playkicking" are intermediate play patterns between the more rough and tumble play forms such as "wrestle" and the approach-withdrawal play forms like "chase."

This pattern is distinguishable from the "footstamp" in that the direction of a "playkick" is more outward than that of the "footstamp" and the "playkick" is delivered from a wide variety of positions, lying down, sitting, dangling, etc. The "footstamp" is usually delivered from a bipedal or quadrupedal stance.

Playslap (Fig. 41)

This pattern consists of an open palm slap administered about the body or head of another chimpanzee in a playful manner. If one play partner is considerably larger than the other, for example, an adult and an infant, the larger partner may also receive "playslaps" about the limbs. The larger partner does not return these "playslaps" but may orient a "finger tickle," "playbite" or "gentle pull" toward the smaller chimpanzee. If both individuals are of approximately equal size, "playslaps" are traded back and forth.

The playful slap can be behaviorally distinguished from the aggres-

sive slap by the distance the elbow is raised above the upmost plane of the head immediately before the slap is administered. If the slap is aggressive, the elbow will be raised noticeably above the top of the head, but if the slap isa playful one the elbow will be raised no higher than the top of the head. An exception to the criterion occurs when two "playslaps," one with each hand, are administered simultaneously. In this case, one elbow may be raised clearly above the head as long as the other elbow is kept below the top of the head. Aggressive slaps are often less forceful than "playslaps" but regardless of the intensity, the receiver of such a slap usually does not respond with a playful gesture of his own if hit with an arm that was raised high above the head.

Poutkiss

The "poutkiss" involves a gentle, brief placement of the edges of the lips to another's body. The lips may be in the normal position or the upper lip may be very slightly protruded. Infants were the most frequent recipients of "poutkisses" in the Oklahoma group. "Poutkisses" were usually oriented to the lips, eyes, or browridge and were sometimes followed by grooming.

Present (Fig. 44)

In the chimpanzee,this pattern assumes a wide variety of forms. In the simplest type, the initiator merely stands quadrupedally and orients his ano-genital area toward the recipient. Both legs and arms are held straight and there is a brief pause in movement. The typical response to such a present is either no acknowledgement or a touch of the ano-genital area. The "present" in this form was not correlated with dominance and occurred in numerous contexts.

Present-back (Figs. 43 and 45)

This is a form of the "present" which involves orienting the lower back toward a recipient by assuming the present position and slightly bending the knees. It is usually accompanied by a look over the shoulder toward the recipient. This posture may be acknowledged by the recipient, but typically does not lead to further interaction.

Present-crouch

In this posture the knees and elbows are flexed and the ventral surface is lowered toward the ground while the posterior is oriented toward the recipient. The initiator typically looks back over his shoulder. The "present-crouch" is usually assumed when an attack by a higher ranking individual is imminent.

Pull on (Fig. 46)

"Pull on" was one of the most frequently observed play patterns in the Oklahoma colony and was observed across all age ranges. It was by far, the most common pattern that mothers used in play with their own or other infants. Typically, an infant would "dangle" by one arm just above his mother, so that his feet hung in front or to the side of her head, and then wait for the mother to respond. If the mother appeared to ignore him he would swing to and fro while kicking his legs freely about her head and displaying a "playface." Mothers then reached up and began "pulling on" the toes, feet, or fingers of the infant with one hand. Mothers usually played with infants in this fashion for 15-20 minutes, only occasionally looking toward the infant and generally displaying no "playface" of their own, but appearing quite relaxed. Juveniles also elicited play from mothers by "dangling" in a similar fashion. The "pull on" was typically used to initiate or reinitiate play and then it dropped

out.

The "pull on" could be distinguished from its more aggressive counterpart, "stretch pull" because the limb being pulled upon was never hyperextended by the initiator of the pattern.

When juveniles initiated a "pull on" toward infants the pattern was sometimes increased to a "stretch pull" if the infant tried to move away or otherwise avoid the invitation to play.

The "pull on" appeared in the infant play repertoire between 8 and 9 months of age and was observed in individuals of all ages.

Punch

In this pattern, a blow was delivered with the knuckles of the second and third joints. The "punch" was administered quickly and the hand and arm were withdrawn immediately, often in preparation for another blow. The arm was extended horizontally, and the hand was never observed to be raised above the initiator's shoulder level. The "punch" was delivered upon the face, head, and shoulders of the recipient, often striking the recipient directly in the nose. Recipients usually made few attempts to resist "punches" and often appeared to be stoically waiting them out. The less reaction they displayed to "punches" the more likely was the aggressor to tire of the activity. "Punches" were typically delivered only toward smaller individuals.

Push

Chimpanzees may place the palm of their hand or foot, or the back of their forearm, or their shoulder, against another and shove lightly. Often this is a signal to the other individual to move, but, playful "pushing" is also seen.

Seat bounce

In this pattern the ano-genital region is placed against the body or hand of another individual and bounced up and down. It differs from "thrusting" in that there is typically no dorsal or ventral bodily contact and the movement is performed mainly with the legs, as opposed to with the lumbar region. Whimpering infants may be approached and comforted by a "seat bounce" and likewise, an individual who is mildly distressed may rush to another and "seat bounce" against him.

Sit on (Fig. 47)

This pattern is performed mostly by infants and is oriented toward larger individuals. Generally an infant "sits on" the head or shoulders of another individual, but they may "sit on" other portions of the body if the recipient is reclining. When oriented toward the mother, or other adult female, the infant may sit calmly upon this individual for 10 minutes or longer. When oriented toward a juvenile, "sitting on" is brief and is followed or preceeded by some type of embrace or play.

Slap (Figs. 58 and 59)

The "slap" pattern consisted of raising the arm high over the head until the elbow was above the topmost portion of the head. The whole arm was then moved forcefully downward until the palm struck the back of another animal. The "slap" was usually delivered from a bipedal stance, but tripedal "slaps" were also seen, especially if the recipient was considerably smaller than the aggressor. The height of the upraised arm was especially significant for this pattern in that an extremely powerful "slap," delivered without raising the elbow above the head, was ususally responded to as play.

Stretch pull

The "stretch pull" involved movements identical to those described for "pull on" except that the motions were executed more forcefully. Typically, the initiator took hold of a free limb of the recipient and began to pull, slowly but powerfully. The pull continued until the recipient's limb was slightly hyperextended. At this point the initiator ceased pulling but continued to use enough force to cause the limb to remain in this hyperextended position. The recipient either tried to struggle free or began to "hoo whimper" and scream loudly, until the initiator let go or until a third chimpanzee intervened on the part of the recipient.

This pattern was usually displayed by larger individuals toward smaller ones. Injuries never resulted from "stretch pulls" and their function seemed to be more one of harrassment than true aggression. The older the recipient of the "stretch pull" the more likely he was to try and struggle free rather than scream. While mothers never oriented the "stretch pull" toward their own infants, they did occasionally orient this pattern toward other infants.

Thrust (Figs. 48, 49 and 50)

In this pattern the ventral pelvic area is repeatedly and rhythmically pressed against another chimpanzee. When males "thrust," the pattern is typically accompanied by a penile erection, even in infants. Females "thrust" less frequently, but even infant females have been observed to display this pattern. "Thrusting" often seemed to function as a reassurance pattern, both for infants and adults and was displayed repeatedly during introductions of unfamiliar infants or juveniles.

Ventro-dorsal embrace (Fig. 60)

In this pattern one individual places one or both arms around the other while standing or sitting behind the other. Both individuals may then move about quadrupedally together in this position. Infants frequently orient "ventro-dorsal embrace" toward one another during play and exploration. The "ventro-dorsal embrace" is also seen between adults during social excitement.

Ventro-ventral embrace (Figs. 61 and 62)

This pattern consists of the placement of one or both arms around the shoulders and back of the partner while one or both partners press their ventral surfaces in contact. "Embraces" generally lasted from 1 to 5 seconds, although they may revert to a form of ventral clinging, which continues for a period of several hours. This form of reversion occurred when 2 juvenile males were introduced to the mother-infant group. They immediately "embraced" one another and sat, with their arms and legs around each other's back until they were removed from the group.

The "embrace" occurred most frequently between mothers and infants. Mothers "embraced" their infants when they had been out of contact for a relatively long period of time, when presented with a favorite food, and when the infants moved past them during play. Mothers also "embraced" other infants under similar circumstances, though much less often than they "embraced" their own infants.

Waist clasp embrace (Fig. 63)

The behavior involves a clasping of the legs around the waist of another chimpanzee while hanging from a support with one or both hands. If only one hand is used, the other is then placed about the body of the recipient. The pattern can be executed either in a ventro-dorsal or

ventro-ventral manner. It has only been observed among infants, lasts from 2 to 60 seconds and is initiated and received by infants of either sex. Male infants frequently, though not always, display a penile erection when performing this pattern. In a typical "waist clasping" sequence, two infants brachiate about the cage, with one leading and the other following. One infant then stops, looks toward the other infant, and waits for it to approach. The approach is followed by a "waist clasp embrace" and the two infants may brachiate a short distance in unison while embracing.

Wrestle (Fig. 51)

This pattern has been identified for most primate species. It involves an intertwining of the arms and legs of two individuals, generally in a prone position. The limbs of each individual are held or pulled into various positions. "Wrestling" is a broader term than most of the others in this repertoire since it refers to a chain of differing events whose duration and sequence is highly variable. Distinct patterns such as "pull on," "playbite," "playslap," etc. were recorded as "wrestle" when they occurred in rapid succession. When they occurred separately and were interspersed with approach-withdrawal play or pauses, such patterns were recorded individually.

"Wrestling" appeared in male infants at approximately one year of age, and in female infants 4 to 6 months later. By the juvenile period, "wrestling" was the most frequent type of play behavior between peers.

GESTURES and POSTURES

Arm headcover (Fig. 64)

The arms are placed across the top of the head with the hands down on

either side of the head. The pattern occurred both during play as a response to being tickled about the neck and shoulders and prior to play as a signal to another of a desire to play.

Bend away (Fig. 65)

During this pattern the displayer typically assumed a tripedal or crouched bipedal stance to one side of the recipient. The arm nearest the recipient was flexed at the elbow and the wrist and held in front of the displayer as he leaned slightly away from the recipient. The gesture was typically oriented toward older or more dominant individuals and there was a slight pause in the displayer's movements as he assumed and held the "bend away" posture for a second or two. Infants began to display this gesture at about 9 months.

Clitoral rubbing

This pattern may occur in adult females during social stress. It involves an exaggerated rubbing of the vaginal area against the floor or other smooth surface. Movements may be backward and forward, or circular.

Infant females sometimes exhibit clitoral rubbing with the heel during play with younger infants.

Dangle (Fig. 67)

Among infants,"dangling" was the most frequent play pattern and occurred in both locomotor play and social play. The typical method was to hang by one arm from an overhead support while revolving the body as much as 360 degrees, and kicking the legs freely. Infants up to 3 years of age often "dangled" in this fashion for 10 minutes by one arm and by alternating arms they could "dangle" and play for 2 hours or more with only brief pauses for rest. They began to incoroprate "brachiation" into

the "dangle" pattern between 12 and 15 months of age. Regardless of the length of time they "dangled," infants never appeared to become tired. By contrast, they were sometimes observed to sag against their mothers and breathing heavily for a minute or two after an especially vigorous "chase" or rough and tumble playbout.

Juveniles also "dangled" by one arm, but after 3 years of age "dangling" by two arms became increasingly frequent until late adolescence when the two arm "dangle" was common while the one arm "dangle" occurred infrequently and in some cases disappeared entirely. The two armed "dangle" prevented the individual from rotating his body freely and the one armed "dangle" seemed to be preferred until the increasing body weight apparently made it more tiring. Adults were definitely capable of performing the one armed "dangle" though and it is difficult to be certain that body weight was the deciding factor which increased the use of both arms or whether developmental preferences were partially responsible. In any case, as the two armed "dangle" became more frequent, so did the performance of wild, daring leaps.

Extend hand (Figs. 68 and 69)

In this pattern, the displayer slowly and hesitantly held his hand toward the face of another while looking directly at the recipient. The palm of the hand was usually vertical and the knuckles were slightly bent. The gesture was frequently oriented toward more dominant individuals when the subordinate was uncertain as to the propriety of approach. It also occurred, perhaps as a form of appeasement, after minor agonistic episodes or when a mild disagreement appeared eminent.

Head down (Fig. 70)

This pattern consists of lowering the head near the ground, usually

with both legs remaining almost straight, the knuckles placed near the head, and the arms flexed. It is a posture used to solicit play and also occurs during play. It is displayed frequently by all age-sex classes, with infants showing the pattern as soon as they are able to stand quadrupedally. Often the back of the head is placed against some part of the play partner's body and then the partner is pushed with the head and shoulders. This posture, like the "lie on back" pattern, appears difficult to resist and even non-playful adult females have been observed to reach out and tickle another adult who adopts this position.

Hold out hand (Fig. 71)

In this gesture the hand and arm are extended toward another chimpanzee. The palm is generally upward, though it may occasionally be slightly vertical. (The arm extended with the palm downward is regarded as a different gesture.) The gesture was used to request an object in the possession of another individual or to request the presence of another individual. In some instances the hand may be moved back or forth to "beckon" to the recipient of the gesture. The gesture was performed without regard to dominance status and appeared in a wide variety of contexts. It first occurred at approximately 9 months.

Hunch (Figs. 72 and 72a)

This is a raising of the shoulder region accompanied by a lowering of the head. This pattern typically occurs during the "glare," the 'bipedal swagger," the "charge," and in conjunction with other agonistic patterns. It also appears during greeting and is almost invariably accompanied by pilo erection.

Hurry shake (Fig. 73)

The arm is bent at the elbow and at the wrist and the hand is shaken

rapidly in the lateral plane (i.e., back and forth as opposed to up and down). This occurred when one chimpanzee wanted to cling ventrally (or ventrally embrace) to another, but the body of the recipient was not in the appropriate posture (ex., arms were folded across the chest, etc.). The recipient usually responded by exposing the chest, turning around, approaching, etc., so that clinging was possible.

Lie-on-back (Fig. 74)

This pattern involves reclining on the back, usually with the legs and head drawn upward to the body. The pattern appears during play, where it often serves as an initiator of a playbout, and during greeting between infants or juveniles. When the "lie-on-back" occurs during a greeting, the response is typically a "ventro-ventral embrace," so that both youngsters end up lying on the ground, one on top of the other.

Penile rubbing

Starting at approximately 2 years of age, infant males occasionally display brief penile rubbing after a penile erection occurs. The rubbing is done with the first and second toes of the foot.

Rigid tantrum (Fig. 56)

This pattern has only been observed in infants and seemed to be a rather stereotypic response to the momentary loss of the mother. The infant screamed loudly and its body appeared to become stiff. Usually it clung rigidly to the nearest available object with arms and legs bent. The body shook, giving the appearance that the infant was attempting to let go or move away. Mothers rushed rapidly to such infants and gathered them into the ventral position. The tantrum terminated as soon as the infant clung to the mother.

Touch behind head

In this pattern one individual approaches another and touches him behind the head or on the back of the neck with the fingertips. The palm of the initiator is typically raised above the head of the recipient and the arm is stretched until the fingertips, but not the palm, touch the back of the recipient's head. It is used as a request to another to approach or follow the initiator.

Infants begin to display this pattern at approximately 6-8 months and the initial occurrences are correct in form, though often clumsy.

Raised Palm (Fig. 57)

When displaying this gesture, the chimpanzee sits or stands and looks directly at another individual while raising one arm until the palm of his hand faces the recipient. The gesture is similar in form to the arm hand position adopted by human beings during "waving," but the chimpanzee moves neither the arm nor the hand back and forth. The posture may be held from 5 seconds to a full minute in some cases and is used as a command or strong request to come. It is typically seen when other attempts to make contact with the recipient have gone unheeded. It is a silent, strangely forceful and imploring gesture. The gesture appears to be a broken off, modified form of the "touch behind head," and occasionally has graded into that gesture.

Temper tantrum

This violent pattern typically erupted after a series of "rising hoo whimpers." When it occurred, the chimpanzee abruptly threw himself upon the ground, screaming loudly with "open-mouth-bared-teeth"

and a frenzy of limb movements. Individuals slapped and grabbed at themselves and surrounding inanimate objects. "Temper tantrums" lasted from 5 to 30 seconds and typically ended as abruptly as they began with the performer only mildly perturbed afterward. "Temper tantrums" occurred among all age-sex classes but seemed most frequent in juveniles. They appeared to be a frustration response, occurring when an individual was prevented from doing something he wanted to do very badly. Mothers tried to comfort their offspring during tantrums, but comfort was usually refused until after the tantrum.

Wristbend

In this gesture, the wrist was bent and the back of the wrist was held toward the face of the recipient. The "wristbend" frequently occurred in contexts similar to the "bend away" and was possibily a low intensity form of that gesture. The chimpanzee performing the "wristbend" was usually either seated or in a crouched bipedal stance while extending his wrist toward the recipient. The gesturer alternately looked down towards his arm and then at the recipient's face, usually with the "wide-eyed" expression.

MOTHERS and INFANTS

Chest expose (Fig. 80)

The arms are held back from the chest as the mother (or other initiator) leans toward the infant. The infant climbs into the ventral po-

sition.

Cling (Figs. 75 and 77)

In this pattern one hand or foot grasped the mother's hair, as the infant engaged in other activities.

Dorsal carriage (Fig. 8)

The infant rides on the mother's back, clinging with the hands. The infant may ride high on the shoulders or low in the lumbar region. When being transported for short distances the infant may ride with his head toward the mother's genital region or crosswise, but the infant's body is generally oriented in the same direction as the mother's if it rides very far.

Gather ventral (Fig. 79)

The fingers of one hand are placed gently behind the infant's back and the hand follows the infant as it climbs into the ventral position.

Hand dangle (Fig. 83)

In this position the mother takes the infant's hand in her own and holds the infant away from her body, dangling it by one hand. Infants were held this way as mothers rested and sometimes, even when they moved about. The pattern was common for some mothers, highly atypical for others.

Hand-to-object

Mothers of young infants sometimes held the infant's hand up to the wire, a tire, etc. and tried to place or curl the infant's fingers around the object.

Hold hand behind (Fig. 82)

This is a signal used by mothers to move their infants into the ventral position. The arm is raised at the shoulder and held behind the

infant's buttocks. The hand is bent at the wrist and the fingers curl slightly forward.

Lateral carriage

The infant's venter is held against the mother's side as the infant clings to the mother's dorsal and ventral surfaces with hands and feet. Some mother-infant pairs used this position in preference to the ventral position.

Lean out

Infants between 3 and 6 months of age spend a great deal of time leaning away from the ventral position without actually moving out of it. This may involved leaning backwards or sideways, but typically the arms, head and upper chest are held away from the mother's venter, while the abdomen and the legs remain against her venter.

Leg or arm cling

In some cases infants may cling to the mother's leg or arm as she moves. Such clinging was usually done only for short distances.

Palm or forearm carry (Fig. 54)

Young infants are occasionally carried, ventral surface down, in the mother's palm or on the underside of her forearm as she moves tripedally.

Place-in-front (Fig. 52)

Mothers of non-mobile infants sometimes disengaged their infant's hands and feet and placed it on the ground in front of them. They held the infant's hands or kept the palm of their own hand gently around the infant as it sat or lay on the floor in front of them.

Pull-up (Fig. 81)

Mothers moved infants out of the ventral position by disengaging the

infant's hands and pulling it out from the venter. Often they lay on their backs as they did so and thus the infant was pulled upward. The infant is groomed, tickled, turned about, and gazed at as it is held in this position.

Side sitting cling

In this position the infant sits or stands next to the mother, but clings constantly to her venter with one hand while exploring or playing with the feet and the free hand.

Tail tuft touch (Fig. 84)

As an infant walks by, adults often reach toward it with a bent index finger and briefly touch the infant just under the tail tuft.

Ventral carriage (Fig. 78)

In this pattern the infant clings to the mother's venter with both hands and sometimes with both feet. If the mother is sitting, her thighs may be drawn up behind the infant so that the infant's ventral surface is held against her own ventral surface, but the infant has no need to cling. When carrying very young infants in this position, mothers may support them by walking with a crouched gait so that their thighs are under the infant, or by walking tripedally with one hand under the infant's back.

Figure 1. "Bipedal locomotion" by infant during locomoter play.



Figure 2. Brachiate



Figure 3. "Double footstamp" by infant male.



Figure 4. "Single footstamp" by infant as he clings to his mother with one hand.

Figure 5. "Freefall" by infant during play.

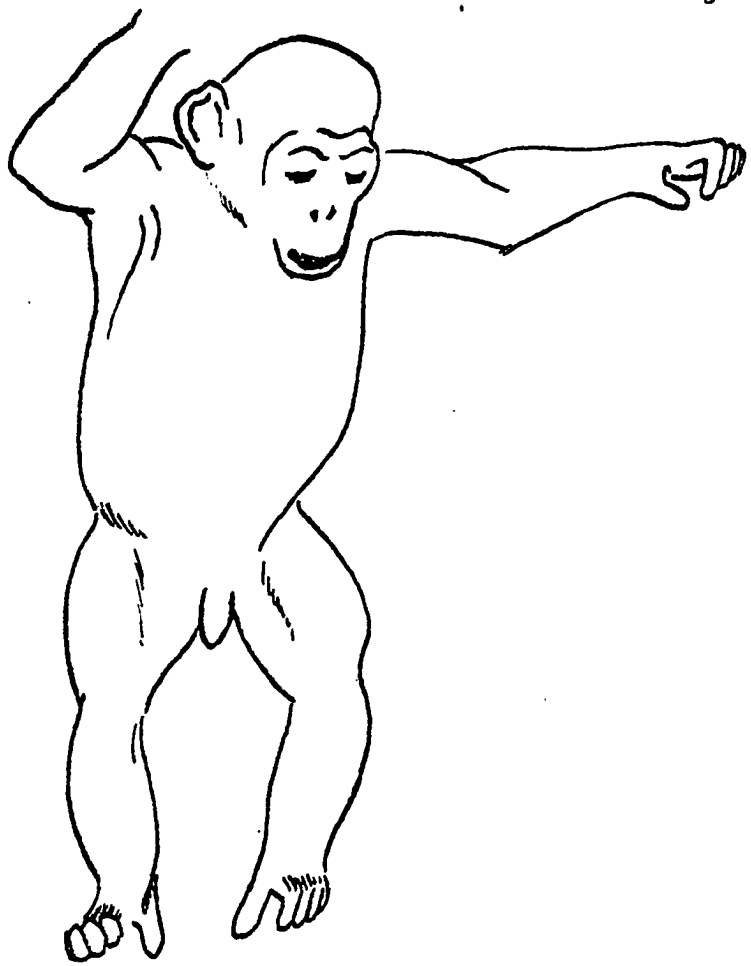




Figure 6. Gallop



Figure 7. Infant (left) "crutches" and displays grin face as mother watches.

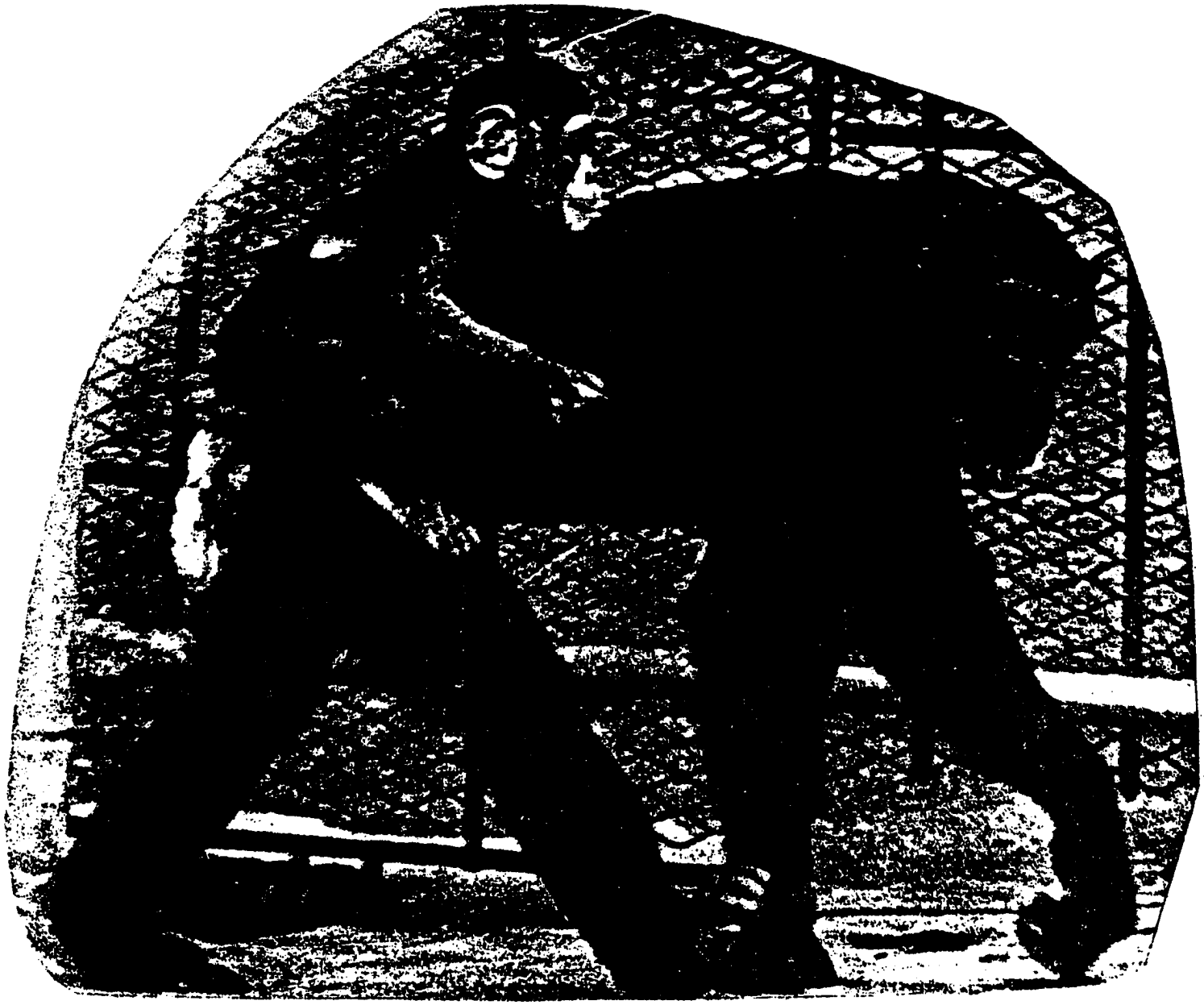


Figure 8. "Quadrupedal locomotion" by mother who carries her infant in the dorsal position.

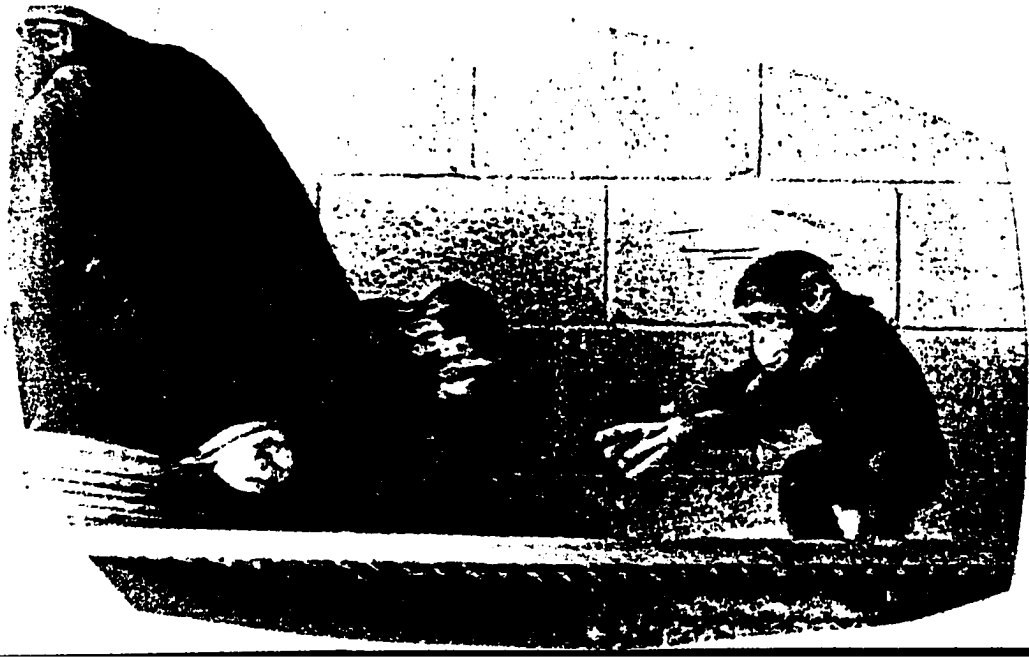


Figure 9. The infant on right performs "jump" during locomoter play as a younger infant (left) watches closely.

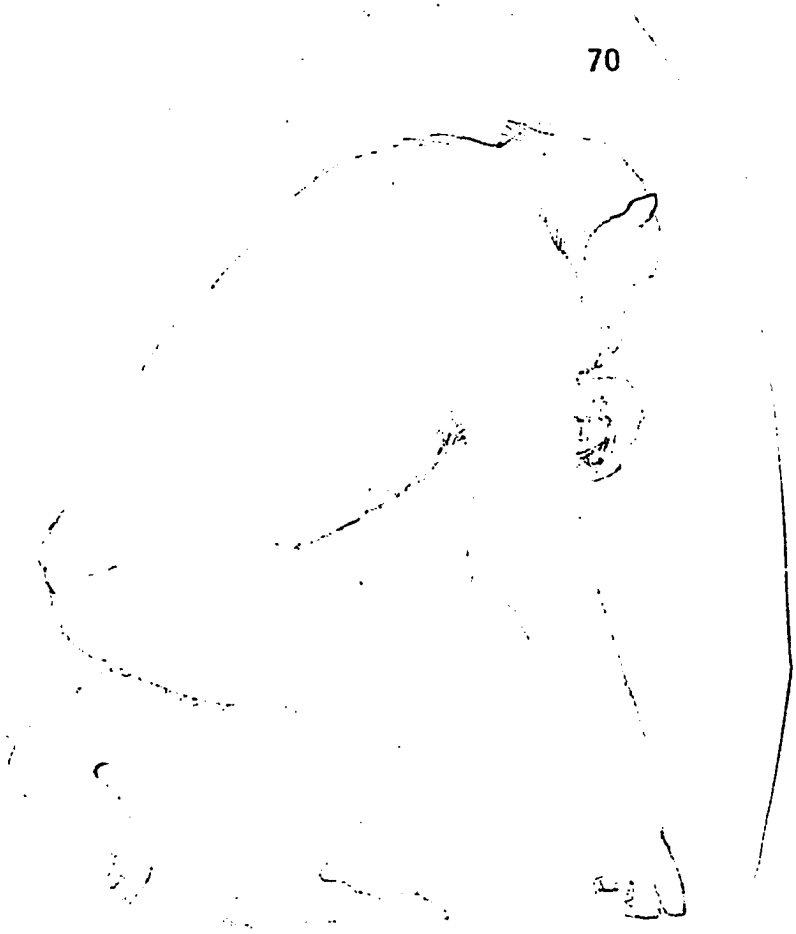


Figure 10. "Tripedal locomotion"

Figure 11. "Ugh bark," note that the mouth opening is made by dropping the lower lip. (below)





Figure 12. "Ough bark," note that the mouth opening is made by raising the upper lip.



Figure 13. Lip bulge

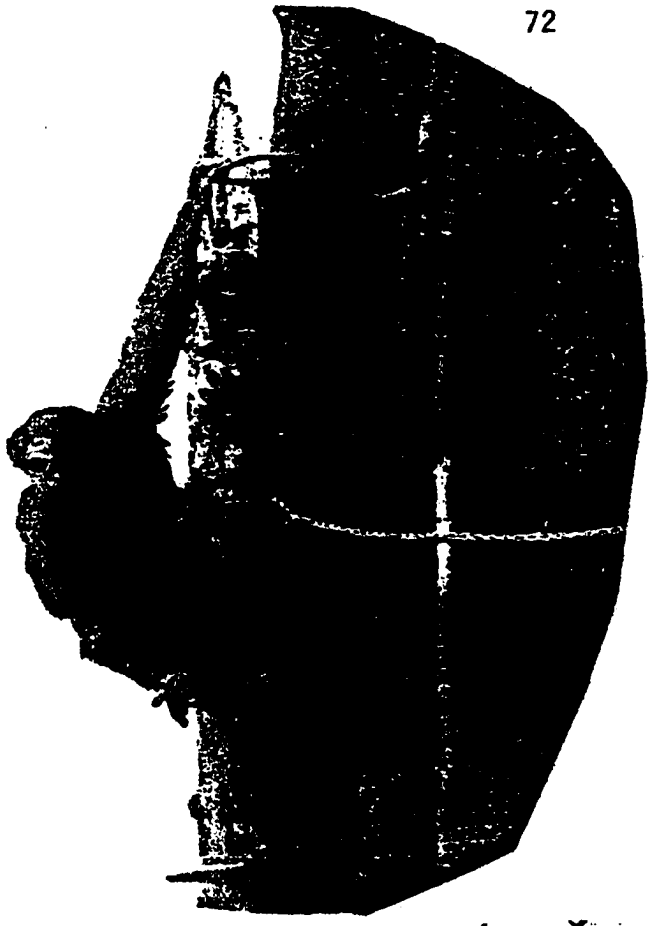


Figure 14. "Pant hoot" in response to similar calls from another group.



Figure 15. An infant and a juvenile display mutual "look at" before exchanging playslaps.

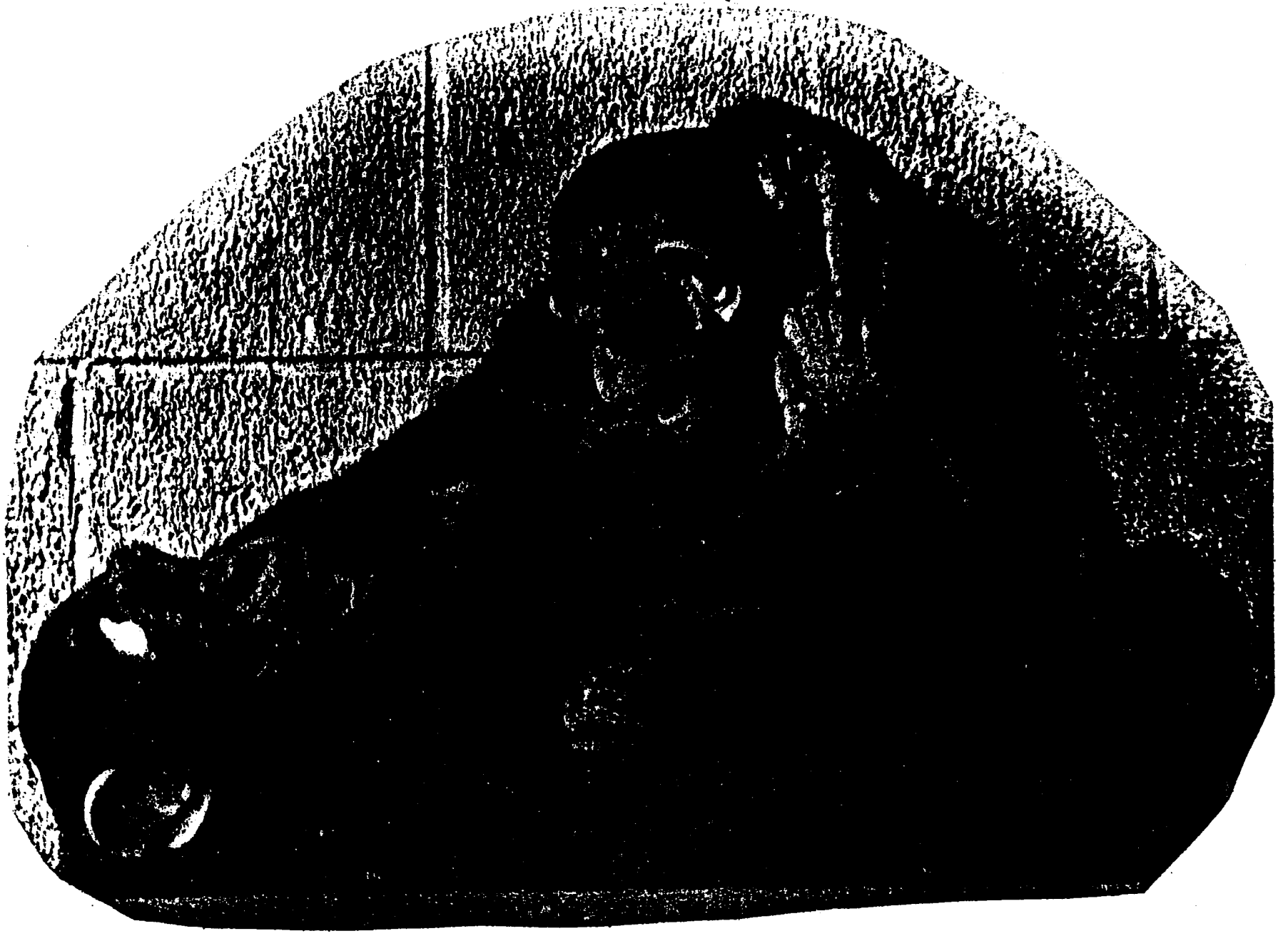


Figure 16. Play face (Infant, on top, shows "full play face" and juvenile, bottom, shows "half play face")



Figure 17. "Open-mouth-bared-teeth-and-gums"



Figure 18. "Raucous scream." Tongue protrusion is often, but not always, a component of this vocalization.

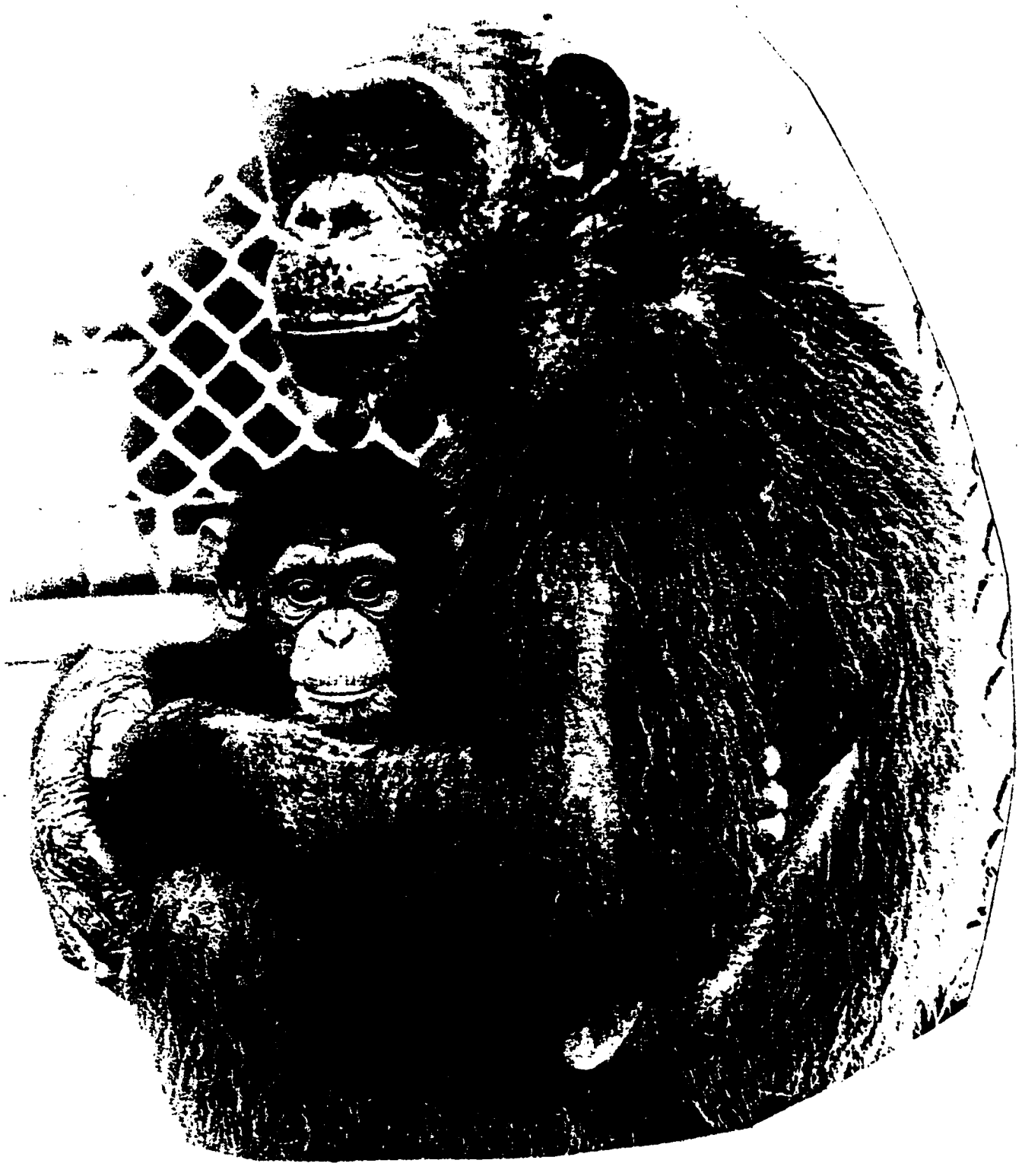


Figure 19. Normal face. "Normal face" is shown only by infant, mother shows pucker of mouth corners. Note that the eyelids of both individuals are visible.



Figure 20. Infant orients "hoo whimper" toward mother when juvenile approaches in "head down" position to solicit play.



Figure 20a. Infant shows silent pout face toward his mother (not pictured) while clinging to another mother.



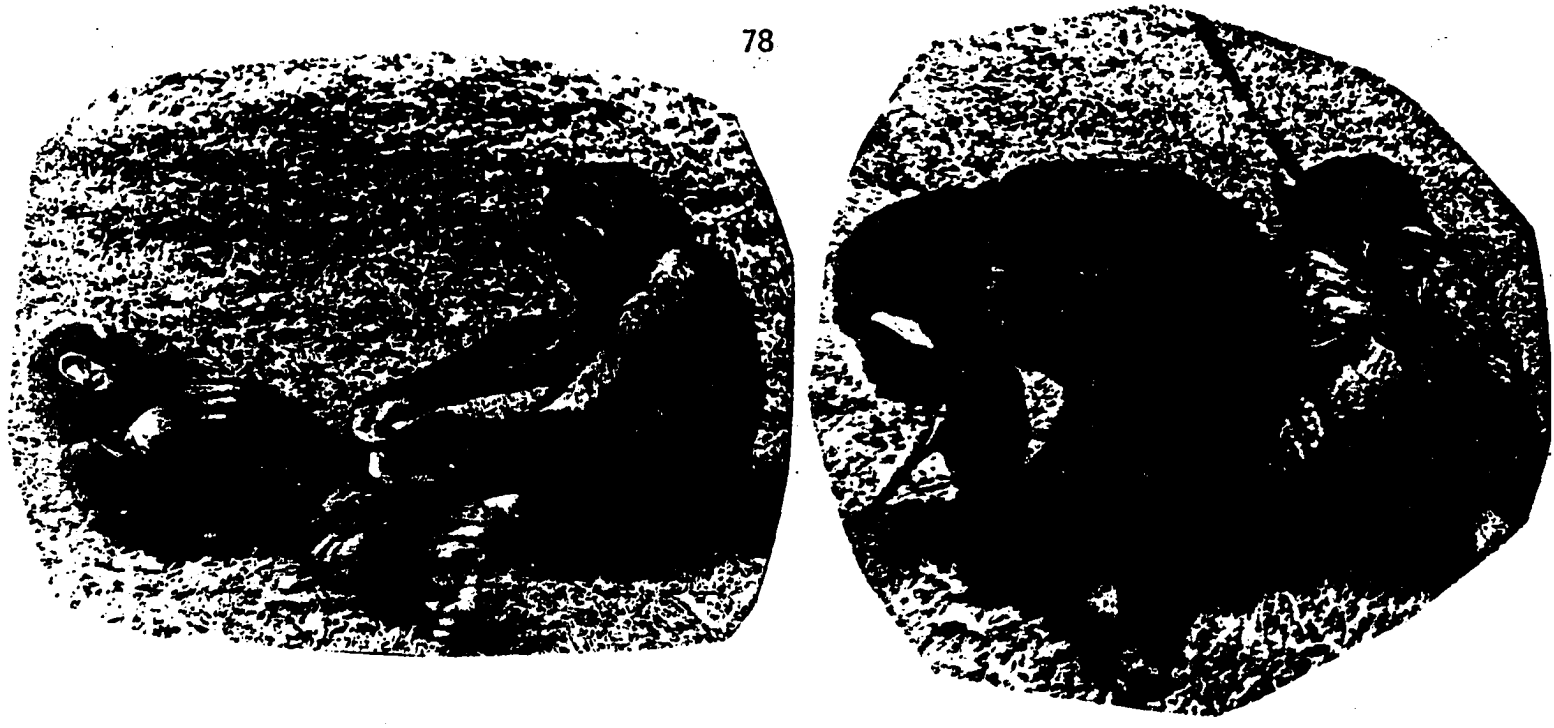
Figure 21. Wide eyes face



Figure 22. Arm around back



Figure 23.
Mutual arm around embrace



Figures 24. Ano-genital inspection



Figure 25. Chase

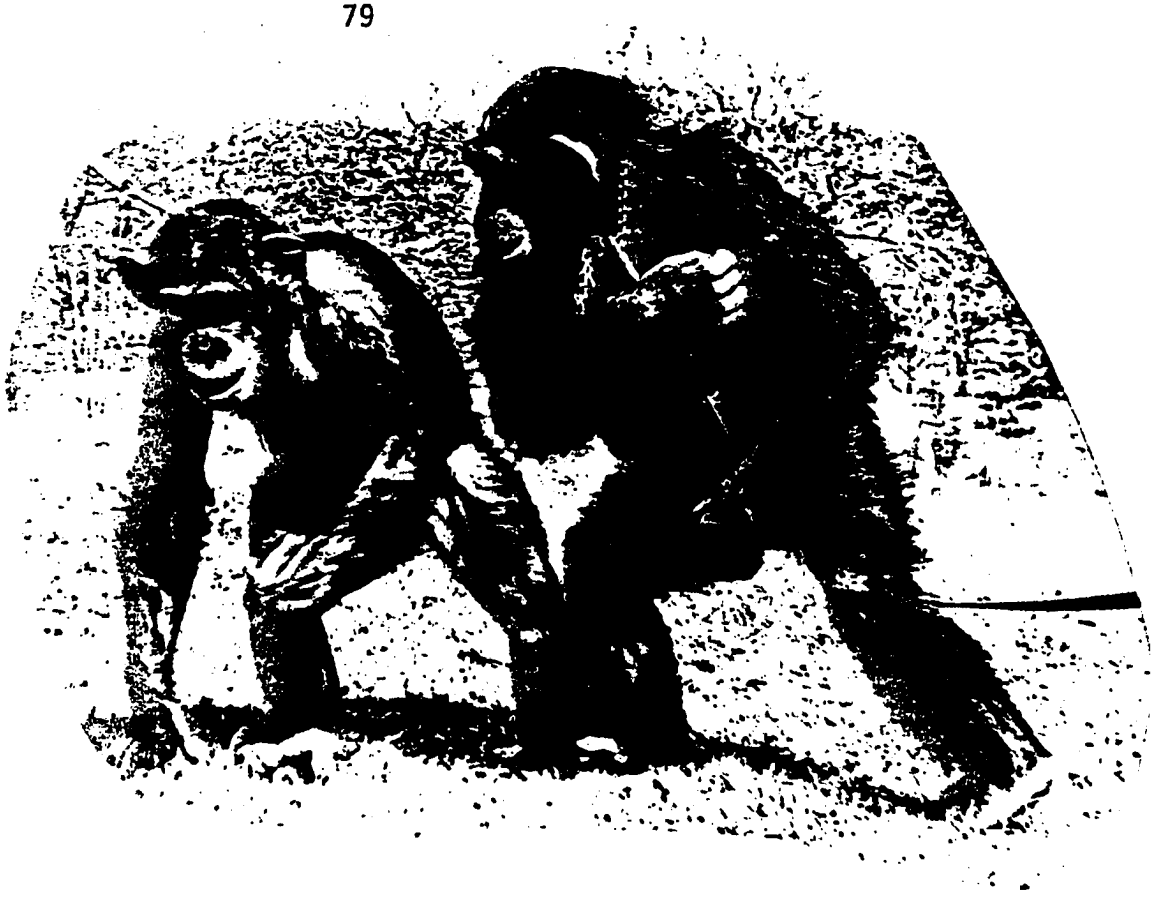


Figure 26. The juvenile on the right prepares to give a playful "backhand thump."

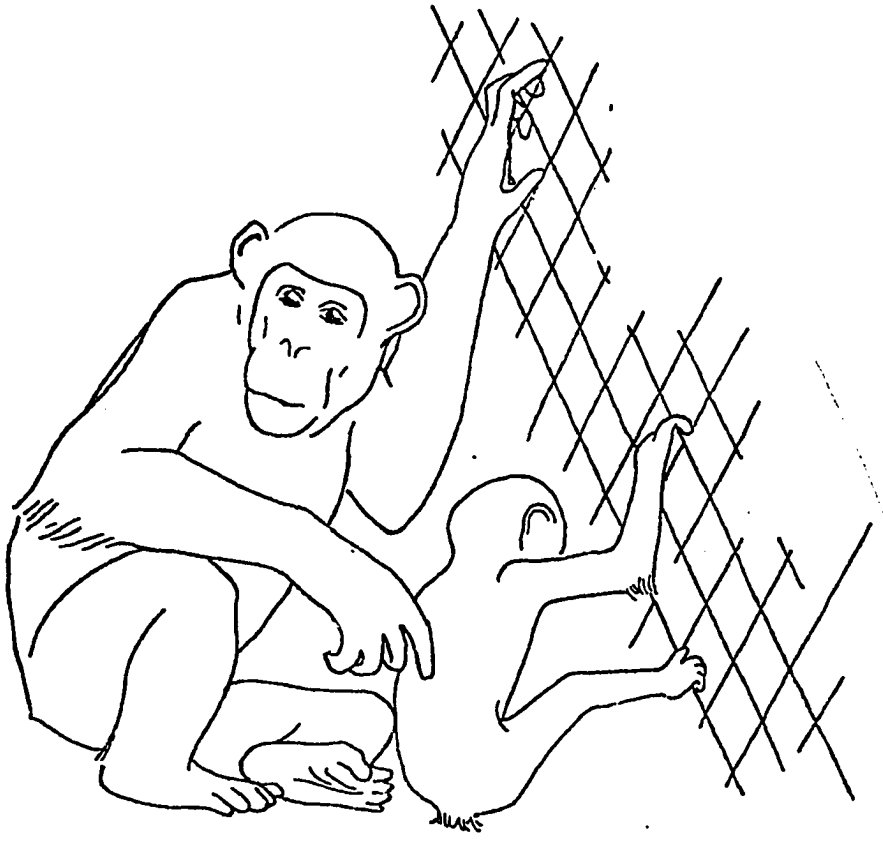


Figure 27.
Finger tickle



Figure 28. Mother "dental grooms" her infant.

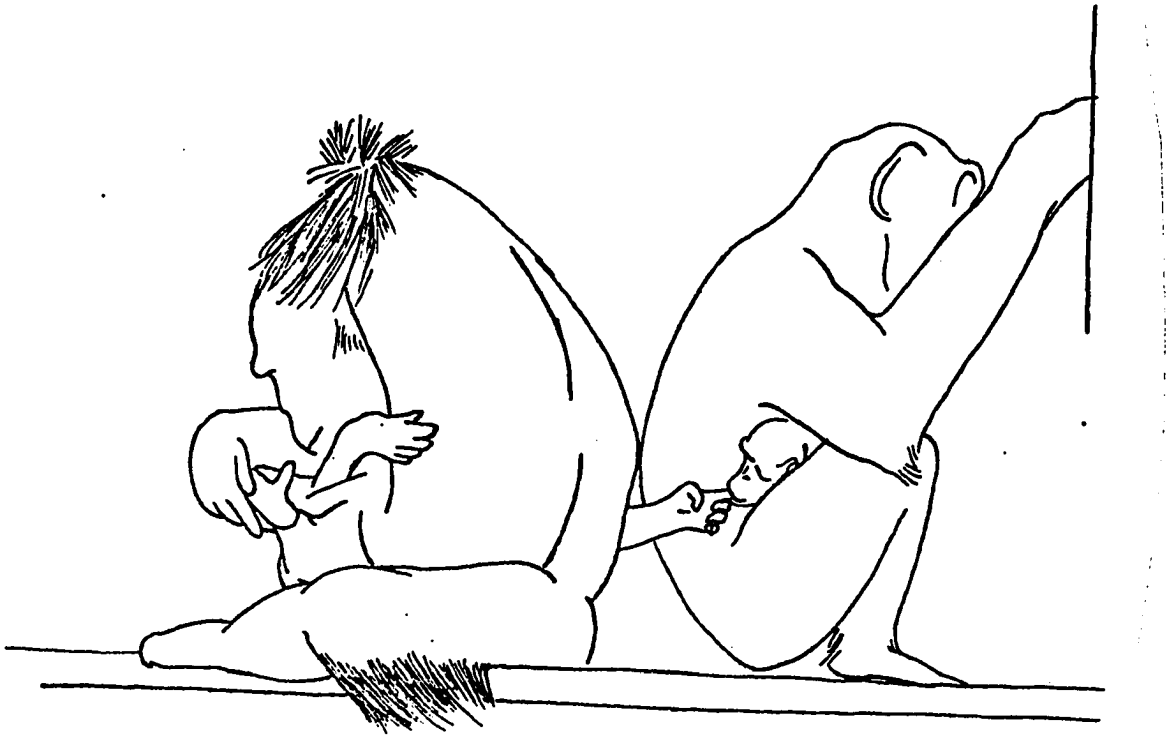


Figure 28a. Mother holds infant's feet in her own while grooming anal region.



Figure 29. Hairhold

Figure 30. (below) The infant on the left leans out of mother's lap as she grooms him and offers a "finger-to-mouth" gesture to a nearby infant.





Figures 31 & 31a.
Head touch

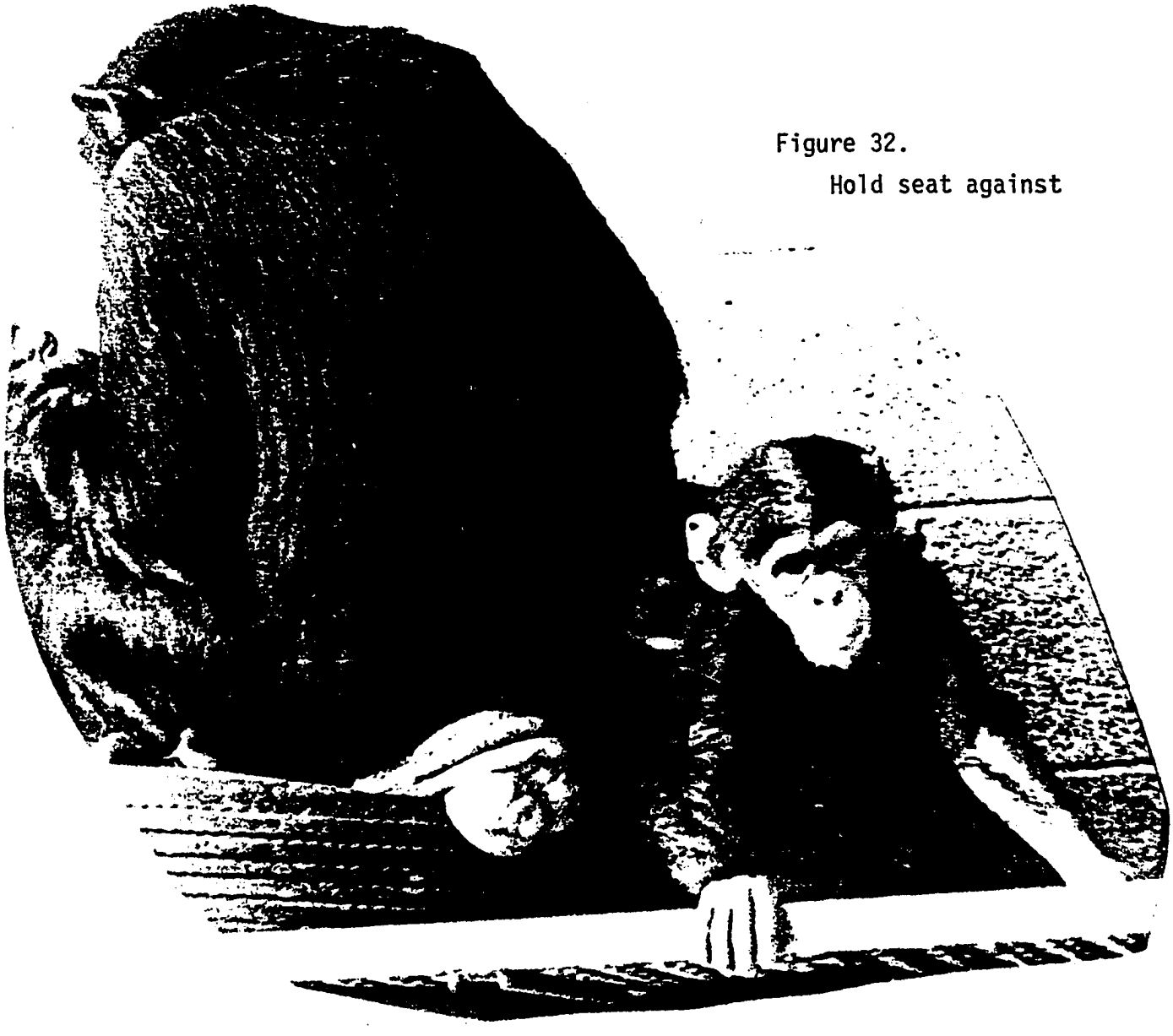


Figure 32.
Hold seat against



Figure 33. Lipbeg

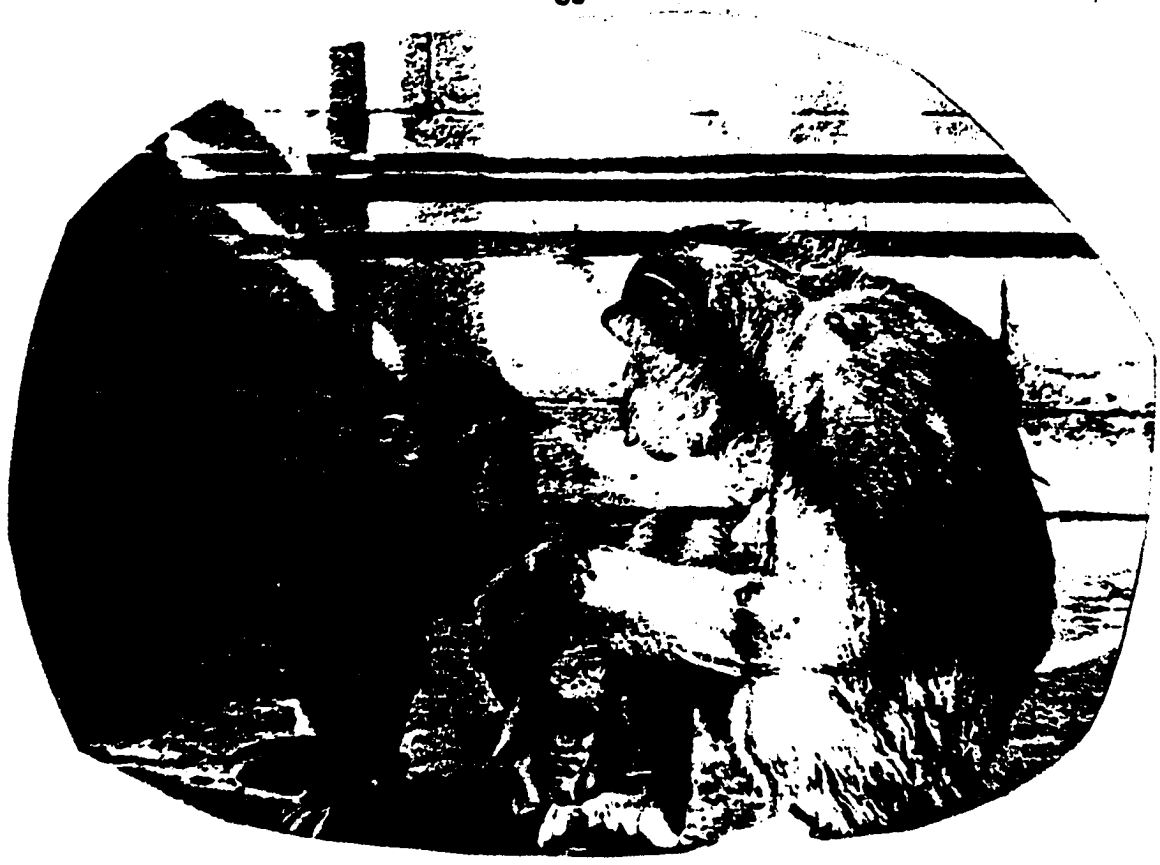
Figure 34. Mouthcover



Figure 35. Peer



Figure 36. "Double-handed pat"





Figures 37 & 38. Infant approaches mother who gives "pant hoots." Mother responds with "open mouth kiss."



Figure 39. Playkick



Figure 40. Playbite



Figure 41.
Playslap



Figure 42. Infant displays "handclap" and gains the attention of the group.



Figure 43. Present back

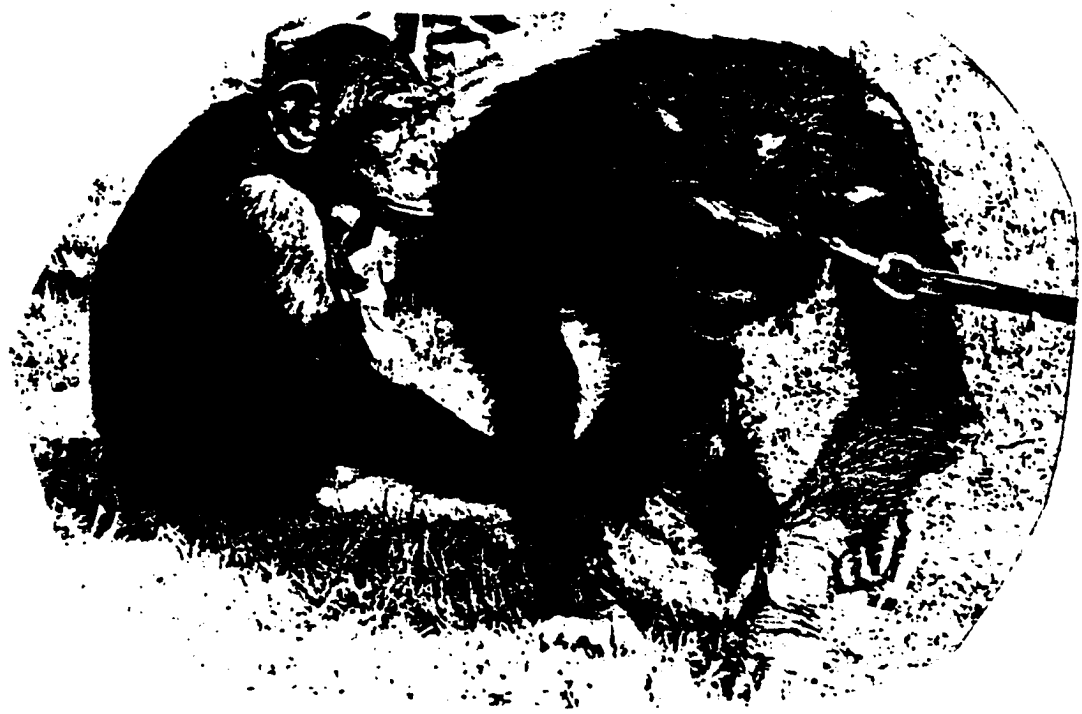


Figure 44. "Present" by juvenile female. Juvenile male responds with genital inspection.



Figure 45. Juvenile male orients "back present" toward juvenile female. She responds with a knuckle touch.

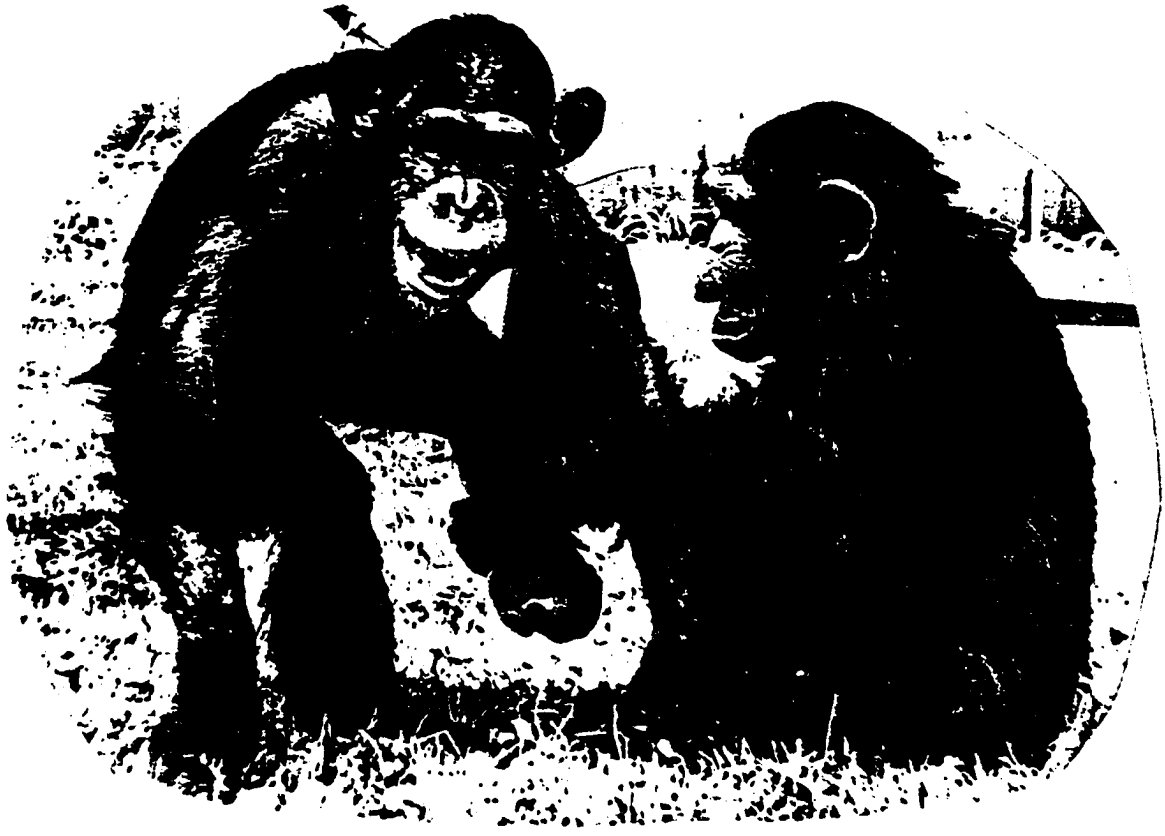


Figure 46. The juvenile on the right "pulls on" the foot of the juvenile on the left. Note that the pull is gentle and does not hyperextend the leg of the recipient.



Figure 47. Infant plays with her mother's ear as she "sits on" her shoulder.



Figure 48. Juvenile male positions adolescent female for thrusting.



Figure 49. Mounting and intromission.

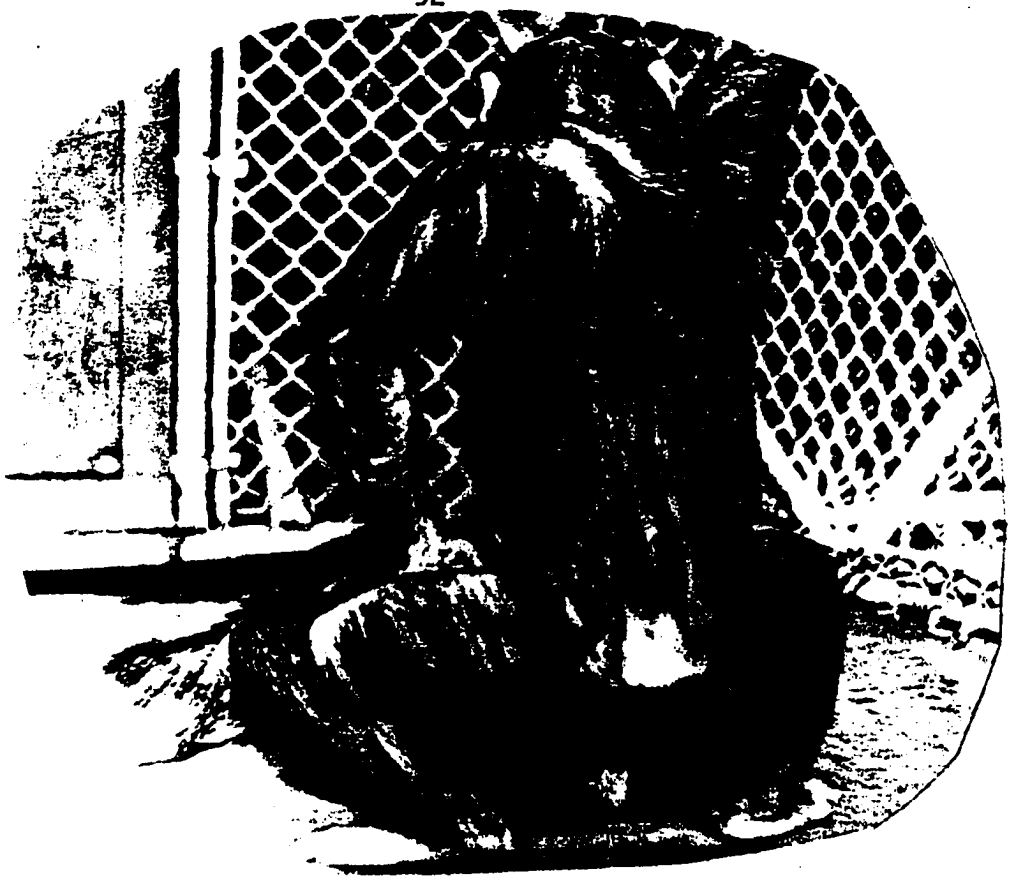


Figure 50. Thrusting. Note the extreme crouching of the female.



Figure 51. Wrestle

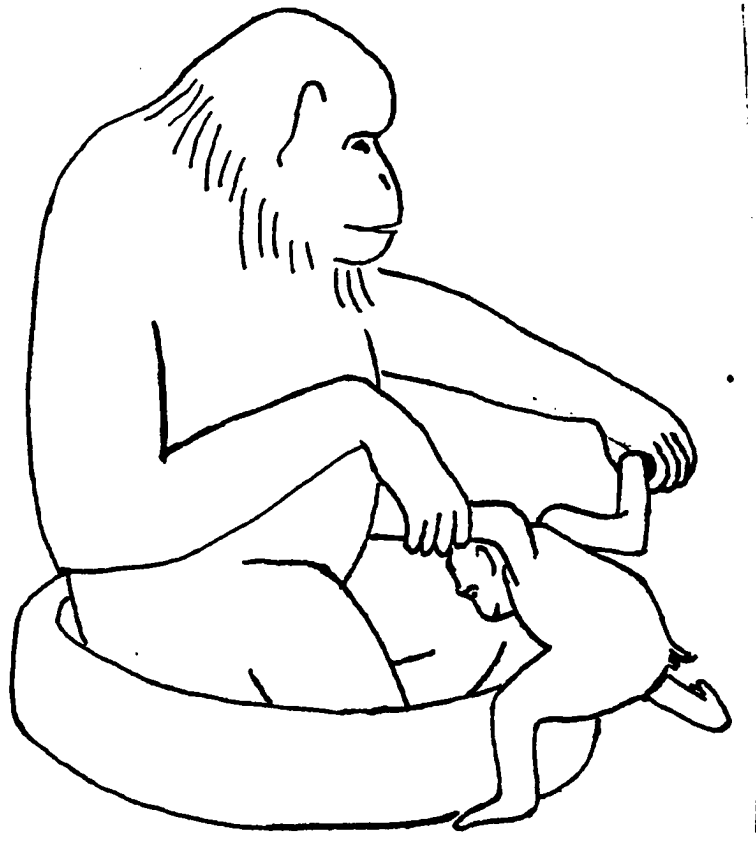


Figure 52. Mother pulls 4 month-old infant away from her venter and "places in front."

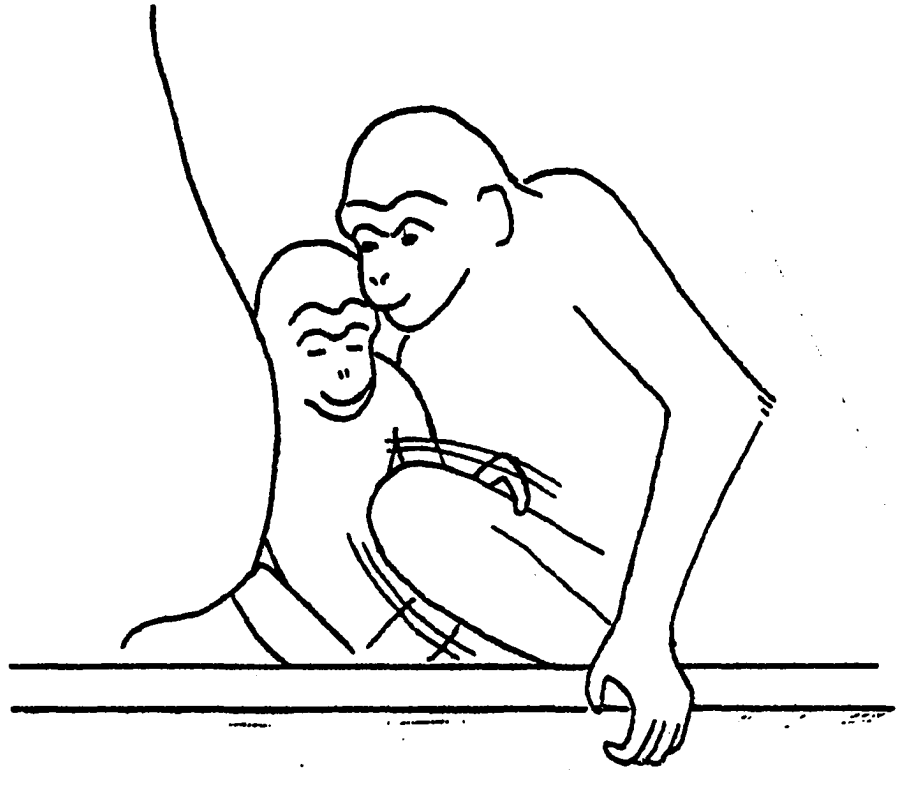


Figure 53. Juvenile exhibits "leg shake" toward infant who remains clinging to its mother with one hand.

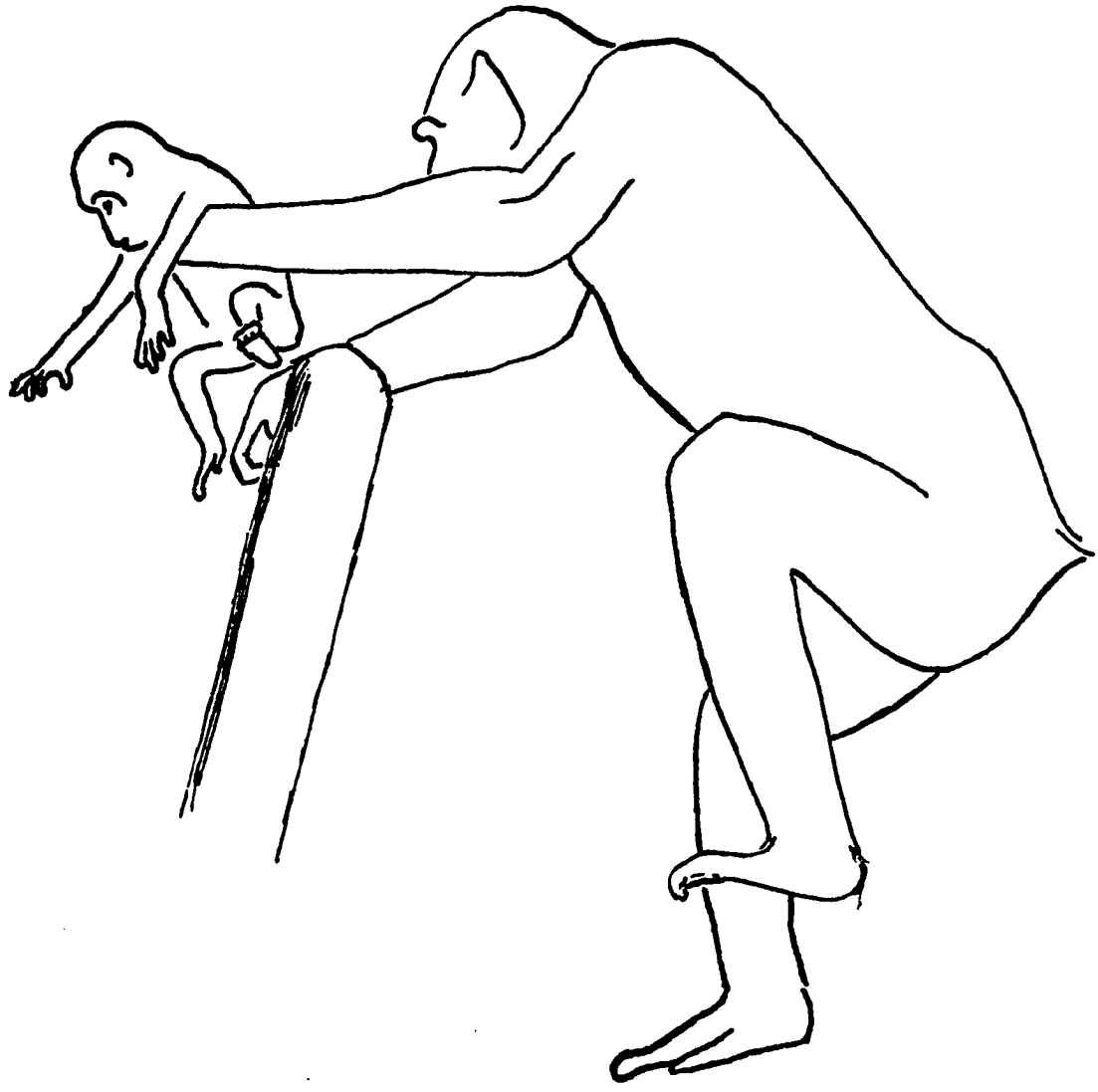


Figure 54. Young mother uses "palm carriage" with small infant as she climbs onto a tire.

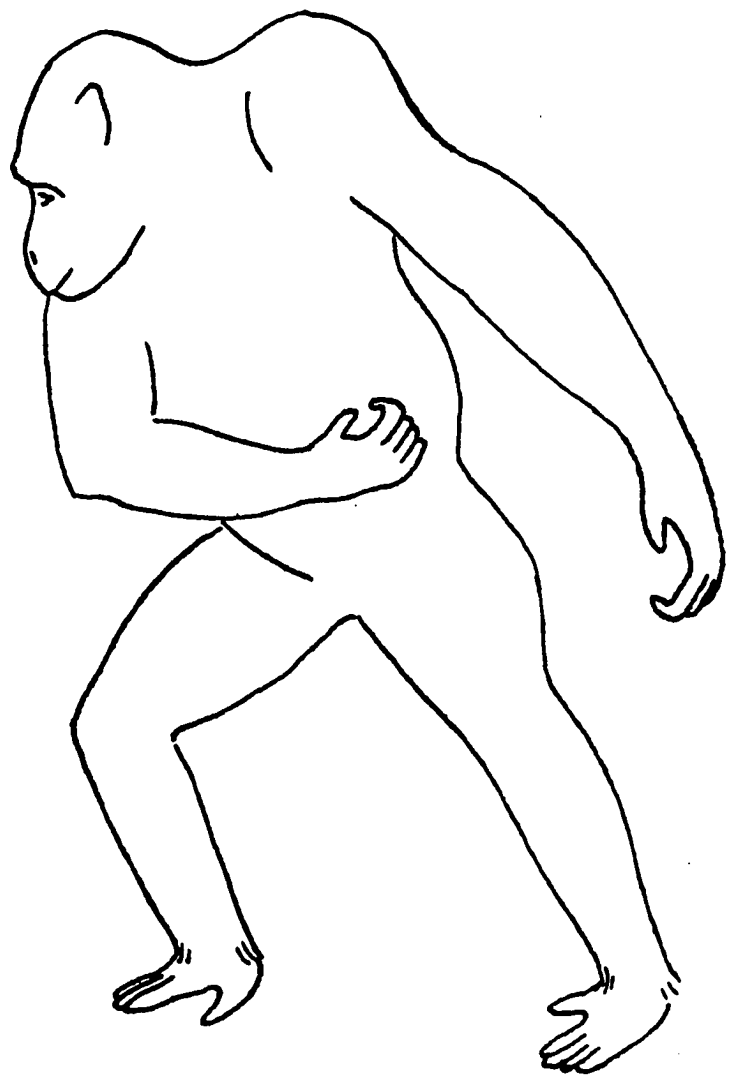


Figure 55. Adult female shows mild "swagger" coupled with bipedal approach.

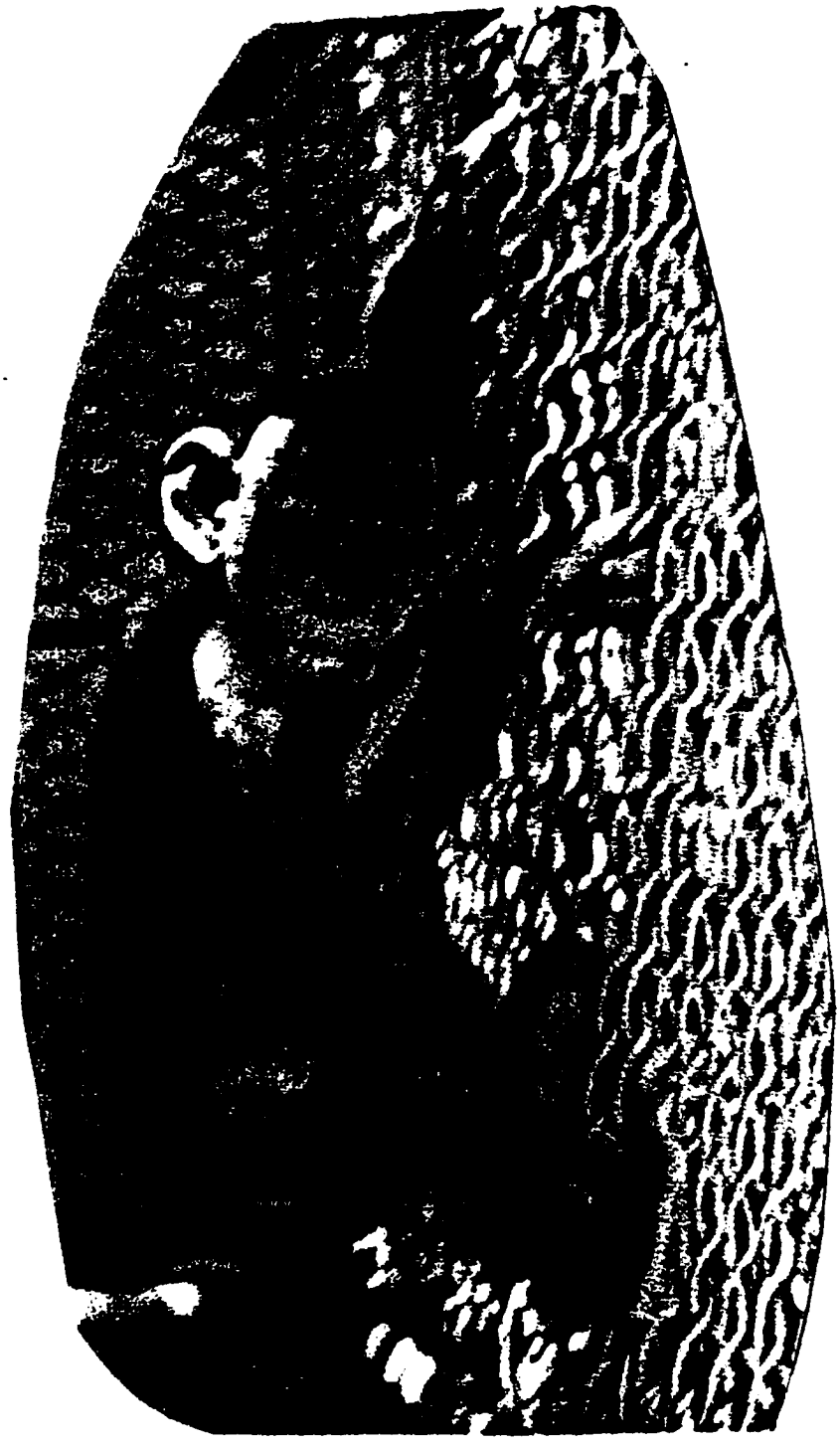


Figure 56. Male infant displays "rigid tantrum" upon being unable to find his mother.

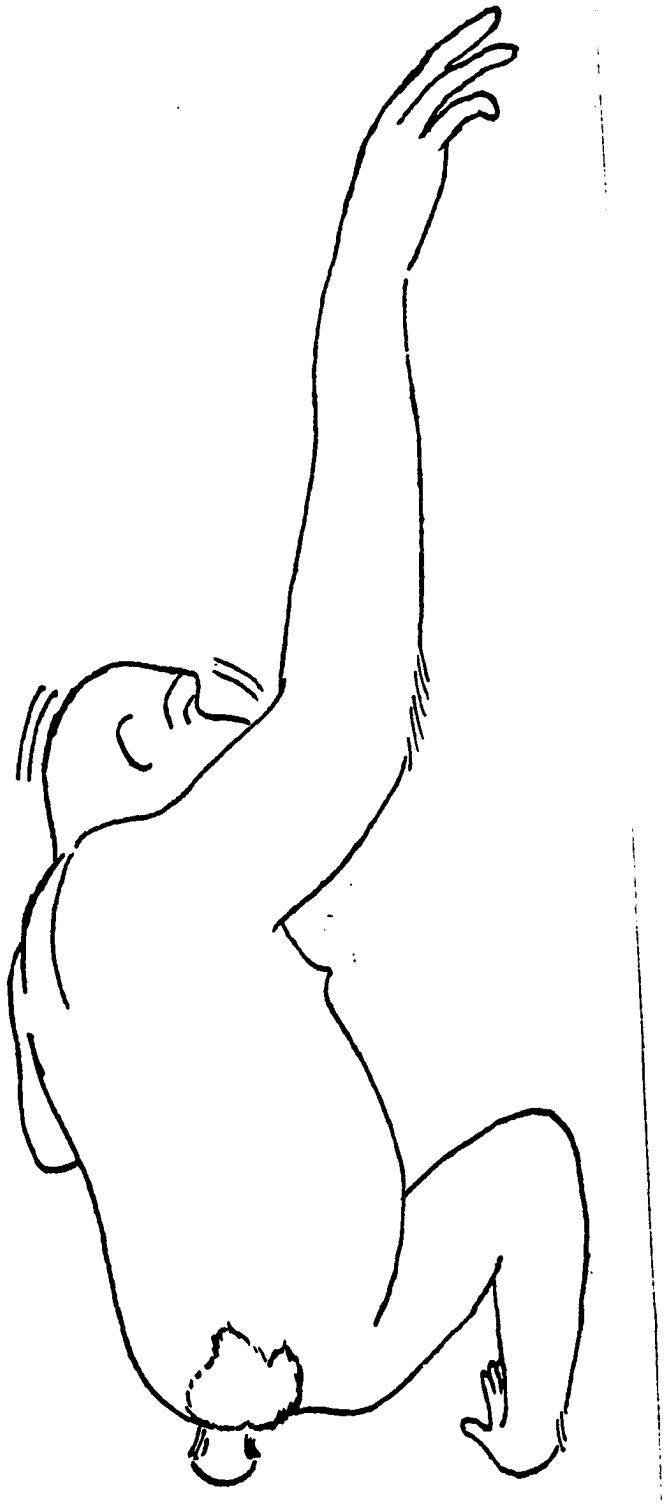
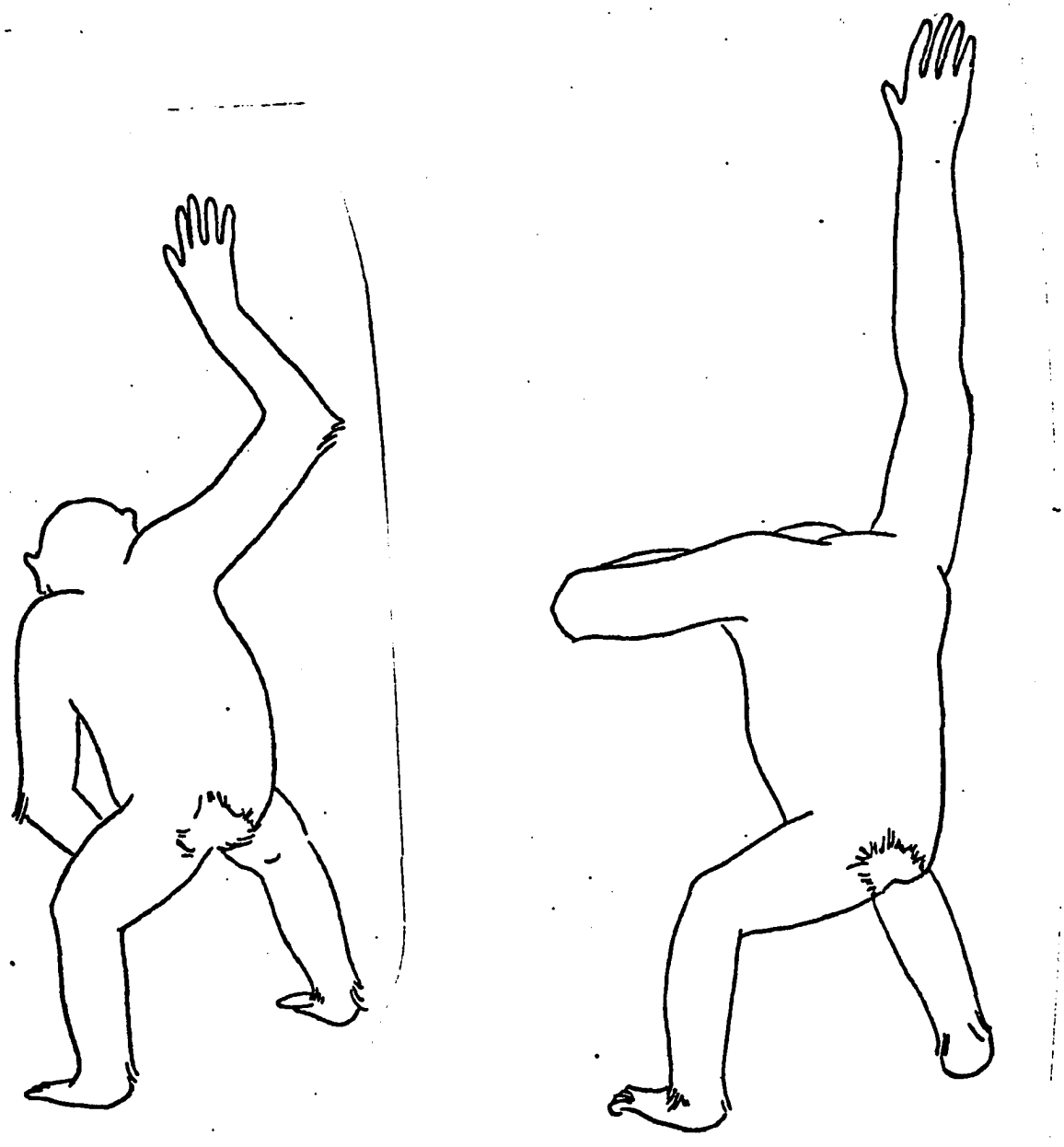


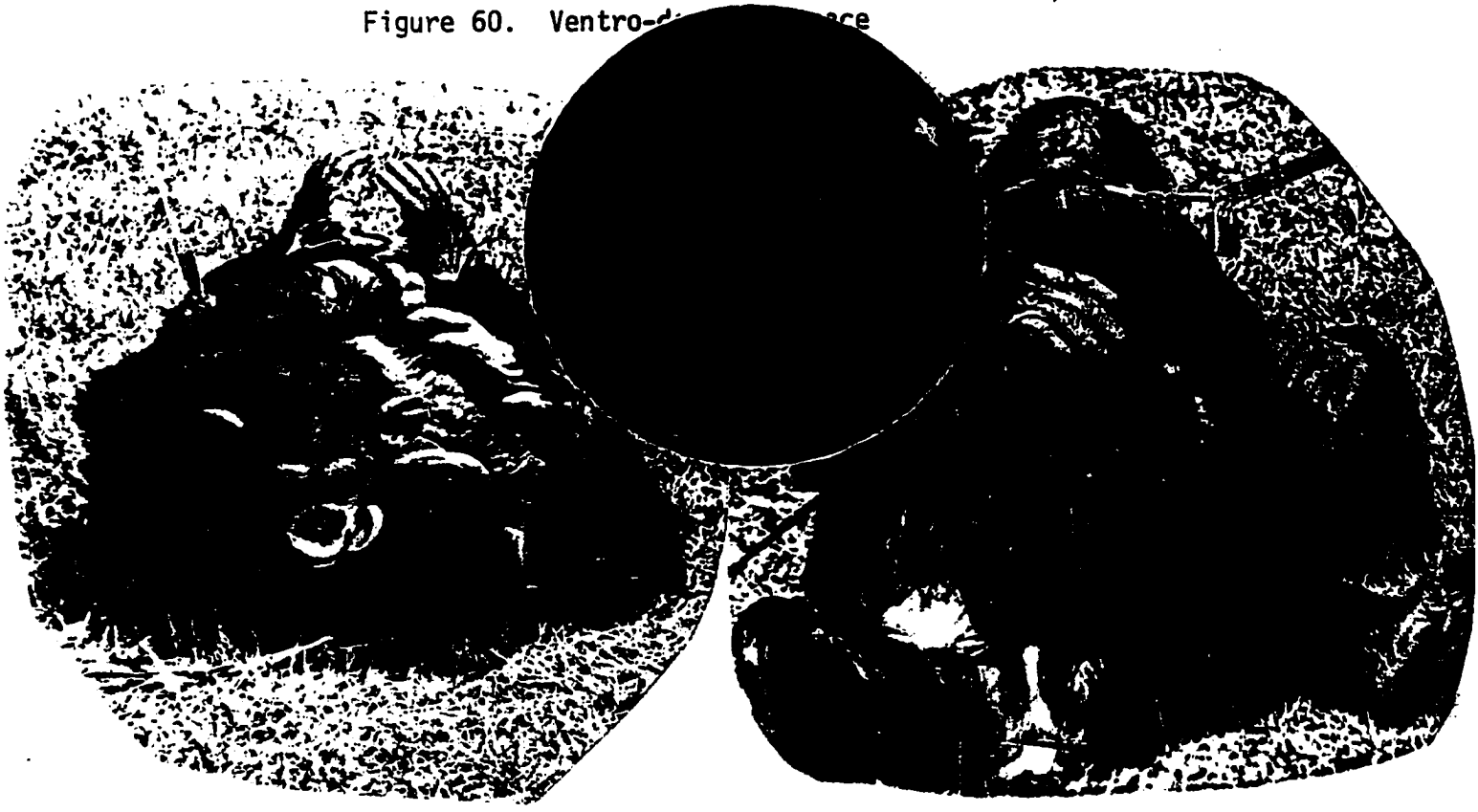
Figure 57. Mother orients "arm raise" and "head nod" toward her three-year-old male infant who is avoiding her.



Figures 58 and 59. Juvenile male displays aggressive slap. Head is lowered just prior to delivery of slap.



Figure 60. Ventro-d[illegible]ce



Figures 61 and 62. Ventro-ventral embrace



Figure 60. Ventro-dorsal embrace



Figures 61 and 62. Ventro-ventral embrace



Figure 63. Waist-clasp embrace



Figure 64. Arm headcover

Figure 65. Bend away

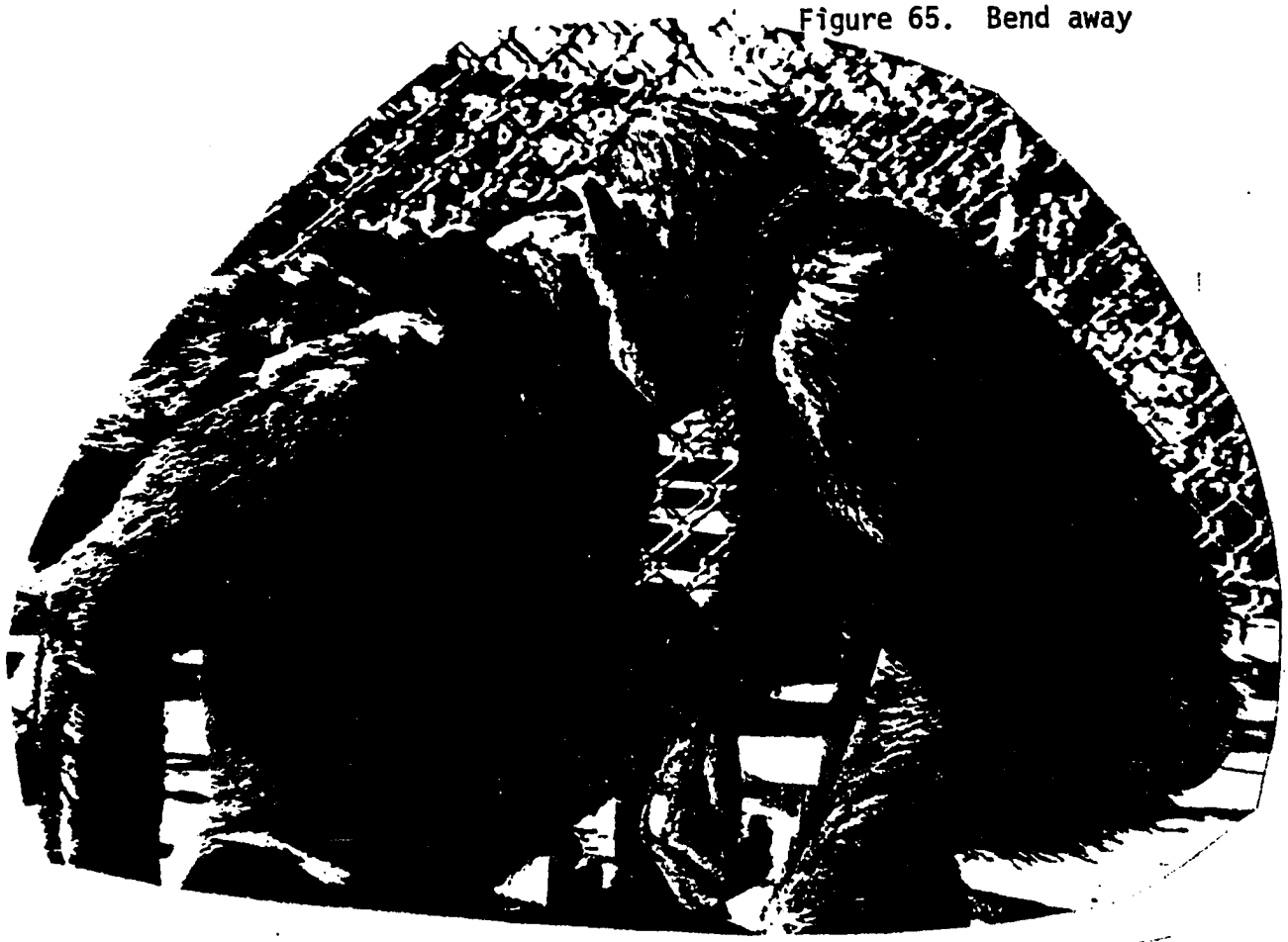


Figure 67. Dangle





Figure 68. Extend hand

Figure 69. (below) Infant female orients an over-hand "extend hand" toward her mother.



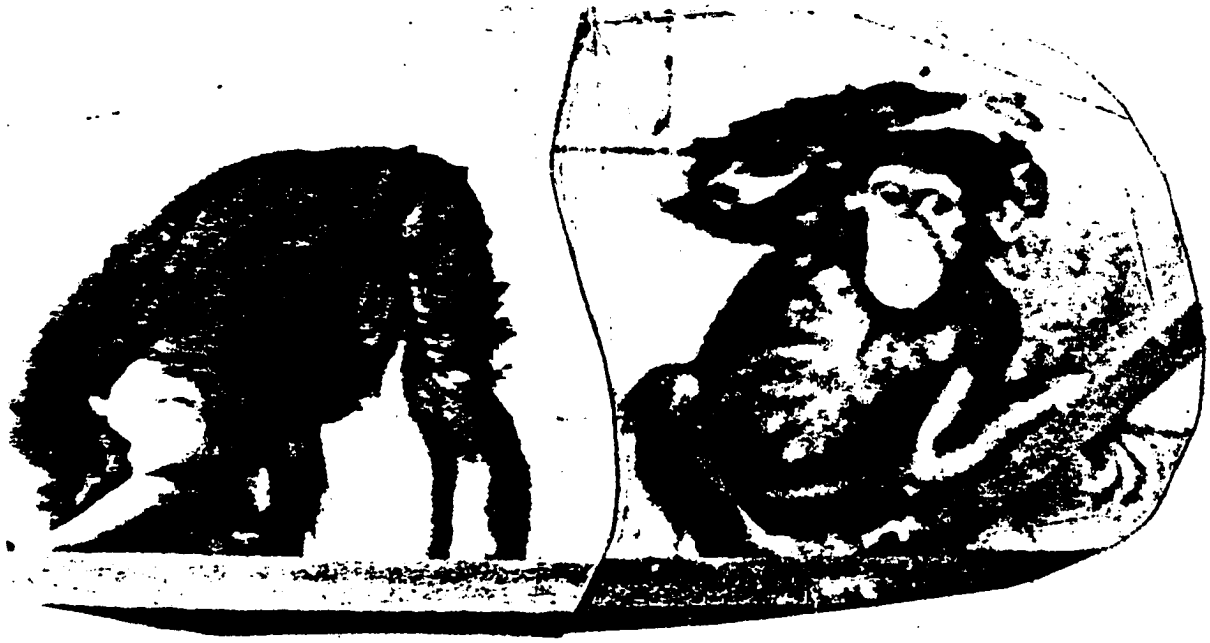


Figure 70.
Head down

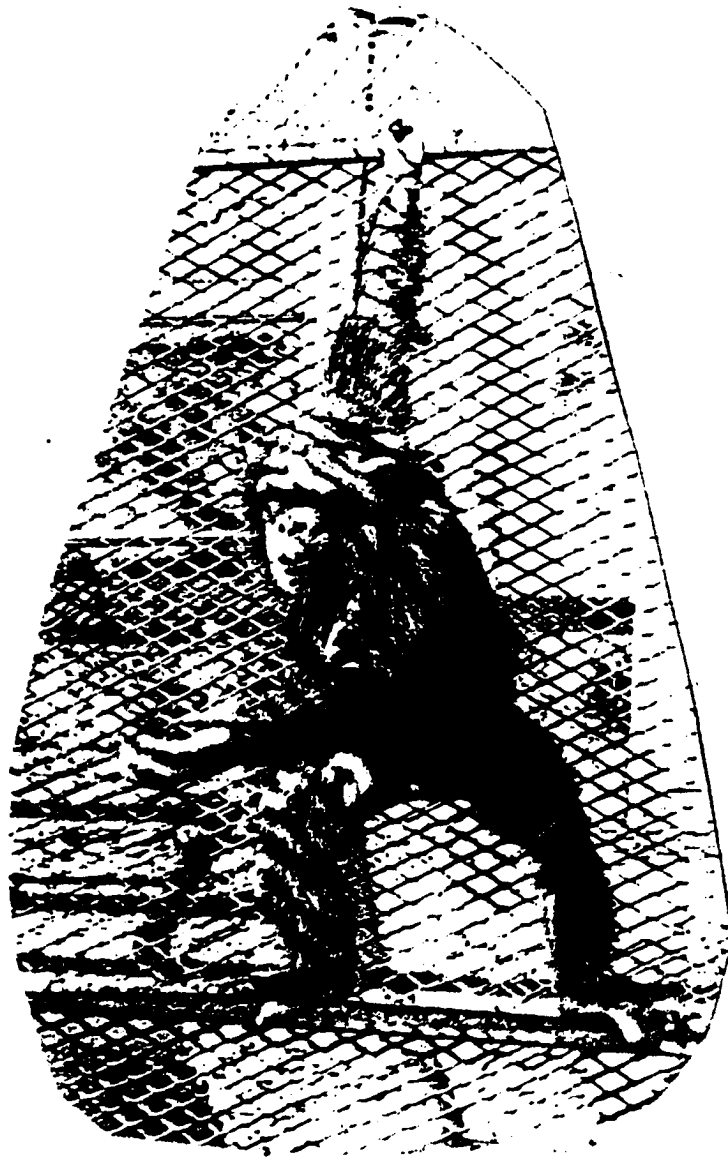


Figure 71.
Hold out hand

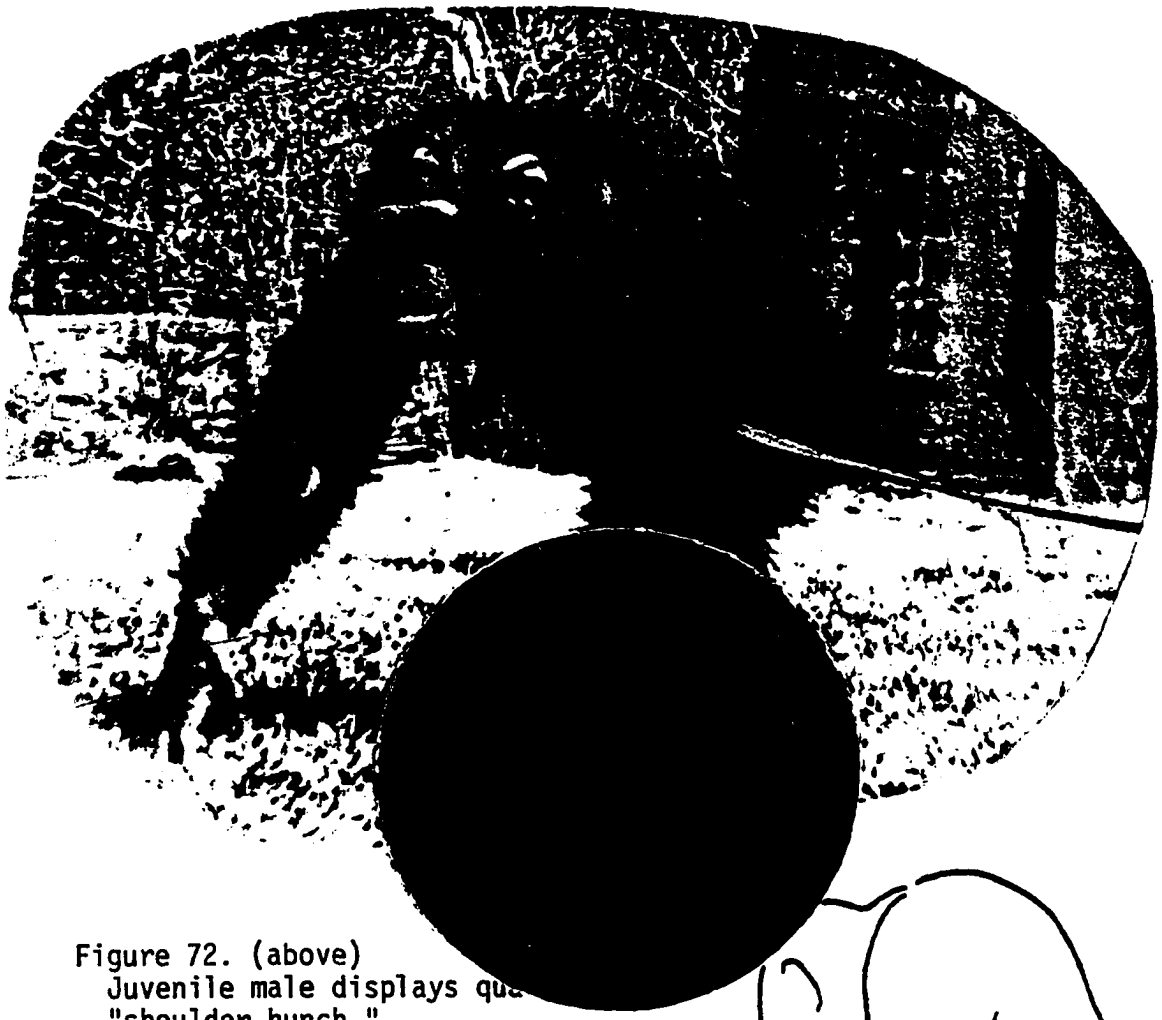


Figure 72. (above)
Juvenile male displays qua
"shoulder hunch."

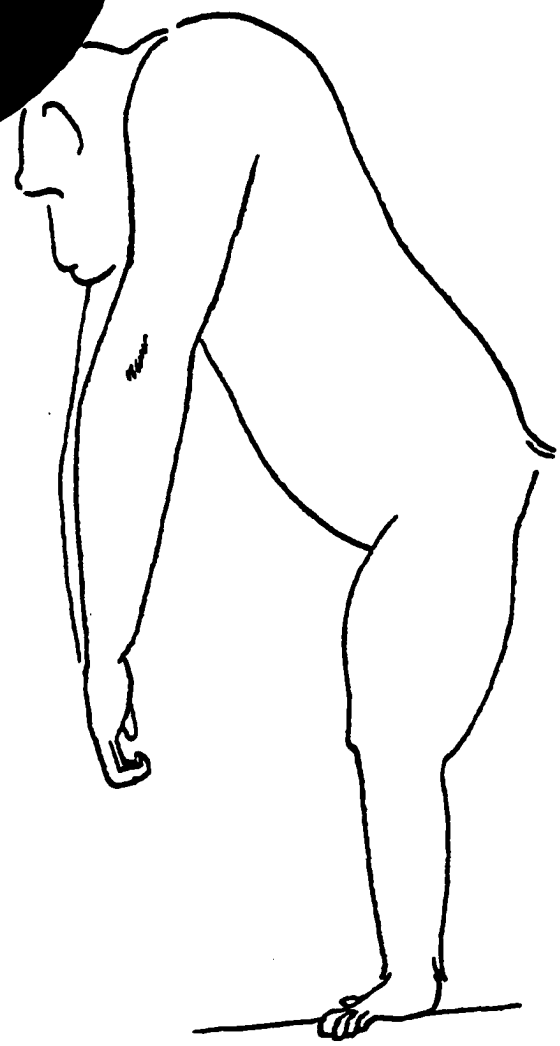


Figure 72a. (right)
Adult female shows bipedal
"shoulder hunch" accompanied
by bulged lips.



Figure 72. (above)
Juvenile male displays quadrupedal "shoulder hunch."

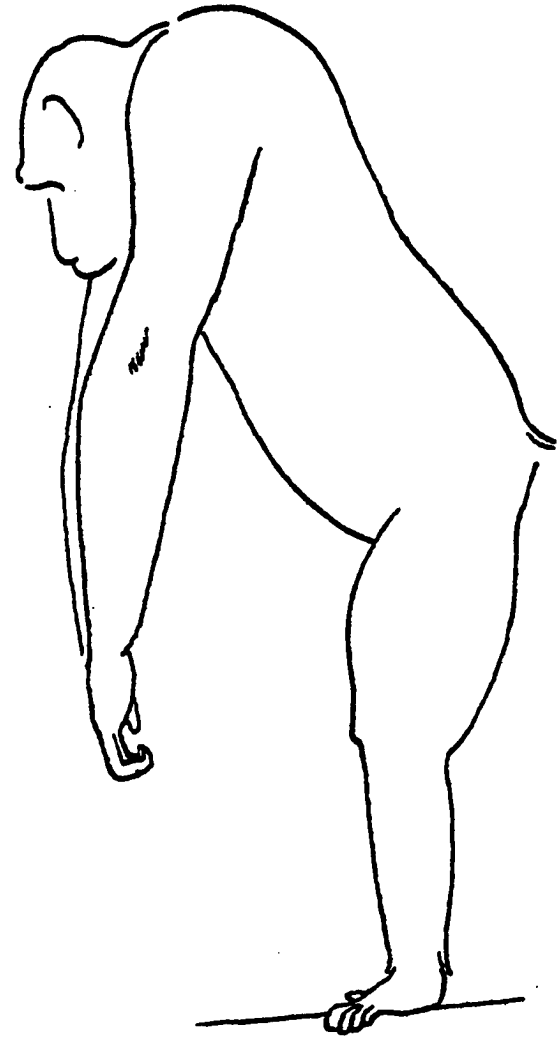


Figure 72a. (right)
Adult female shows bipedal "shoulder hunch" accompanied by bulged lips.



Figure 73. Hurry shake

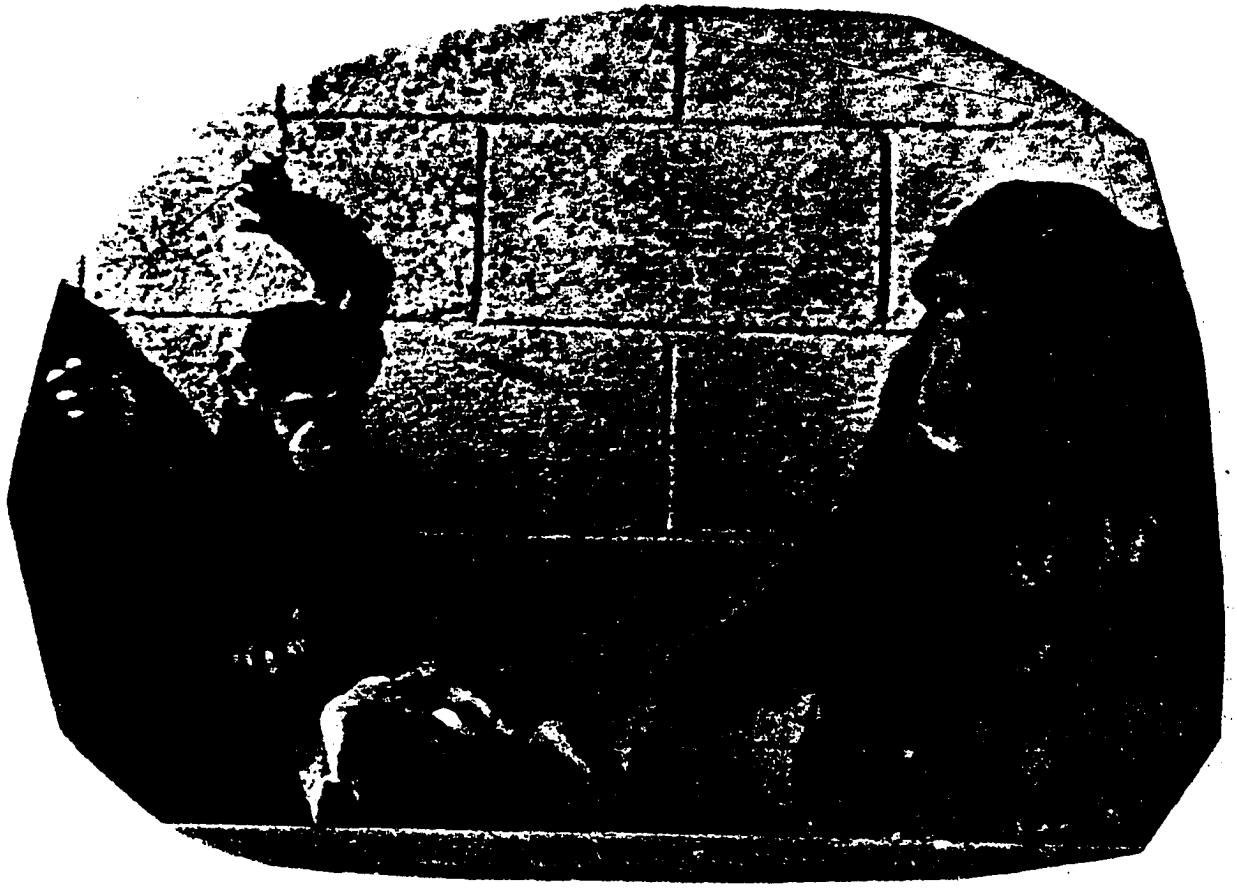


Figure 74. Lie on back

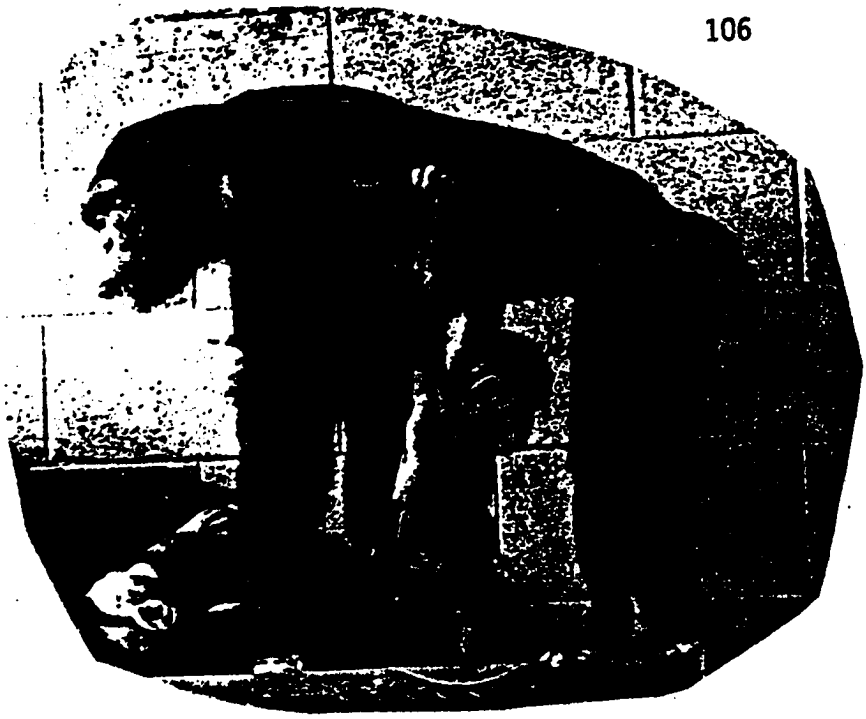


Figure 75. Ventral carriage with infant dangling by hands



Figure 76. Ventral carriage



Figure 77.

Infant "clings" to his own mother with one hand while playing with another mother.



Figure 79. Gather ventral

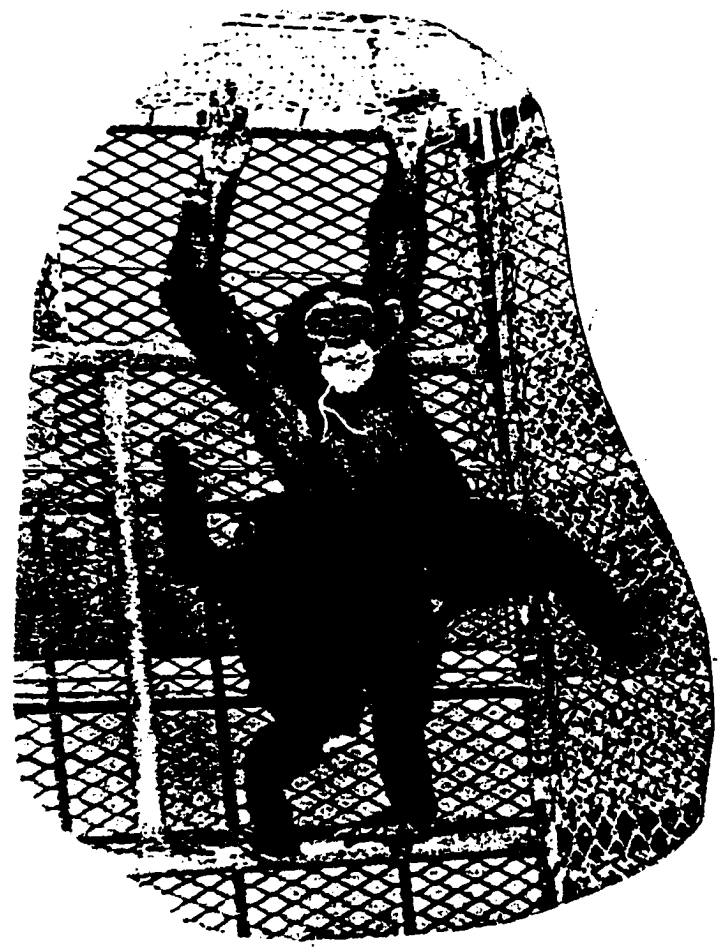


Figure 80. Juvenile orients a "chest expose" toward an infant, but is "ignored."



Figure 81. Mother "pulls up" young infant.

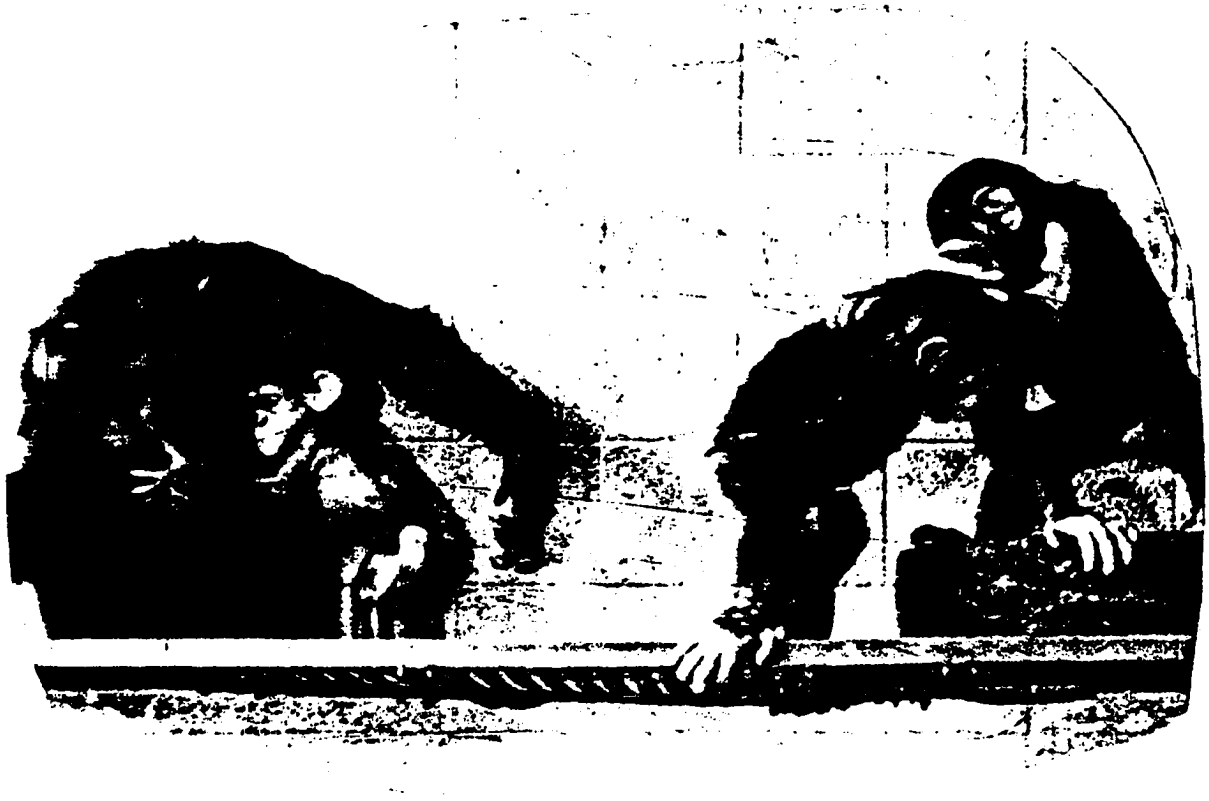


Figure 82. Mother (left) signals her infant to climb ventral with a "hold hand behind" as 2 older infants begin to play close by.



Figure 83. Mother in the center "hand dangles" her infant.

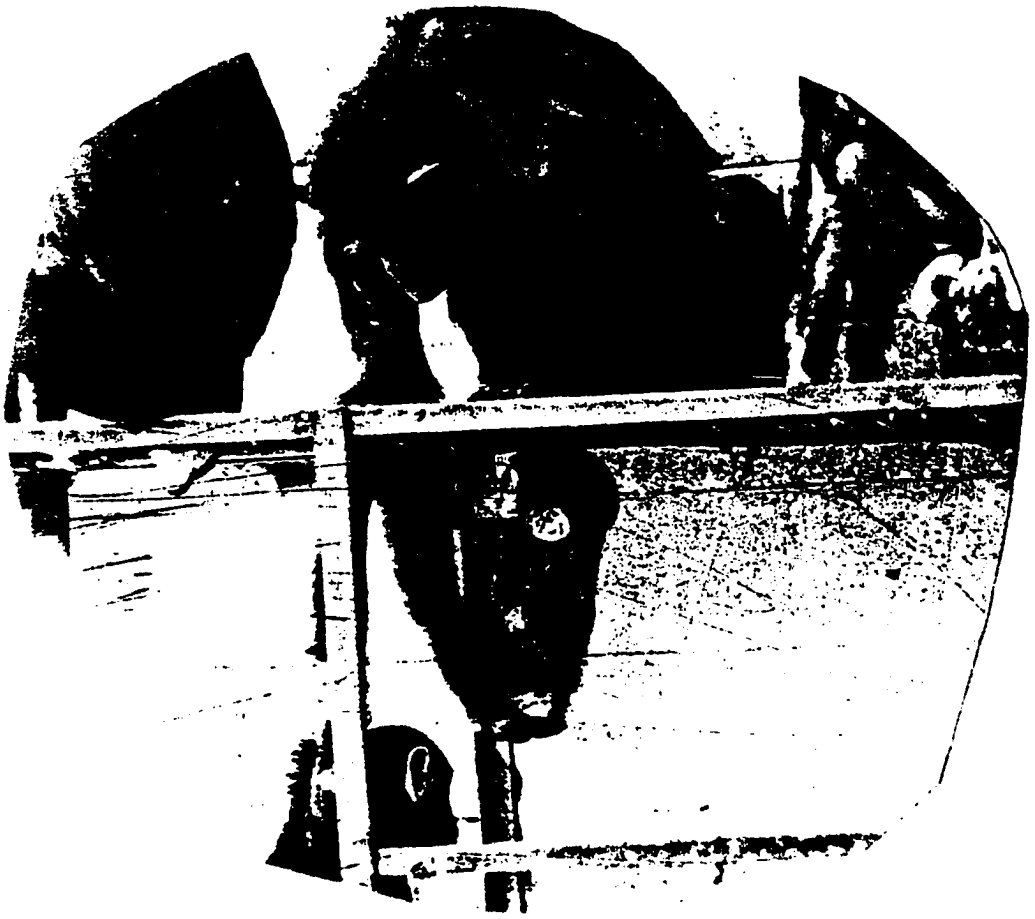


Figure 84. Mother performs "tail tuft touch" to her infant as the infant plays below her.



Figure 85. Lip-tongue kiss



Figure 86. "Full closed grin" given by human reared juvenile female.

All photographs were taken by the author. All line drawings were done by Gloria Steffen and were made either from photographs or video-tape taken by the author.

PART II

BEHAVIORAL INTERACTIONS AMONG CAPTIVE, GROUP-LIVING MOTHER, JUVENILE, AND INFANT CHIMPANZEES (*Pan troglodytes*)

INTRODUCTION

Studies of maternal behavior among captive chimpanzees have typically employed mother-infant pairs who are either housed in isolation or, at best, provided with the company of one adult female or one adult male (Yerkes and Tomilin, 1935; Tomilin and Yerkes, 1935; Bingham, 1927; Rogers and Davenport, 1970). Presumably, mother-infant pairs are isolated in order to eliminate any possibility that the infant might be harmed by other chimpanzees, and to allow the mother to care for the infant without interference. The presence of other chimpanzees can provide a real threat to the infant's life. Recently, an infant born into a social group at Lion Country Safari in California was taken from the mother shortly after birth and carried by the adult male. The infant died in a few days from starvation (personal communication, P. Middgett). Such is not invariably the case, however, and mother-infant pairs housed in social groups have adjusted well at Stanford, Lion Country Safari in Florida, and at the Institute for Primate Studies in Oklahoma.

Van Lawick-Goodall's (1968) observations of mother-offspring relations among wild chimpanzees of the Gombe Stream National Park, indicate that frequent and varied interactions with all age-sex classes are typical of mother-infant pairs. An important element of maternal care among wild chimpanzees is the protection of the new infant from the overzealous attention of other individuals, and an important element of infant development is the interaction, with individuals other than the

mother, which takes place within bounds typically set by the mother. These aspects of maternal care and infant development, along with many others, are absent when captive mother-infant pairs are housed in isolation.

Studies of rhesus macaques (Hinde and Spencer-Booth, 1969), baboons (Rowell, 1968), and squirrel monkeys (Kaplan, 1972) have demonstrated that maternal behavior and the mother-offspring relationship are significantly affected by the presence or absence of social companions. Maternal behavior among group-living captive chimpanzees has not yet been studied, however, the presence or absence of social companions may be more significant for the chimpanzee, and other great apes, than for lesser primates. Individual patterns of maternal care vary widely among chimpanzees (Van Lawick-Goodall, 1968; Rogers and Davenport, 1970) and among gorillas (Fossy, 1975). Further, many primiparous captive chimpanzee and gorilla mothers display inadequate maternal behavior (Nadler, 1974b). Van Lawick-Goodall (1968) suggests that this is because "some experience normally gained by wild females before the birth of first infant is sometimes lacking in captive females" (p. 223). A second interpretation is offered by Nadler (1974a), who notes that most captive gorilla mothers do show adequate maternal behavior for at least several days after the birth of the infant. The maternal behavior starts to disintegrate when the mother becomes agitated, paces back and forth across the cage, and fails to respond to the infant's screams or to support it adequately. If the mother can be adequately calmed, appropriate maternal behavior reappears. Nadler (1974a) cites several examples in which when "provided with the companionship and distraction of a familiar animal, that (the) mother also terminated her mistreatment

of the infant" (p. 71). A similar phenomena with a captive primiparous chimpanzee was observed by Savage, Temerlin, and Lemmon (1973). Nadler (1974b) points out that although early experience may play a part in determining the adequacy of maternal care, its effects have been confounded by the conditions of captivity which typically include small living quarters and no social companions.

A study of mother-offspring relationships among group-living captive chimpanzees seems warranted for several reasons. Learning apparently plays a greater role in determining the quality and fashion of maternal care among the great apes than among lesser primates. Captivity and its associated conditions may therefore alter chimpanzee maternal patterns more extensively than those of lower primates. The aspects of maternal behavior which are altered, and the alterations themselves may provide insights into similar phenomena in our own species where learning plays an even greater role in determining maternal patterns. Furthermore, inadequate maternal care, which has frequently been observed among isolate-housed chimpanzee mother-infant pairs may be, in part, a function of the social environment and not solely the result of inadequate experience, as has been previously supposed (Rogers and Davenport, 1970). This too, may provide us with insights which have applicability to our own species. Though the human family unit is widely regarded as the social group of mothers and young infants, with the increasing fragmentation of the extended family in western culture, many mothers are finding themselves alone with their young children for much of the day. The new stresses and loneliness produced by the absence of the extended family intensifies the parent-offspring relationship (Yorberg, 1973) and may in some cases lead to depression and inconsistent

maternal care (Radl, 1973). Mothers who not only lack the stable relationships provided by an extended family, but, in addition, are unable to establish any lasting social ties with others in the community often show gross infant neglect, lack of proper infant feeding, inconsistent punitive behavior, and intermittent infant rejection (Pavenstedt, 1967). A better understanding of the chimpanzee's social environment, the mother's relationship to that environment, and the effects of different social environments upon chimpanzee maternal care and infant development should provide helpful hypotheses for the further investigation of similar problems in our species.

The purpose of the present study is to investigate chimpanzee maternal behavior in a captive social group of mothers and infants. Individual differences in maternal care are noted and emphasized as opposed to being lumped together. Patterns of group interaction, including mother-infant, mother-other-infant, infant-infant, and mother-mother interaction are investigated in detail. Hopefully, this work will provide normative data and a typical picture of the maternal behavior in a social group of captive chimpanzees. Additionally, some attempt is made to explore the dynamics of the mother-infant communication process.

The majority of observations herein were made during a one-year study of a captive group of chimpanzees comprised of one multiparous female, her juvenile male and infant female offspring, and two primiparous females and their infant male offspring. Regular observations of this group are continuing at the time of writing and the group now consists of 6 mothers and their offspring. All mothers have been peer-reared since the infant or juvenile period of development, and all were originally wild caught. Visual, tactual, and auditory access to other

age-sex classes of chimpanzees is permitted at all times. Occasionally, unrelated adult males or juveniles have been temporarily placed in the mother-infant group. Observations were taken for as long as possible between the hours of 9:00 a.m. and 4:00 p.m. each working day except when illness or other unavoidable events occurred. Approximately 3 hours per day were devoted to recording data from the mother-infant group. Other aspects of chimpanzee behavior were studied during the remaining portion of the day. These studies involved direct interaction with chimpanzees other than those in the mother-infant group. Although the findings of those studies are not directly relevant to this paper, many of the following comments on mother-infant patterns were undoubtedly influenced by the author's personal interaction with other chimpanzees. Nuances of postures, gestures, vocalizations, etc. are difficult for an observer to notice unless they are responded to distinctly by the recipient. However, when the observer becomes the recipient, these differences are learned rapidly. Additionally, if the chimpanzee is willing to overlook certain inadequacies in the human anatomy, hypotheses regarding the signal value of various behavior patterns may be tested by the observer.

Quantitative, through the minute data on play, grouping, contact, and grooming, was recorded by noting the beginning and end of each of the above activities on a standarized time sheet. Participants were identified by their initials and the general quality of the activity was described. Running descriptions of interactions were made several times each day using a symbol shorthand notation system. The above data was supplemented by the extensive use of photographs and videotape.

CAPTIVE MOTHERS AND NEWBORN INFANTS

The post-parturitional behavior of six mothers (including one mother twice) was observed for different periods of time varying from 1 day to 2 years. In one case, an infant which was premature died within one day of birth and its twin sibling had to be taken from the mother, and in 2 other cases, infants were taken from their mothers at 2-4 days of age for research purposes. Most of the data in this section was obtained from 2 primiparous and 2 multiparous mother-infant pairs. These four births occurred within an 8 month period between November 1973 and July 1974 and observations are continuing on three of the pairs at the time of writing.

These mother-infant pairs were observed intensively within 1 to 5 hours following parturition. All mothers were wild caught and peer-reared, none rejected their infants and all infants (except the premature twins) were observed nursing within 48 hours following birth.

Multiparous mothers were carrying their infants low in the ventral cradle when first observed and the placenta was still attached (refer to Table 1 for background information on each mother). One primiparous mother, Peggy, lay on her back with her infant clinging, head down, to the calf of one leg. Approximately 3" of umblicus was still attached to the infant, but the placenta was absent, presumably eaten. The other primiparous mother, Cindy, cradled her infant ventrally. For the first 2 days she typically cradled the infant quite high, at or above nipple level. The placenta was still attached to the infant. Mothers either

TABLE I

PAST BIRTH RECORD OF MOTHERS

NAME	Number of previous infants	Sex of infant	Age of mother
Carolyn	4	♀, o	20 yrs.
Carolyn	6	o	20 yrs.
Wendy	2	♀	16 yrs.
Mona	2	o	16 yrs.
Mimi[1]	1*	?	12 yrs.
Peggy[2]	0	♀	11 yrs.
Cindy[3]	0	♀	8 yrs.

[1]Mimi delivered an infant (thought to be premature) during conditions of group stress when a large number of chimpanzees had to be crowded into an extremely small space for hurried cage repair. The infant was killed at birth during a group fight.

[2]Peggy had the opportunity to observe mothers and infants in an adjacent cage for several years and, prior to delivery, she was housed with Wendy and an infant.

[3]Cindy was reared with younger chimpanzees and frequently carried 2½ to 3 year olds in the ventral position when she was an older juvenile and adolescent. She also was able to observe mother and infants in adjacent cages.

allowed the placenta to drag behind them as they moved or they carried it by the cord. Cindy was careful to wrap the cord around her arm so that no tension was placed on the umbilicus when she moved (Figure 1). She also repeatedly hit at any flies which attempted to land on the placenta. Though most mothers briefly touched or poked at the placenta with their fingertips, none held it in their hands or sat with any portion of it in contact with their bodies. All placentas dropped off before the end of the second day and mothers ignored them once they became detached from the infant. In one case, the umbilicus was accidentally severed by a guillotine door as the mother was being moved to another cage several hours after delivery. An adult male, who was caged with this mother, picked the placenta up and carried it around in front of him by the umbilicus, just as the mother had done. The mother appeared unconcerned.

New mothers supported their infants with their arms, thighs, or hands as they sat or moved. Multiparous mothers appeared to be able to move more easily and generally supported their infants more adroitly than primiparous mothers. Both primiparous mothers attempted to support their infants with 2 or 3 limbs, but their infants frequently slipped out of position. Infants of primiparous mothers appeared to be less able to briefly support their own weight than did infants of multiparous mothers, but this difference may well have been a function of the multiparous mothers' craddling agility. Multiparous mothers supported their infants with their thighs and the palm of one hand when moving. They placed their hands so that the palm ran vertically along the infant's back, with the middle or the index finger curled loosely under the infant's genitals and the wrist or forearm supporting the infant's head.



Figure 1. Cindy moves with umbilicus wrapped around her arm.

Thus, even if the infant did not cling at all, the entire surface of its trunk was held firmly against the mother's venter. The primiparous mothers did not support the entirety of their infant's trunks. Cindy either held one thigh up tightly against the infant's back and allowed the infant's head to drop backward or held the infant's head firmly in the crook of her arm and allowed the infant's trunk to fall backward (Figure 2). Peggy pulled both her legs close to her body and moved in a crouched stance, taking very short steps and holding her hand against the infant's head as it clung to her calf or thigh. The infant repeatedly slipped from her grasp and whimpered loudly. She hurriedly pressed it to some surface of her leg or body, seemingly without regard to the orientation of its head or ventral surface. The infant did not vocally object to being cradled backwards or upside down, but repeatedly stretched its arms and legs outward, making grasping motions with its hands and feet. During the afternoon of the second day, she began carrying the infant in the typical ventral position. This occurred gradually and was preceded by grooming and repeated inspections of the infant. During inspections, Peggy pulled the infant an inch or so away from her body and touched, groomed, and peered at it, paying particular attention to the face, navel and genital regions. When the infant whimpered, she would quickly put it down, often orienting the head upward if she had been inspecting the face and placing the ventral surface down if she had been inspecting the navel. By the end of the second day, the primiparous mothers supported their infants as did multiparous mothers, though their movements were still hesitant. Both primiparous mothers appeared somewhat dazed when first observed. Their eyes were glazed and they could easily be approached and touched through the wire. Multiparous



Figure 2. Primiparous mother supports infant's head but allows the infant's posterior to dangle away from her venter.

mothers appeared extremely placid and were unusually friendly, but all appeared to be normally alert. All captive mothers spent the majority of their time either sitting or reclining during the first 2 to 3 days following parturition, but the primiparous mothers spent considerably more time lying down than did multiparous mothers. Mona and Wendy spent 45% and 68% of the first day after birth lying down while Cindy and Peggy spent 83% of the day reclining.

It appeared that all mothers looked at their infants more frequently on the first day of life than on succeeding days, but data on the number of times per minute that a mother looked directly at her infant was obtained only for Cindy. She looked at the infant 10.8 times per half hour on day 1, 4.8 times per half hour on day 2, and 3.3 times per half hour on day 3 (Figure 3).

The most impressive facotr of maternal behavior among captive chimpanzees was the high degree of variability in both the type and quantity of mother-infant interaction patterns. For example, Wendy did not groom or pull her infant up from the ventral position until the evening of the first day. Only 2 grooming bouts were seen on that day, they were directed toward the infant's genital region and were very brief, lasting 5 seconds or less. Wendy accompanied the grooming movements with loud, exaggerated teethclacking or lipsmacking noises such as are usually produced when new chimpanzees are introduced to the group or when older infants and juveniles first begin grooming adults. She appeared concerned about the location of the placenta, putting it first to the right of her, then to the left, then back and forth again several times whenever she moved to a new location. She barked at other chimpanzees when they got too close to the placenta or attempted to touch it. The infant



Figure 3. New mother "hoo whimpers" to infant as she rearranges its position.

was kept completely surrounded by her arms and legs and it was difficult to glimpse any part of it much of the time. When she lay down she kept her head curled forward toward the infant instead of resting it on the shelf as she normally did. She frequently placed her lips gently on the top of the infant's head and occasionally placed her open mouth, with lips pulled over her teeth, over the infant's head. The infant vocalized, very softly, only twice during the first day. It was first observed nursing between 13 and 16 hours (estimated) after birth.

Carolyn was pulling her infant out from her body and grooming it when first observed between 3 and 7 hours (estimated) following parturition. Teethclacking and lipsmacking were not heard although the grooming was frequent and bouts were long, ranging from 2 to 28 minutes. Carolyn's infant vocalized repeatedly when pulled out of the ventral position, averaging 40 vocalizations per hour during the morning of the first day after birth. Carolyn repositioned or cradled the infant in response to persistent vocalizations, but seconds later she would again pull the infant out from her venter and begin inspecting or grooming it. Touching the lips to the infant's head or placing the open mouth over the head were not seen, although they could have occurred since Carolyn's back was often turned toward the observer and she spent most of her time on a high shelf which made observation difficult. Twice during day 1 she was observed to detach one of the infant's hands, hold it to the wire and attempt to curl the infant's fingers around the wire. Other colony mothers have been observed to do this also, but not until their infants were 2 to 3 months old. Carolyn's infant was first observed nursing between 8 and 11 hours (estimated) after birth.

Individual differences in maternal care persist throughout the mother-infant relationship and are a function of both the mother and the infant.

Infant Removal

Two infants and one mother were studied for a short period (2 to 6 hours) following infant removal at 2 and 10 days of age. Mothers were sedated with sernulin during infant removal and although the infants may have ingested some of the drug by nursing before the mother was fully immobilized, both infants were awake and appeared alert when removed from their mothers. Both infants protested vigorously immediately upon removal. They vocalized with open-mouth-bared-gums repeatedly and their screams attained an intensity and frequency considerably greater than had ever been emitted while they were with their mothers. One infant attempted several times to bite the chin and neck of an attendant. Neither quieted until presented with either a nipple or bottle. In one case the nipple was the breast of the infant's non-lactating human surrogate mother and in the other it was a baby bottle filled with milk.

Carolyn (who had her four previous infants removed after birth for experimental purposes) was observed as the effects of the sernulin began wearing off following her infant's removal.[1] Within an hour, Carolyn began moving about the cage in an uncoordinated manner, falling or slipping occasionally. She put her hand in the "groin pocket" between her stomach and thigh and felt this area repeatedly. She rubbed her hand

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[1]Sernulin does not actually produce a state of unconsciousness, but rather an extreme lack of corrdination resulting in immobilization. In most cases chimpanzees appear to be asleep or exceptionally groggy and in some cases vocalizations, suggestive of hallucinations occur. When Carolyn's infant was removed her eyes were open and she watched the infant being taken from her.

along the inside of both thighs, about her venter and between her legs. She looked down at her thighs and stomach, looked about the cage and looked down at her thighs and stomach again. She placed her hand in the "groin pocket" and cradled her thighs up close about her head, pulled her hand out, looked down where her hand had been, and replaced it. These behaviors were repeated over and over again, as though she did not recall that she had just looked at or felt that space between her thighs and her body. This looking behavior disappeared when Carolyn was fully recovered from the sedative. She then simply sat and looked at the door through which her infant had been carried out of the colony (Figs. 3 and 4).

CAPTIVE MOTHERS AND THEIR INFANTS

Attentions resulting from captivity

The ontongeny of mother-infant interaction patterns among captive chimpanzees is quite similar to that described for wild chimpanzees by Van Lawick-Goodall (1968). Hence, this section will not duplicate that work with descriptions of carriage, nursing, etc., but will instead, concentrate on patterns which appear to be rather a direct function of captivity. The captive environment is less complex and generally unstimulating. Consequently, captive mothers often devote an unusually large amount of attention to their infants.

When the infant is very young, this attention is manifested in the form of repeated infant grooming and inspection behavior. The mother may also provide the infant with extensive support whenever she moves. Although wild mothers support their young infants, support by captive mothers is frequently so excessive that travel of any distance would be

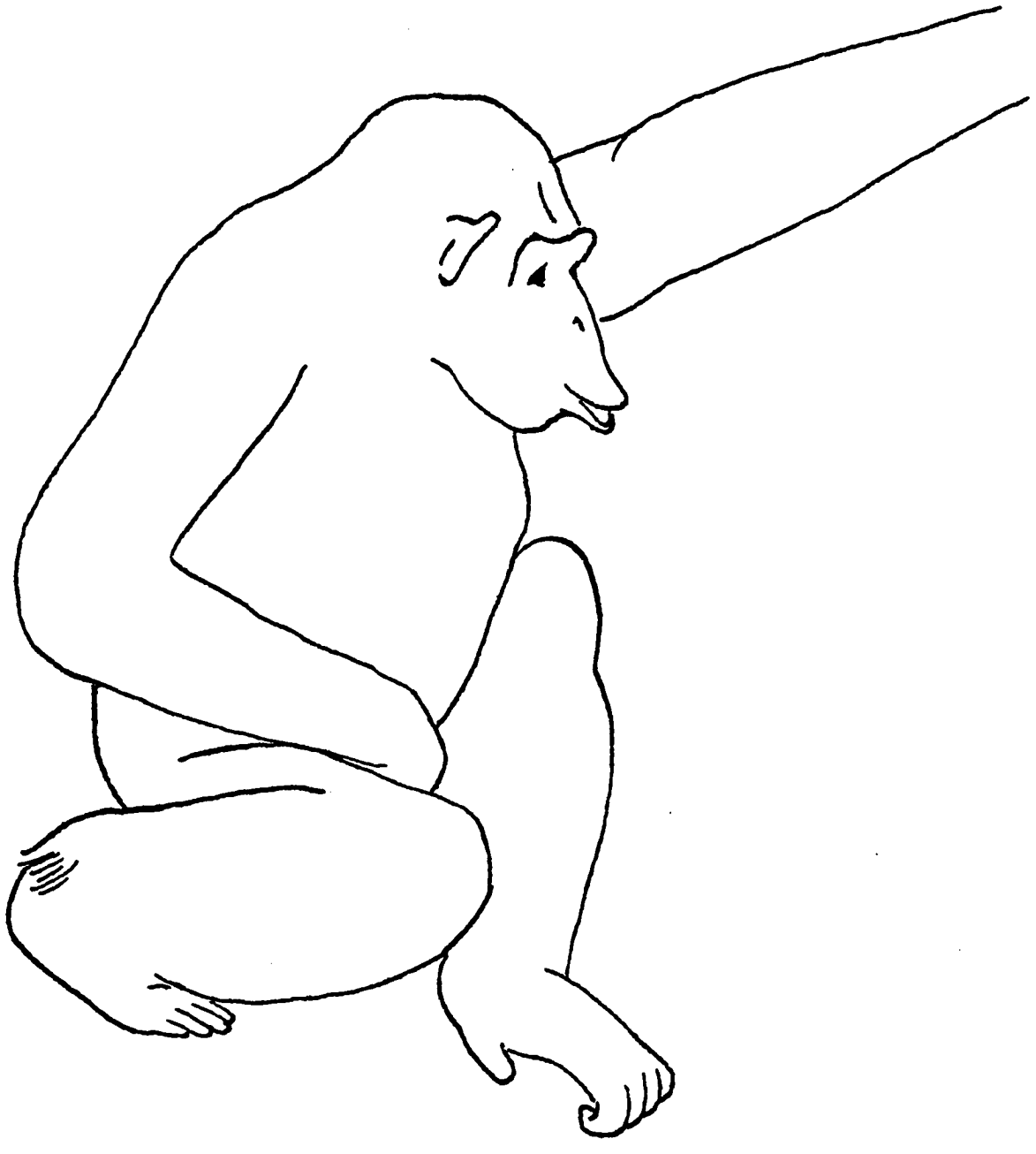


Figure 4. Carolyn groggily supports herself with one arm while she feels her abdomen looking for her infant.

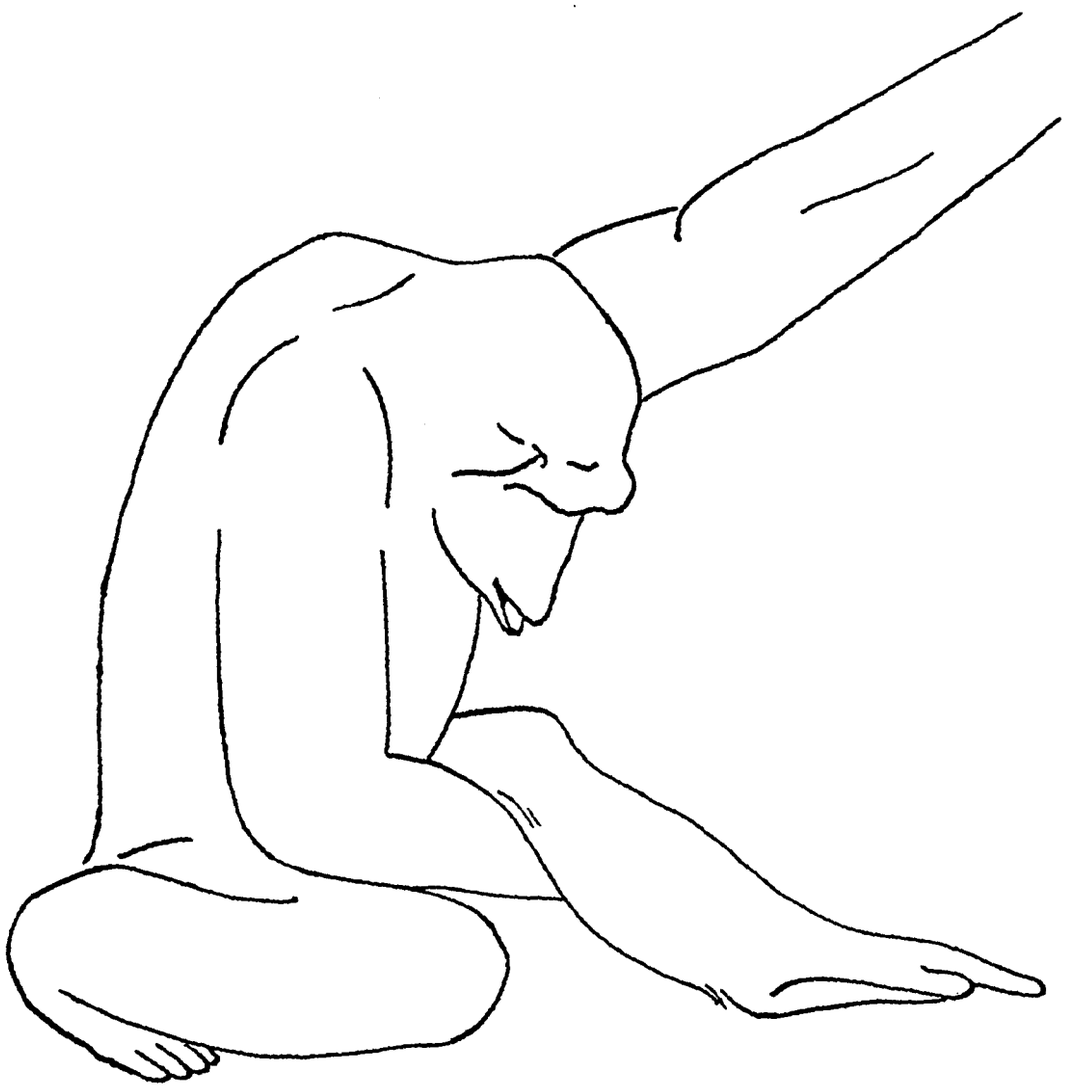


Figure 5. Carolyn groggily looks at her abdominal area and searches under her legs for the infant.

impossible. As the infant matures, mothers spend a great deal of time encouraging infants to move out of the ventral position.

Four mother-infant pairs have been observed during the initial stages of contact-reduction. In these pairs, the first complete break of contact occurred between 3 and 6 months of age, with male infants initiating contact breaks before female infants. Prior to the first complete break in mother-infant contact, many forms of contact reduction occurred. Early forms of contact reduction were typically instigated by the mother and objected to by the infant. Later forms were predominantly instigated by the infant.

In each of the 4 pairs observed during this period, the mothers appeared to have their own individualistic ways of reducing contact, the one factor in common being that the main function of each mother's behavior was to move the infant out of ventro-ventral contact but not completely out of contact. Moving the infant out of the ventral position was often preceded by a repetitive disengaging of the infant's hands, as though the mother were irritated by the constant clinging. Infants ceased clinging only momentarily when mothers disengaged their hands, however, and then the mothers would move them out of the ventral position. Mimi did this by pulling Meshach up by both hands and holding him away from her, or by placing one hand under his seat and sliding him around to her side so that he sat on the shelf next to her (Figure 6). Wendy turned her infant around and put it's stomach against her forearm or thigh, or sometimes sat the infant on her knee and let it lean against the wire (Figure 7). Mona sat in the middle of a large tire, turned Daniel around, placed his stomach against the rim of the tire and curled his arms across the top (Figure 8). She



Figure 6. Meshach inspects his mother's genital area after she moves him around to one side to decrease ventral contact.

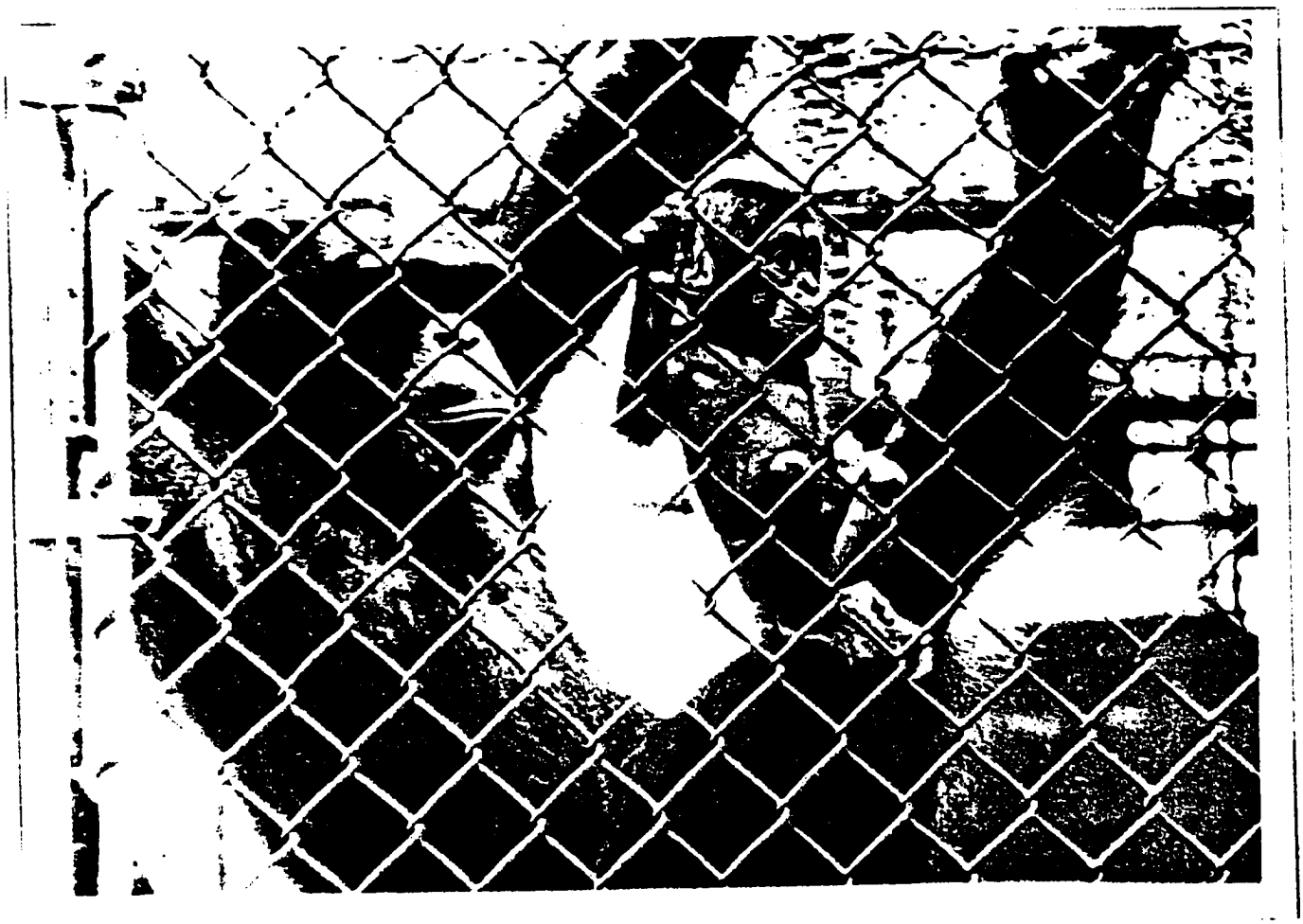


Figure 7. Wendy lets Jane hold onto the wire while she supports her with one knee.

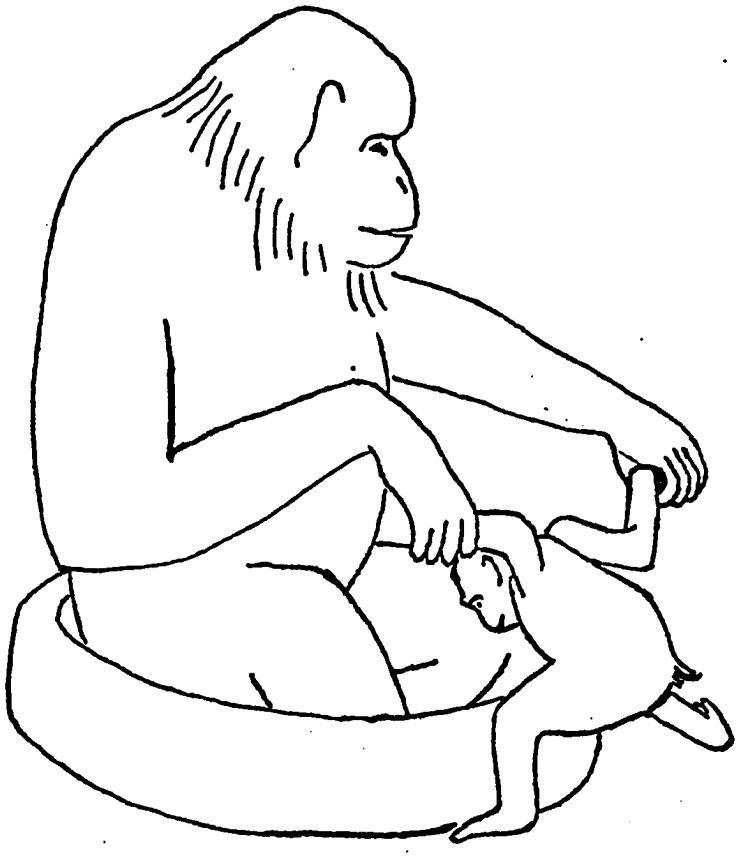


Figure 8. Mona decreases contact with Daniel by placing him in front of her on the floor.

also lay on one side, and placed Daniel, venter down, against the inside of her forearm. Cindy held Abigail by one hand and dangled her under the shelf. Occasionally, she placed Abigail on her head (Fig. 9).

Infants of 2 to 3 months of age objected vocally when moved out of the ventral position, and early attempts to place infants in other positions were brief (1 to 5 minutes), but frequent. Typically, the infant began hoo whimpering within a few seconds after it was moved. The mother looked down in response to whimpers, patted the infant, made slight adjustments in her position or in the infant's position, etc. As the infant's whimpers became louder, the mother's movements became more hurried until finally the infant screamed and the mother quickly hugged it to her venter. Abigail differed noticeably from all other infants in this regard. When completely out of ventral contact, she simply dangled limply by one arm as Cindy held her hand. She did not hoo whimper and made no effort to reattain the ventral position. At 2 to 3 months, she was often away from her mother's venter for 20 to 25 minute periods. It was difficult to discern whether Abigail's aberant behavior was a function of Cindy's unusual habit of dangling the infant by one arm, or whether it represented an atypical low arousal level on the part of the infant. In either case, this pattern was almost certainly intensified by captivity and an infant treated in such a fashion in the wild would probably not survive.

Several patterns of reducing ventral contact and increasing locomotor independence were shown much less often than those described above, but were demonstrated by most mothers at some time. In one such pattern, mothers held infants out in front of them by both hands and let the infant sit or stand on the floor.



Figure 9. Cindy and Mona sit together on the shelf with their infants. Cindy (right) decreases mother-infant contact by dangling Abigail by one arm.

This pattern is similar to that of human mothers who often turn their infants toward them and let the infant stand or sit in their lap. In this position, the chimpanzee infant exercises its legs by repeatedly straightening the knees with a pushing motion, just as do human infants. Additionally, since the chimpanzee infant is held by its hands instead of under its armpits as is the human infant, the infant strengthens its arms by flexing the elbows and pulling upward. Mothers may also stand their infants next to a tire or other impediment and, holding the infant's hands, assist it in climbing over the hurdle. They may hold the infant out in front of them and gently bounce it up and down and they may place the infant's hands on, and curl its fingers around, the wire, encouraging it to climb.

Captive mothers also paid considerable attention to the excretory functions of their infants. Young infants were regularly held a few inches away from their mother's body if they were about to defecate or urinate. The mother typically observed the process intently and in some cases wiped feces from the infant's anal region afterward. At other times, the infant's feces were ingested by the mother.

Beginning at around 3 to 5 months, infants start to actively participate in the process of contact reduction. They often begin by leaning far back against their mother's knees while she sits. They flail their arms about, attempting to make tactual contact with nearby objects or other chimpanzees. They appear especially attracted to the mother's face, waving their hands about, trying to touch her mouth and eyes, and grasping the hair on the side of her face. Mothers did not restrict this leaning, reaching, and grasping, unless their infant happened to grasp another chimpanzee. They then disengaged the infant's hand and

tucked it into their venter, or moved a few feet away from the other individual. When the infant began attempting to climb out of the ventral position, mothers approached and sat near the wire or other climbable object to facilitate this process. The infants grasped the wire and pulled themselves toward it, while keeping one hand or foot in contact with the mother. As they gained confidence in their locomotor ability they began letting go of their mothers for short periods. At this point, they also started to cling ventrally to other chimpanzees for a minute or two.

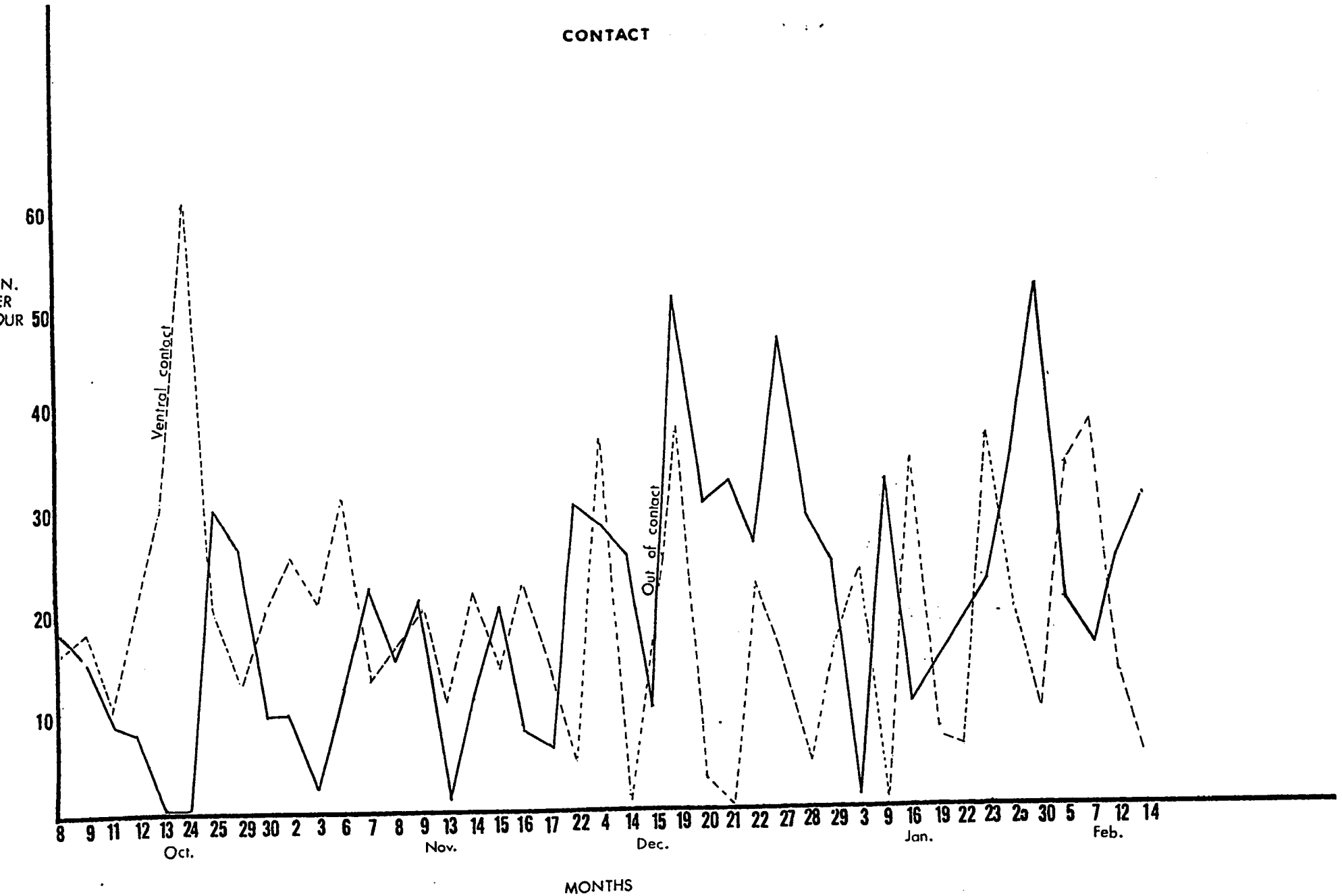
Patterns of affection and infant tolerance

Affectionate patterns were very similar to those described previously by Van Lawick-Goodall (1968) for free-ranging chimpanzees. Affection behaviors included nuzzling and playbiting the infant's shoulder. This pattern occurred frequently, when infants climbed back into the ventral position, and during general group excitement. Mothers also placed their mouths, with lips covering the teeth, over the infant's face and head. They held their noses against the infant, patted them, and gazed at them during play. Mothers displayed a great deal of tolerance and patience toward infants who stamped on their heads, pulled the tender hair around their face, jumped up and down on them as they tried to sleep, interferred with grooming bouts, took food from them, refused to cling when the mother wanted to move outside, etc. Although mothers rarely displayed irritation with regard to the activities of their infants, they were clearly irritated by many conditions of captivity and often the infant was the brunt of behaviors resulting from such irritation. Sometimes they detached their infant's hands and left

Figure 10. (following page)

Amount of time spent either completely out of contact (solid line) or in the ventral position (dotted line), by Meshach.

(When these two figures do not equal 60 minutes, the difference is the amount of time spent in non-ventral contact.)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Out of contact
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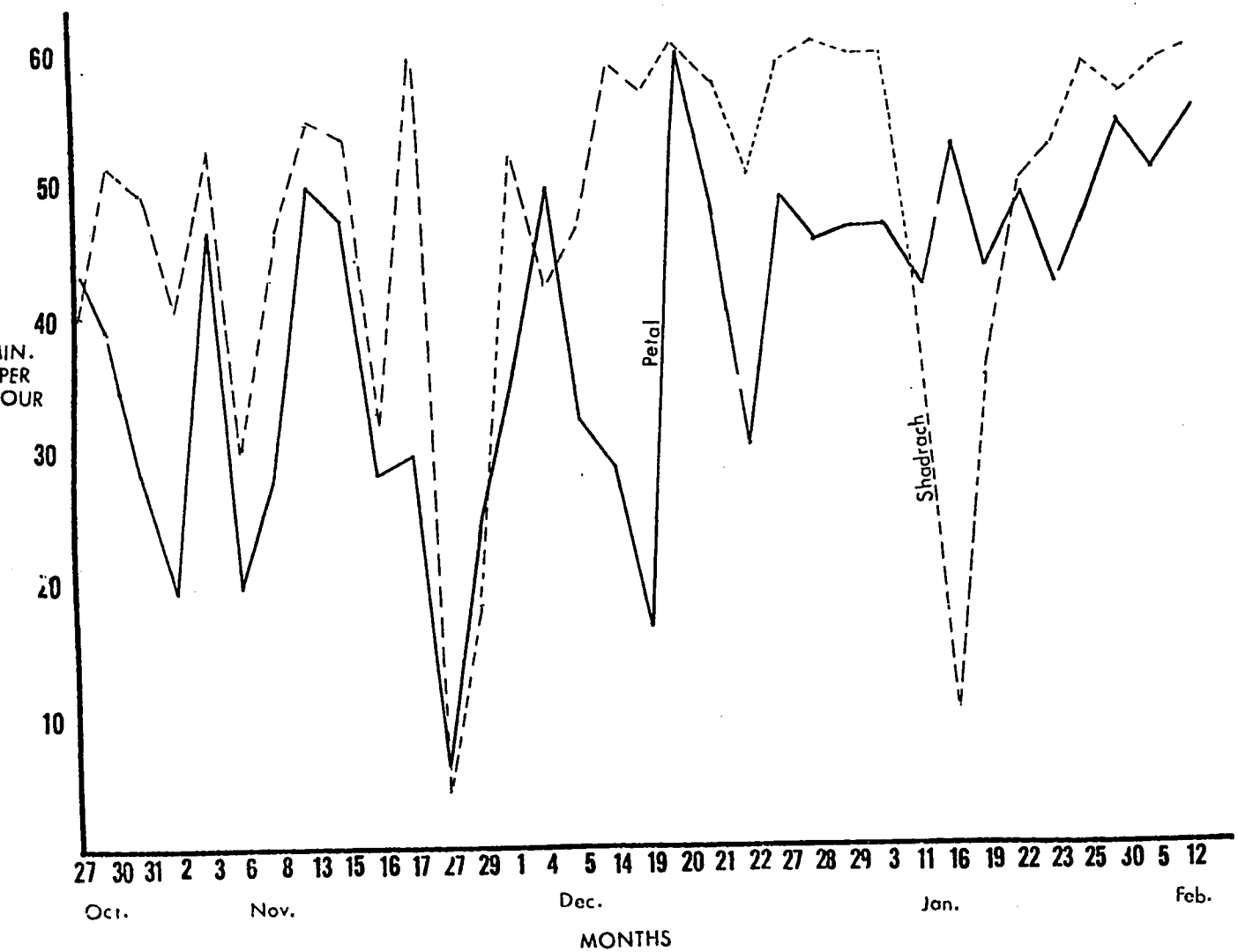
CONTACT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it whimpering and clinging to another mother as they paced the cage in agitation. They occasionally insisted on an intense hair-pulling type of body grooming or a painful "pulling" form of genital grooming. They abruptly terminated nursing bouts and they stole fruit from their infants by chasing the infant and, if it did not drop the fruit, squeezing its mouth until it spat the fruit out.

Mother-infant communication

The behaviors of mother and infant were so well coordinated that overt communication between them was typically unnecessary or very subtle. Often mothers merely looked toward the infant and it approached and clung ventrally, or they touched the infant's hand and it climbed out of the ventral position. Other patterns included the head nod, which functioned as an approach signal; a soft ‹‹oughh›› vocalization, which functioned as a ventral-cling signal; an upraised arm with palm down and elbow straight, which was employed as a command to approach; and a bipedally front to back sway, which was used when an infant refused to cling ventrally. Signals to cling dorsally entailed a wide variety of postures, most of which included an orientation of the dorsum toward the infant, a pause, and a look over the shoulder at the infant. The "leg-back" signal as described by Van Lawick-Goodall (1968) was not observed.

Mother-infant contact

Contact between mothers and their mobile infants was initiated and terminated by infants in 90% of all observed cases. The total amount of contact for any given day varied dramatically in the case of any individual infant. Figure 10 illustrates the amount of time Mimi and Meshach were observed in contact during the 4 month period from October to Janu-

ary. This was the period of initial contact reduction, as the first complete breaks between this mother-infant pair occurred near the end of September. Figure 11 demonstrates the same sort of daily variability for Shadrach and Petal who were 2 years old during this period.

MOTHER-OTHER-INFANT INTERACTIONS

Non-mobile infants

Interactions between mothers and the very young infants of other mothers were infrequent. When interactions did occur, they were generally preceded by some gesture toward the infant's mother. Such gestures included glancing from the mother to the infant several times, approaching the mother and sitting next to her rather stiffly while looking at her infant with rounded eyes, and grooming the mother. If the mother merely sat still in response to these gestures, her infant was then touched by the other mother. Touching of other infants was typically done with an extended index finger, with the lips, or with both. Infants were usually touched under the chin, on the stomach, or on the tail tuft. If the infant's mother did not intervene during the touch, play or grooming followed. These grooming and play interactions normally lasted less than 1 minute and grooming was accompanied by teeth clacking and lipsmacking. Play consisted of gentle prodding with a finger or nibbling of the stomach and shoulders. Mothers typically intervened at some point during interactions between their young infants and other mothers. Intervention took many forms, including turning their back on the other mother, drawing their thighs up about the infant, repositioning the infant, interposing their hand or forearm between the



Figure 12

Figures 12 through 16. In this series of consecutive photographs, Wendy (second from right) requests permission to touch or groom Mona's 4-month-old infant. Wendy first orients a fingertip head-touch toward Mona (Fig. 12) then, as Mona ignores her, she places her palm on Mona's forehead (Fig. 13). Mona continues to ignore the request and so Wendy moves around to the other side and touches Mona's shoulder (Fig. 14). Still ignored, Wendy shows closed-teeth face and touches Mona's forearm in a more direct attempt to indicate her desire to touch the infant (Fig. 15). Finally, as a last resort, Wendy actually attempts to gently pull Mona's arm away from the infant (Fig. 16). When this is also ignored by Mona, Wendy turns away and grooms her own infant.



Figure 13



Figure 14



Figure 15



Figure 16

infant and the other mother, pulling on the other mother's hand or foot with a playface, grooming the other mother, and simply walking away. Mothers did not threaten or display agonistic reactions toward other mothers who attempted to touch their infants. They did, however, occasionally threaten older infants or juveniles who tried to peer at or touch their infants (Figs. 12-16).

Although most interactions between mothers and the young infants of others were limited to touching, grooming, or brief tickling, other patterns were observed. Sometimes one mother followed another about the cage and repeatedly reached forward and inserted her finger between the infant's foot or hand and its mother's body, thereby disengaging the infant's grip. Some mothers also wrapped their fingers around an infant's leg or arm and pulled it a few inches away from the mother's body. Mothers also patted other infants, hoo whimpered toward them, and held their hands out to them.

Young infants stretched one arm toward other mothers who approached them, sometimes gripping the other mother's hair. Infants who were just beginning to spend a few minutes out of contact with their own mother sometimes clung to another mother when she was nearby. Occasionally, such clinging appeared to be accidental, since infants often did not glance at the other mother before clinging to her, much as toddlers may, without looking up, cling to the skirt or pant leg of an adult whom they do not know. When this occurred, the mother merely reached out, disengaged her infant's hand and drew it to her own venter without interference from the other mother.

Just as mothers did not respond agonistically when other females attempted to touch their infants, other females did not react with aggres-

sion if their approaches toward infants were denied by the mother. Older infants and juveniles sometimes showed pilo erection and foot stamping when their approaches to young infants were checked. They also poked at, or slapped at the infant or mother and then rapidly retreated.

One mother developed the habit of approaching other mothers whose infants were clinging ventrally, and poking the infant in the back until its mother began playing with or grooming her. In this case the poking did not appear to indicate an interest in the infant, but rather a desire to interact with the other mother.

Mobile Infants

Interactions between mobile infants and other mothers were frequent, complex and varied. By this stage, the infant was capable of agile independent locomotion and his use and understanding of gestures and vocalizations was relatively sophisticated.

The most frequent type of interaction was play. Mother-other-infant playbouts were initiated by both mothers and infants. Though all infants played daily with other mothers, all mothers did not play regularly with other infants.

The nature of such play is difficult to describe accurately in abstract terms. Two running descriptive prologues are thereby included to give the reader a "feel" for the character of this type of play. The first is a playbout between Pampy, the dominant female, and Meshach, 20 month old son of the middle ranking female. The descriptive prologue is taken from a videotape of the playbout and illustrates the reciprocal nature of play. Each action is either responded to by the recipient or is repeated in a similar or slightly altered form until the recipient does respond.

> Petal (daughter of Pampy) and Meshach play while dangling above Pampy. Pampy initiates play with Meshach by reaching up and pulling on his arm. As she pulls, eye contact between them occurs. Meshach then tries to push Pampy's hand away from his feet. In response she raises her other hand and pulls on him. He lets go and drops to the shelf beside her. Pampy places the palm of one hand behind his head and the palm of the other behind his tail tuft. Meshach displays a grin face then leans into Pampy's stomach with a playbite. Pampy tickles Meshach's thigh with her fingertip, Meshach pushes her finger away. Pampy moves her hand back and pauses. Meshach touches Pampy's hand, Pampy does not respond. Meshach then turns toward Pampy with a half play face and playbites Pampy's hand while playslapping her shoulder. Pampy embraces Meshach with both arms then gives him a mouthcover. As she moves her face away from his, Meshach playbites her hand, Pampy again embraces and mouthcovers Meshach.

The above description represents 40 seconds of play. The entire bout lasted 3 minutes and included interspersed play between Petal and Meshach as well as continuing play between Meshach and Pampy. It terminated when Meshach's mother went outside and he followed. Many of the patterns described above were repeated numerous times. Several others also occurred including, Meshach tugging on the hair of Pampy's leg, Meshach embracing Pampy about the head with one arm, Pampy finger tickling Meshach's ribs and stomach, Pampy squeezing Meshach behind the neck with thumb and index finger, and Pampy touching Meshach's tail tuft.

For purposes of comparison, a descriptive prologue of play between Mimi, the middle ranking female, and Shadrach, the 30-month-old infant of the low ranking female, is also presented.

> Shadrach and Meshach (Mimi's son) play on the shelf next to Mimi. Shadrach orients a half play face to Meshach. Mimi looks at Shadrach and holds his arms and in response he turns toward her and puts an arm over her head. She playbites his neck and he then adopts the arm-headcover position. She pauses and he moves toward her with a playbite then adopts the arm-headcover position. Mimi playbites Shadrach's neck once more, then pauses again. Shadrach begins pulling on her arm and she playbites him again. He adopts the arm-headcover position in response. Mimi

> pauses and Shadrach moves into the head down position, combining it with an arm-headcover. Mimi playbites his back and Shadrach emits audible laughter. With the laugh, Mimi begins playbiting Shadrach with slightly increased pressure, all up and down his back. Petal (daughter of high ranking female) approaches and Mimi pulls on her leg. Petal squeals. At Petal's vocalization Shadrach rushes toward Mimi with a double handed playslap and playbite to her face.

This description represents 35 seconds of play. The entire playbout lasted a total of 4½ minutes and was interrupted by brief exchanges of play patterns between Shadrach and Meshach, Shadrach and Manny, and Mimi and Meshach, as these individuals passed by Mimi and Shadrach. Play between Mimi and Shadrach resumed after each interruption. The playbout terminated when Mimi pinch bit Shadrach's fingers. Shadrach gave high-pitched squeaks with closed-mouth-bared-teeth and held his arms toward Mimi while shaking his hands at the wrist. Mimi put her hand behind his back and he leapt into the ventral position and took her nipple in his mouth for 2 seconds. Mimi then placed her open mouth to his chest and hugged him to her, after which he climbed out of her lap.

Although the above playbouts represent only two of the hundreds observed, they illustrate several factors which are typical of the majority of mother-other-infant playbouts. As in the descriptive accounts, most mother-other-infant playbouts begin when 2 or more infants are playing close by. Holding an infant's limb (without a playface) is a frequent manner of initiating infant play among mothers. Mothers often pause during playbouts and during pauses, infants may terminate the playbout by moving away; but typically they adopt a playposture or orient playslaps, playbites, etc. toward the mother and she resumes play. While affiliative patterns (embrace, mouthcover, etc.) are often directed toward

younger infants during play, they are not generally seen when mothers play with older infants. Another age related difference is that while the tempo and intensity of play never increases during play with young infants, it sometimes does during play with older infants. Additional infants regularly approach during mother-other-infant playbouts, and if one infant is mildly hurt the other infant typically reassures him or attempts to distract the mother.

One of the most obvious differences between mother-infant and mother-other-infant behavior was that although mothers groomed their own infants regularly, they rarely groomed other infants. When they did, they typically groomed the infant's genital area and the infant squeaked, hoo whimpered, and tried to move away. (Occasionally, a mother directed slow gentle grooming to other parts of the infant's body, and it did not object.)

Infants under 2½ to 3 years hardly ever groomed other mothers. But when they did, they often directed their grooming toward the genital region. Both male and female infants, peered at, touched, sniffed, and inserted an index finger into the vulvas of adult females. Genital swellings resulted in increased infant grooming by both male and female infants. Mothers terminated infant grooming after a minute or so by gently pushing the infant away with their knuckles or by covering their genital region.

Infants of 2½ to 3 years were attracted to cuts, abrasions, and other bodily irregularities a few months before they began more typical grooming. Early grooming bouts were often directed toward the recipient's face, just as early attempts to touch the mother had been directed toward her face. Early grooming of other mothers was characterized by exagger-

ated lipsmacking, teethclacking, peering, picking, and repositioning.

In addition to genital grooming, several related mother-other-infant behavior patterns appeared which might be loosely categorized as sexual. A common behavior toward younger individuals was to approach and press the genital region against their abdomen or tail tuft. This pattern was displayed by males and females, though males often interspersed it with facing the infant and thrusting against it. The position was usually maintained for 30 to 60 seconds. Infants directed the genital press only toward other infants but they directed "thrusting against" toward each other and toward older individuals. Both male and female infants were observed to thrust against other mothers, but males did so with noticeably greater frequency. Male infants displayed penile erections during thrusting and thrust against both swollen and non-swollen females.

Thrusting directed toward other mothers was often observed during agonistic interactions. Mothers who had been attacked or threatened and were hurt, hesitant or unable to return the attack screamed loudly and rushed toward male infants (or, in some cases, the male infants rushed to them). The infant then thrust rapidly against the screaming mother until she quieted down. She then typically turned to the infant and embraced him.

On one occasion, a mother pulled a male infant into the ventral position and then began to masturbate by rubbing her genital area back and forth across the shelf. Another mother immediately approached, took the male infant away, and shoved him toward his own mother. (This was the only observed instance of masturbation while holding an infant.)

All mothers carried other infants ventrally and/or dorsally at

times, occasionally while also carrying their own infant. Infants generally paid no attention when their mothers carried other infants, but sometimes they hoo whimpered and followed their mother until she put the infant down and let them cling.

Infants who were frightened, distressed, in potential danger, etc. often ran to the nearest mother and held to her briefly. Mothers caught other infants if they started to fall, embraced them if they were frightened, opened heavy doors for them, gave them mouthcovers if they persistently whimpered, etc. Infants comforted other mothers who were frightened or distressed by clinging ventrally, embracing them, placing a hand or finger in their mouth, turning their shoulder or back to the other mother and holding still while she placed her teeth against them.

In spite of the frequent interchange of affiliative patterns between mother and other infants, agonistic interactions also occurred. On some days, mothers simply appeared to be in bad moods and they stretch-pulled, chased, pinch bit, etc. other infants whenever they came near. At other times, specific infants were selected and mildly harassed. Mothers would, for example, press down firmly on an infant's hand, thus causing it to loose its grip. They would groom the infant's genital region very roughly, take objects away from it, orient threat barks toward it. Actual attacks on infants were not seen.

Infants also harassed other mothers. They foot stamped on metal doors next to mothers who were trying to sleep, they rolled tires at new mothers who were trying to nurse snall infants, and they jumped or fell on mothers who were grooming. While clinging ventrally to their own mothers they even dared to threaten, grab at, or attempt to bite other mothers (even when the mother they were threatening was of higher

rank than their own). Other mothers attempted to ignore such behavior, responding only if the infant persisted. A threat or grab toward such an infant was usually sufficient. Agonistic behavior of the sort described for mother-other-infant pairs was never observed between a mother and her own infant.

JUVENILE-INFANT INTERACTIONS

Interactions between the juvenile male, Manny, and the infants, were frequent and consisted of play, reassurance, carriage and cradling, agonistic and sexual patterns.

Manny carried each of the infants both ventrally and dorsally. Carriage was typically intitiated by Manny, but the infants also solicited carriage at times and occasionally even refused to let go when Manny attempted to set them down or return them to their mothers. When carrying infants, Manny often hurried to another cage and thus out of the mother's sight. Van Lawick-Goodall (1968) reports similar occurrences, which she terms kidnapping, between juvenile and infant siblings.

Manny's behavior toward his sibling, Petal, did not differ noticeably from his behavior toward Shadrach or Meshach during these episodes. However, if the infant objected to being carried by vocalizing and attempting to move away from Manny, Carrie and Mimi approached Manny, causing him to move away from their infants. Pampy rarely approached her son if Petal vocalized under similar circumstances, since a direct stare toward Manny was sufficient.

Manny initiated ventral carriage by dangling in front of an infant as it moved across the top of the cage or along the wire. He oriented his exposed chest toward the infant and often moved his thighs rapidly

up and down while looking at the infant. The same pattern was observed in the adult male Shadow at the Stanford Primate Research Facility. He too employed the gesture to induce an infant to cling ventrally. Manny also gathered infants into the ventral position by placing one hand behind their back or under their buttocks while standing bipedally and exposing his chest. If the infant was hesitant to cling, Manny displayed a silent pout face or a hoo whimper toward the infant. Manny initiated dorsal carriage by orienting his back directly under the infant as it played on the wire or shelf. Manny then looked back toward the infant, sometimes bouncing his seat up and down if the infant did not cling.

Infants also signaled to Manny that they wanted to cling to him. Such signals usually consisted of an outstretched arm, palm up, oriented toward Manny. If the infant was mildly agitated the outstretched arm signal was accompanied by a hoo whimper, pilo erection, and sometimes by a vigorous sideways shaking of one or both hands. Hand shaking was also used as an emphatic ventral cling signal between mothers and infants.

Infants did not always cling to Manny in response to his solicitations and persistent refusals on their part appeared to provoke agonistic responses from Manny. In this respect, Manny differed markedly from the mothers in the group who never displayed agonistic responses if their own or other infants refused to cling. Manny stretch pulled, pinch bit, and pummeled infants with backhand thumps when they refused to cling. Sometimes this resulted in the infant screaming loudly with closed-mouth-bared-teeth and leaping into Manny's arms. More frequently though, the infant's screams caused the mother to rush over

and the infant then leapt into the mother's arms and grabbed at or barked at Manny. As long as their infants did not vocalize, however, the mothers allowed Manny to carry or play with their infants as he wished.

Many of the interactions between the juvenile and the infants might be termed sexual, in that they involved ventro-dorsal and sometimes ventro-ventral embracing with penile erection, thrusting, and kissing. Manny positioned and thrust with penile erection against all three infants. Occasionally, when Shadrach also displayed a penile erection, thrusting was mutual. Thrusting against infants often preceded and followed Manny's copulatory bouts with swollen adult females in adjacent cages, though thrusting against infants was not limited to those circumstances. A typical sequence involving thrusting against infants followed copulation with adult females, as extracted from the daily notes, is presented below:

10:40 Manny and Shadrach play, wrestling and chasing. Manny stops and pulls Shadrach into the ventro-dorsal copulatory position and thrusts against him with a penile erection. Shadrach holds the position while Manny thrusts, Shadrach shows no penile erection. Manny then walks around the cage behind Shadrach, clasping Shadrach around the waist moving bipedally. Manny sits and Shadrach moves away.

10:46 Shadrach rushes bipedally toward Manny while holding both arms outstretched with palms up and hoo whimpers. Manny pulls Shadrach into the ventral dorsal position and thrusts against him with penile erection. Shadrach becomes quiet.

10:51 Manny pulls Shadrach into the ventro-dorsal copulatory position and thrusts against him with a penile erection.

10:55 Manny adopts the ventral solicitation position on the wire and looks toward Peggy (adult female), Peggy presents and copulation ensues.

11:00 Manny approaches and embraces Petal with penile erection while masturbating with his foot.

11:03 Manny adopts the ventral solicitation posture and looks at Washoe, who presents and copulation ensues. Washoe reaches back to touch Manny's scrotum during copulation.

Thrusting against infants was also interspersed with playing with the infant, grooming it and carrying it. Thrusting and penile erections were much more frequent toward younger infants than toward older infants. At the time of writing, Shadrach and Meshach are approaching the juvenile stage of development and are beginning to direct similar behaviors toward young infants. Similar patterns have also been observed during introductions of juveniles and infants. Mutual thrusting appears repeatedly during the first few hours new individuals are placed together.

Although Manny frequently interspersed copulatory bouts with adult females and thrusting against infants, the patterns should not be interpreted solely as sexually motivated. Manny had not yet attained puberty and his copulatory bouts with adult females were not characteristic of the adult pattern in that they involved long periods of thrusting with no ejaculation.

Playbouts between Manny and one or more infants were observed daily. Juvenile-infant play was more vigorous and involved more chasing than infant-infant or mother-infant play and intensity of such play often increased until the infant vocalized by whimpering or screaming.

Manny's irregular play with all infants served an integrative function in the group in that it brought all groups members into closer contact and more frequent interaction. The infants, while often harassed by Manny, became dependent upon him and moved about more freely

when he was a member of the group. (A paper dealing with the effect of Manny's removal from the group is presently in preparation.)

INFANT-INFANT INTERACTION PATTERNS

Infant-infant interactions encompassed, in one form or another, most of the realm of adult social behavior. Sexual patterns, agonistic patterns, maternal patterns, and play patterns were all complexly intermingled in infant-infant interactions. In fact, many behavioral sequences displayed by infants contained components of 2 or more patterns which were typically separated if displayed by adults. For example, grooming with lipsmacking was accompanied by playslaps, and thrusting with penile erection was accompanied by mutual ventral clinging.

Play between infants of less than 18 months was common and differed from the play of older, more agile infants in that aggressive or semi-aggressive patterns were absent, the bouts were very slow paced but often long, they tended to occur when the mothers were resting, and mutual embracing occurred repeatedly. Such episodes are perhaps best characterized as mutual exploration-play-reassurance interactions and they appear to be a function of the constant enforced associations of captivity. Young infants spend longer periods of time away from their mothers, go farther away, and explore more objects when they move about in pairs. They repeatedly embrace each other, instead of making quick forays back to embrace their mothers. In fact, they often move together with leg or arms clasped mutually about each other. A running account of a portion of a typical exploration-play-reassurance bout is presented below:

> Petal and Meshach dangle a few inches apart from the top of the cage. Petal starts to move away and Meshach extends his arm, palm up, toward her. Petal stops, Meshach approaches and they climb along the wire together in ventro-dorsal contact with legs wrapped about each other. Petal stops and looks down, Meshach then looks down. Petal lets go of the wire and drops several inches to the floor. Meshach looks at Petal with an extended hand, palm up, and silent hoo face. Petal approaches Meshach and he pout kisses her as she reaches him. They playslap one another then dangle from the wire with legs mutually clasp about each other's waists while touching and looking at an irregularity in the wire.

Young infants turned to one another and clung, sometimes preferring each other to their mothers, when frightened or intimidated by larger individuals. After clinging to one another briefly they often barked at the larger chimpanzee or bit or slapped out at it, but attacks did not occur much before 2 years of age. Infants also clung to each other upon hearing strange noises or during disturbances in adjacent cages, and afterward they walked about in a ventro-dorsal clasp for several minutes.

As infants approached 2 to 3 years of age, the embracing-clinging components of play diminished and play became faster paced and more vigorous. During introductions, or other stressful conditions, these components reappeared in the playbouts of older infants.

Infants presented, mounted, and thrust against one another as soon as they were able to move about independently. These patterns were directed toward older individuals as described in the section on mothers and other infants, but the preferred partner was another infant. Mutual genital investigation was common. Male infants touched and sniffed the genital regions of female infants. Female infants peered, touched, and placed their lips on the erect penises of male infants. Genital

investigation did not typically precede thrusting, as is the case in the adult pattern. Mounting and thrusting were performed by infants of both sexes and were directed toward infants of both sexes. However, the adult pattern of males mounting and thrusting against females was the most common pattern among infants. Thrusting was solicited by female infants (regardless of whether or not male infants displayed a penile erection) by crouching in front of the male infants and pressing the genital region against their venters. Males not only thrust against female infants when they adopted this posture, they also clung to them, play slapped them, touched the genitals, or sometimes simply leaned on their backs. By about 2 years of age, male infants sometimes preceeded thrusting with bipedal swaggers, foot stamps, and/or chest slaps.

Older infants are strongly attracted to other infants 6 months to 2 years younger than themselves. They repeatedly approach mothers carrying non-mobile infants and pout kiss, pull on, playslap, playbite, grab, press their genital regions against, and try to kidnap these infants. Young infants therefore, have a great deal of contact with other infants before they begin to move about and play with them. Additionally, they learn what pinch bites, grabs, playslaps, etc. feel like while they are safe in their mother's embrace and they do not react fearfully when they occasionally receive rather rough treatment as they move about independently. By contrast, infants who are reared only by their mothers, whimper and scream frequently when they first begin to play with older individuals. Such whimpering and screaming functions to increase harassment by others.

Frequent contact between mobile infants and non-mobile infants began when the younger infants were 2 to 3 months of age. Following is a

description of one such interaction between Meshach (2½ years) and Abigail (2½ months):

> Cindy (Abigail's mother) holds Abigail out on the floor in front of her. Abigail is suspended by one hand so that her knees and feet touch the floor but her body is upright. Meshach approaches and peers closely at Abigail who looks briefly at him. Meshach touches her foot with his knuckles then puts one arm around her stomach and pulls her to his venter, holds her there for 5 seconds then lets go, moves away, then approaches and peers again. He shows a brief silent hoo face as she looks at him then touches her genital area with his index finger, sits down next to her and pulls her to his venter sideways by an arm and a leg, laying her across his lap. Abigail slides out of his lap, he stands, sniffs her genital area, crouches over her and makes a few thrusting motions then moves away.

Infant-infant interactions and dependence are obviously enhanced by captivity. These infant ties have no counterpart among wild chimpanzees, being comparable perhaps to sibling bonds, but more varied and complex. It is too early to ascertain what, if any, will be the effects of such relationships upon adult behavior.

PART III

GROUP DYNAMICS IN A CAPTIVE GROUP-LIVING POPULATION OF MOTHER, JUVENILE AND INFANT CHIMPANZEES

INTRODUCTION

For a 4-month period following group formation the mother-infant group composed of the families listed below,

Mimi (adult ♀)	Pampy (adult ♀)	Carrie (adult ♀)
Meshach (♂ 1-1½ years)	Petal (♀ 1½-2 years)	Shadrach (♂ 1½-2 years)
	Manny (♂ 5 years)	

remained stable, i.e., no individuals were added to or subtracted from the group. In order to elucidate group dynamics, data regarding grooming and play behaviors was recorded 5 days per week. On some days only 2 hours of data were obtained, on others, up to 6 hours of data were obtained. Data collection of all behaviors was randomized throughout each day, the only stipulation being that data were not collected during any unusual occurrence, or during the handling and feeding of the animals. For purposes of summary, the mean number of observed minutes per hour for any given behavior was calculated for each day. Thus, days of 6 hours of observation are given equal weight with days of 2 hours of observation.

The number of individuals in the group were too few to permit statistical testing of hypotheses regarding factors such as age, sex, status, kinship, etc. Nevertheless, it will be seen that some clear and stable trends emerged which are certainly significant in this particular group. For example, each mother spent more time grooming and being groomed by the individuals who were nearest her own rank. Consequently, the mid-ranking mother, Mimi participated in more grooming bouts than either

Pampy or Carrie. While this relationship, and others, can presently be said to hold true only for this particular group, such findings elucidate group dynamics and point the direction for further study.

The graphs presented in the following pages represent the months of October through December. The group was formed in September and for a summary of the first month following group formation the reader is referred to Savage, Temerlin, and Lemmon (1974). Although the groups appeared to be quite stable within 2 weeks following formation (i.e., all individuals in the group approached and interacted freely with one another and aggression was minimal) the daily grooming, grouping, and play measures were still fluctuating 3 months following group formation.

Data were collected on standardized check sheets and the time of onset and time of termination was noted. The criterion for grooming, play and contact followed the typical usage of these terms. A group was judged to be any number of individuals who were within reaching distance of one another or who were obviously interacting though farther apart (ex., a chasing bout). All data was collected by the author. The statistical analysis of this data is continuing at the present and only the play data will be described in detail here.

PLAY

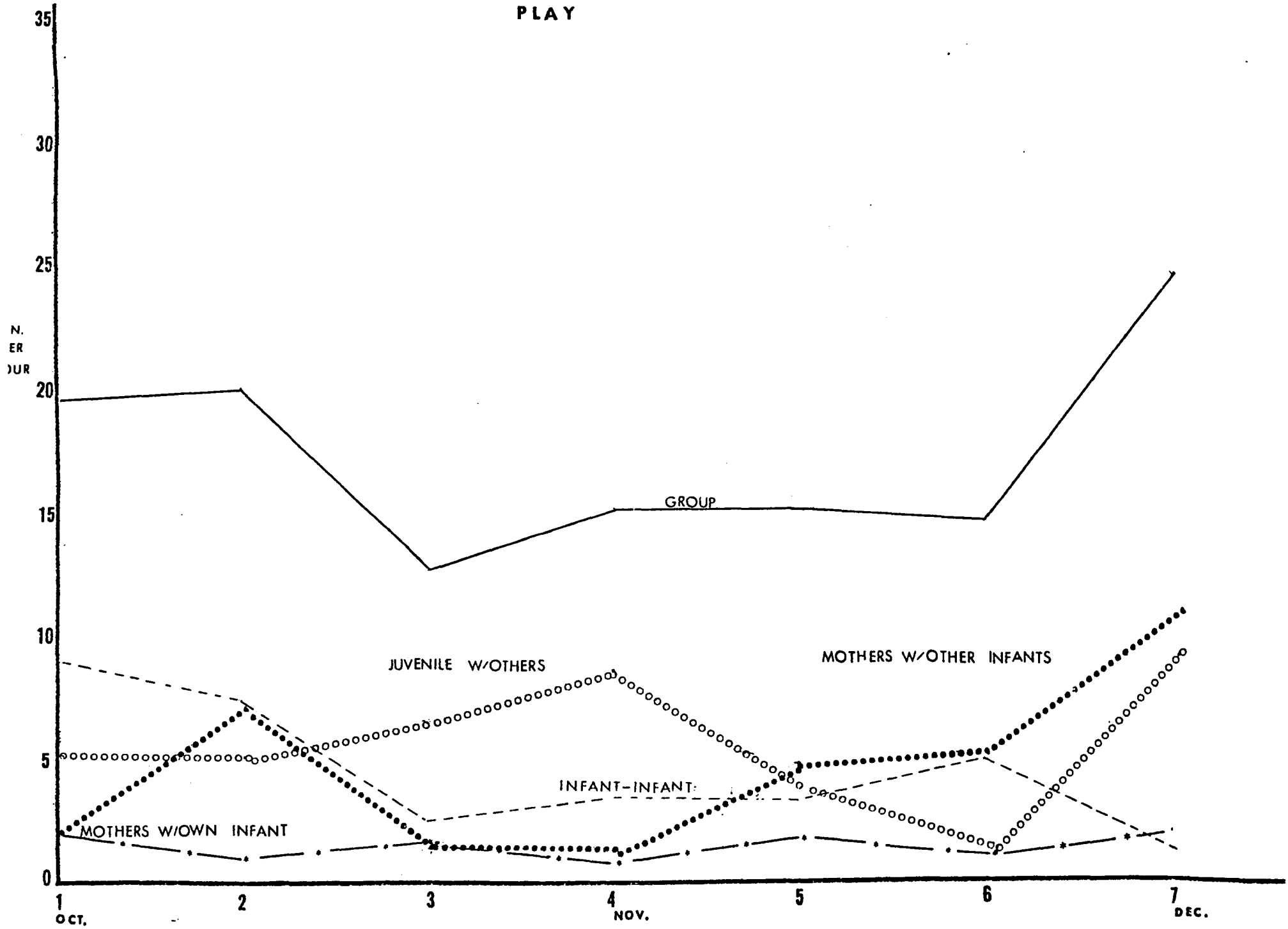
As can be seen in Figure 1, the average amount of group play per hour started out relatively high, decreased, then increased again during the study period. Play groups which included the juvenile tended to become more frequent while overall play was becoming less frequent. Play groups between infants did just the opposite; they tended to become less frequent or remain stable as overall play was becoming more frequent. Play between mothers and their own infants remained relatively

stable throughout the study period, but play between mothers and other infants displayed considerable fluctuation. It is apparent that play within or between various age-sex categories did not fluctuate in accordance with group play and thus the social play of any given individual did not reflect a simple attribute of "group playfulness."

By looking closely at the individual patterning of partner selection and the duration of play between given individuals, it becomes possible to clarify the structuring of play with the group and the "role" or function of each individual with regard to that structure. As can be seen by comparing Figures 2 through 6 , Shadrach, the mobile infant male, participated in more playbouts, with a wider range of partners than any other individual in the group. (Each of the graphs illustrates the daily mean minutes of play per hour with all play partners for a given individual. Play between any 2 individuals was not graphed when the total amount of play over all days was less than 12 minutes.) Petal, the mobile female infant, was the second most playful individual in the group and much of the play behavior displayed by these 2 infants was directed toward one another. Play with Petal accounted for 39% of Shadrach's total social play, while play with Shadrach accounted for 51% of Petal's total play. (The small amount of play displayed by Meshach was a result of his age at the time of study. He was just beginning to engage in social play during this period.) The mutual Shadrach-Petal play reveals a striking periodicity, with an overall decreasing trend. The initial mutual attraction of the infants following group formation resulted in some playbouts of 30 to 40 minute duration. As this attraction decreased, both infants spent more time playing with other individuals and less with one another. Petal's mother, Pampy,

Figure 1. (following page)

Group play between different age-sex categories for the months of October through December.


PLAY
35
30
25
20
15
10
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N.
ER
)UR
GROUP
JUVENILE W/OTHERS
MOTHERS W/OTHER INFANTS
INFANT-INFANT
MOTHERS W/OWN INFANT
1
OCT.
2
3
4
NOV.
5
6
7
DEC.
SIX DAY PERIODS

Figure 2. (following page)

Daily play with each of the other group members by Shadrach, male infant of 2 years.

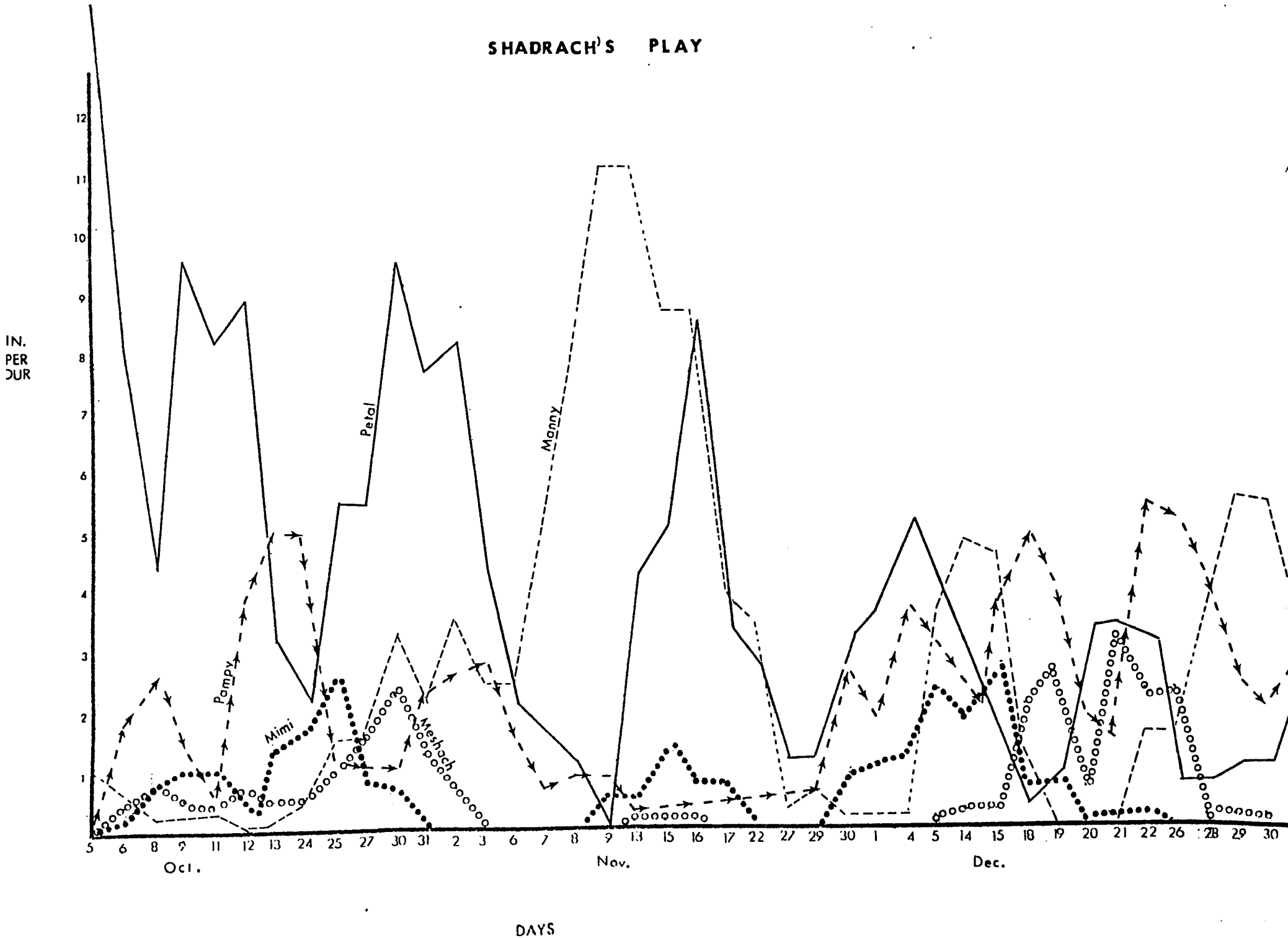
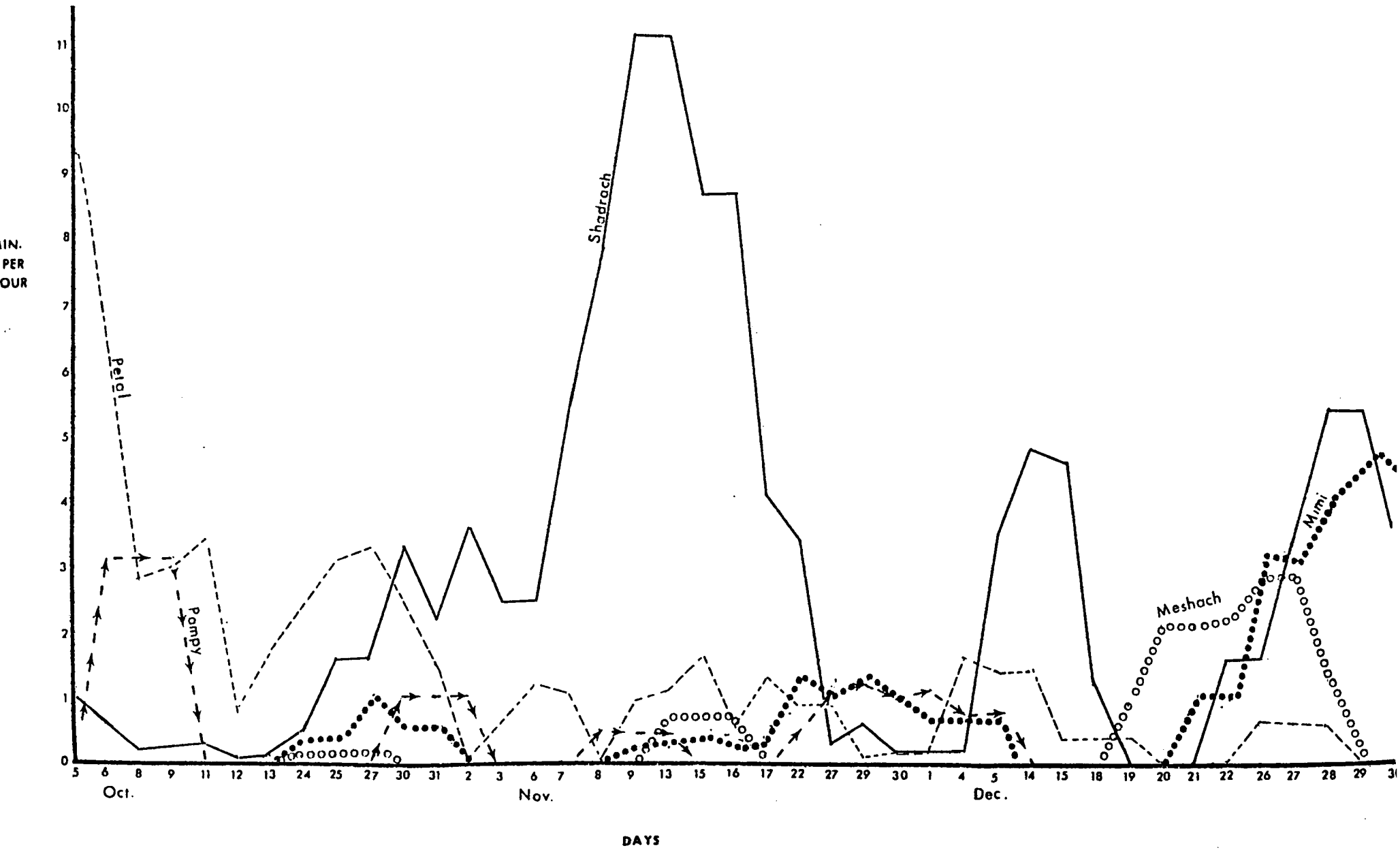

SHADRACH'S PLAY
IN.
PER
OUR
12
11
10
9
8
7
6
5
4
3
2
1
Petal
Manny
Pampy
Mimi
Meshach
5 6 8 9 11 12 13 24 25 27 30 31 2 3 6 7 8 9 13 15 16 17 22 27 29 30 1 4 5 14 15 18 19 20 21 22 26 28 29 30
Oct.
Nov.
Dec.
DAYS

Figure 3. (following page)

Daily play with each of the other group members by Manny, juvenile male of 6 years.

MANNY'S PLAY


IN.
PER
OUR
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10
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0
Petal
Pampy
Shadrach
Meshach
Mimi
5 6 8 9 11 12 13 24 25 27 30 31 2 3 6 7 8 9 13 15 16 17 22 27 29 30 1 4 5 14 15 18 19 20 21 22 26 27 28 29 3
Oct.
Nov.
Dec.
DAYS

Figure 4. (following page)

Daily play with each of the other group members by Petal, infant female of 2 years.

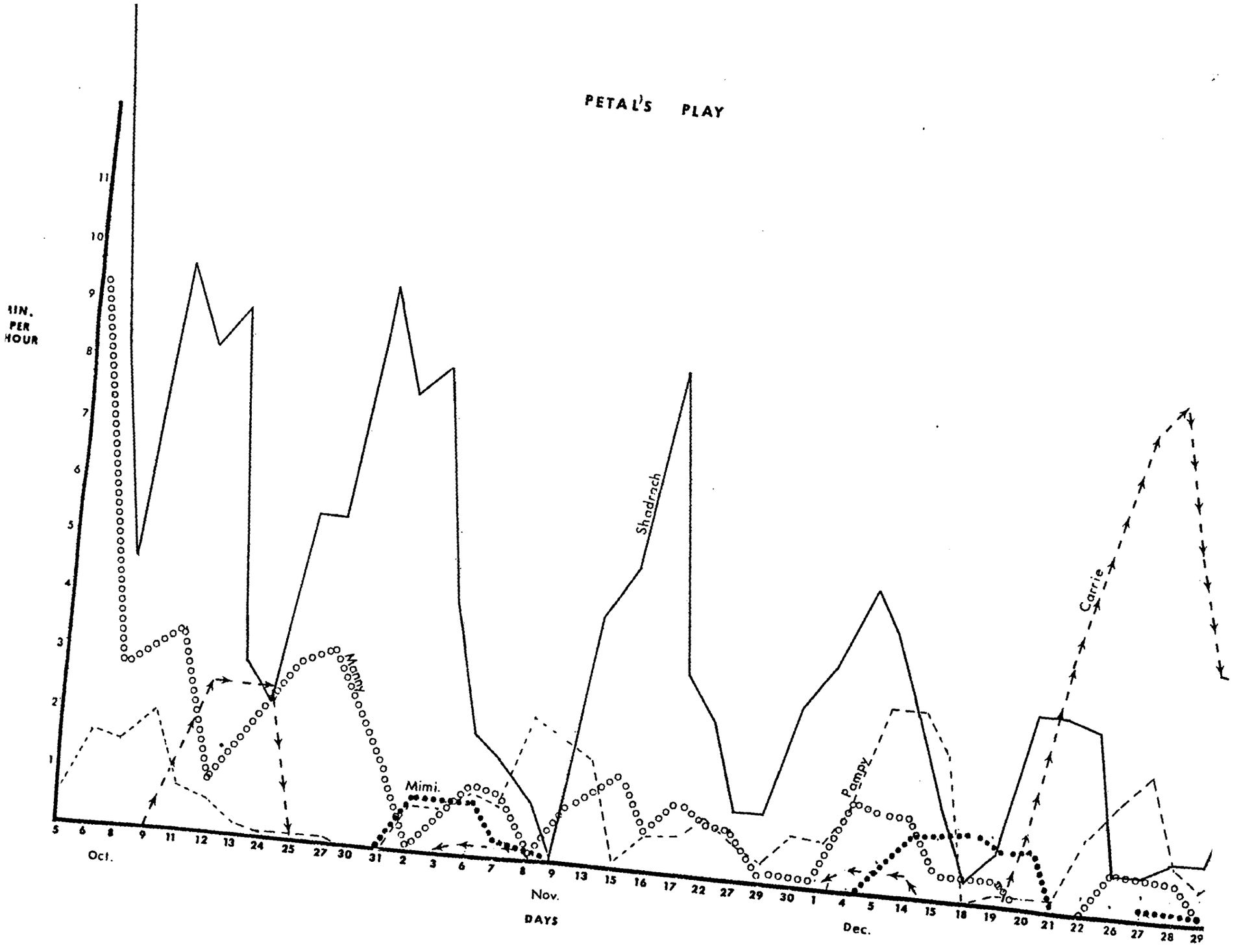

PETAL'S PLAY
MIN. PER HOUR
1
2
3
4
5
6
7
8
9
10
11
Shadrach
Carrie
Manny
Mimi.
Pampy
5 6 8 9 11 12 13 24 25 27 30 31 2 3 6 7 8 9 13 15 16 17 22 27 29 30 1 4 5 14 15 18 19 20 21 22 26 27 28 29
Oct.
Nov.
Dec.
DAYS

Figure 5. (following page)

Daily play with each of the other group members by Meshach, infant male of 1 year.

MESHACH'S PLAY

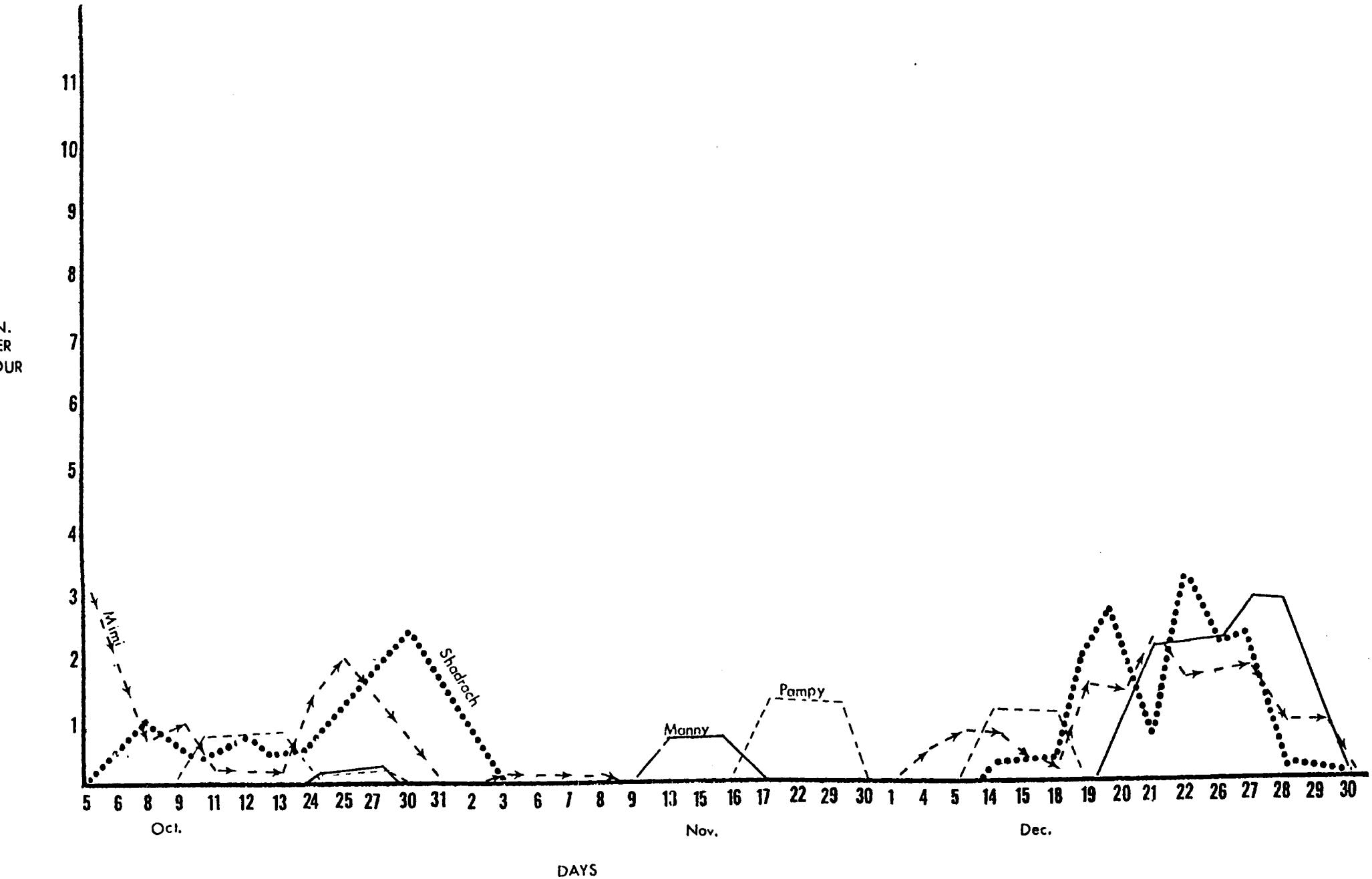
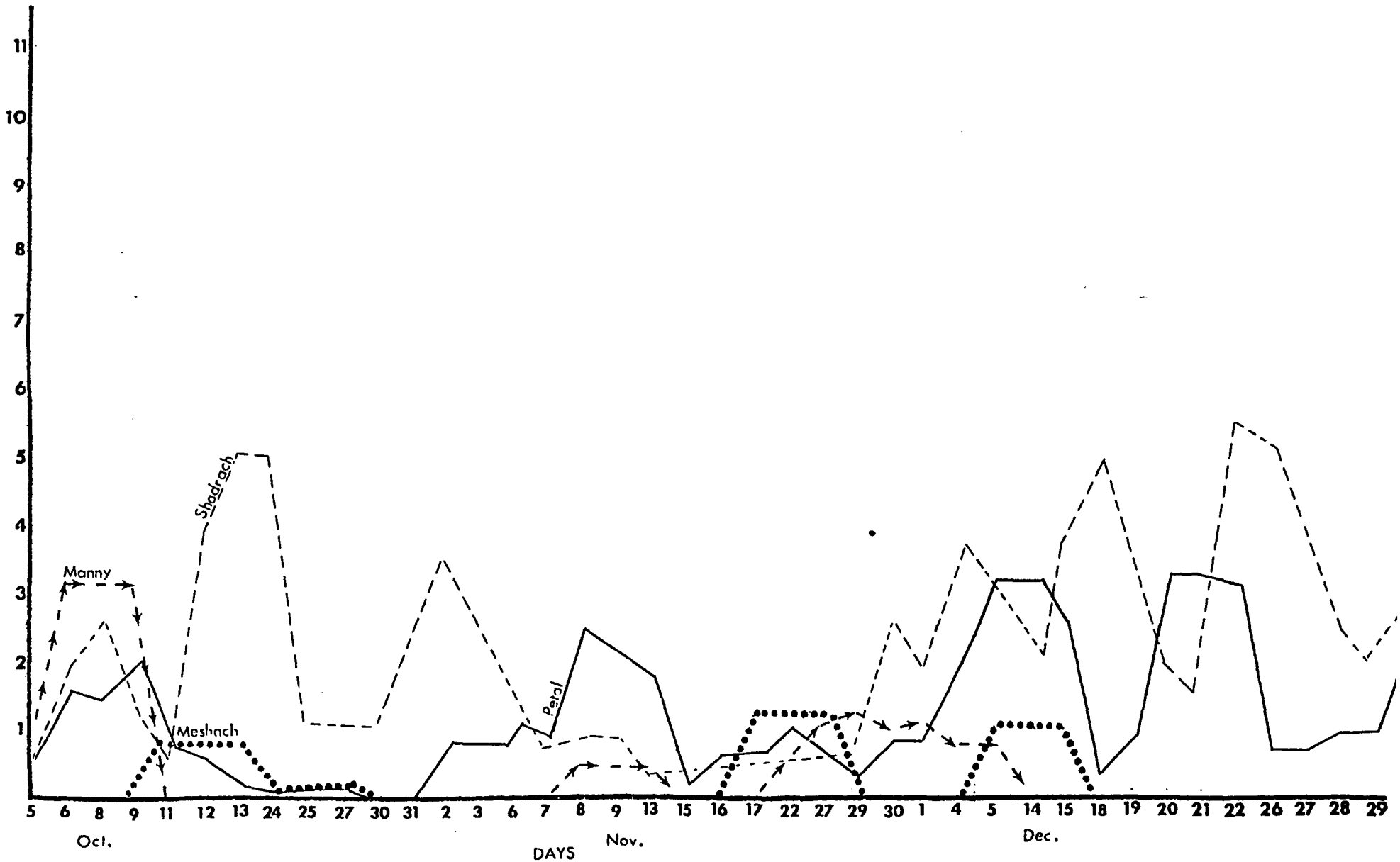


Figure 6. (following page)

Daily play with each of the other group members by Pampy, adult female of 18 years, and mother of Manny and Petal.

PAMPY'S PLAY


11
10
9
8
7
6
5
4
3
2
1
Manny
Shadrach
Meshach
Petal
5 6 8 9 11 12 13 24 25 27 30 31 2 3 6 7 8 9 13 15 16 17 22 27 29 30 1 4 5 14 15 18 19 20 21 22 26 27 28 29
Oct.
Nov.
Dec.
DAYS

began to spend a considerable amount of time playing with Shadrach and simultaneously, Shadrach's mother, Carrie, began to spend a great deal of time playing with Petal. Thus, play between mothers and other infants appears to be facilitated by prior play between the infants themselves.

Prior to group formation, most of Petal's play had been with her older sibling, Manny. Her play with Manny remained high during the first month after group formation then began to drop off noticeably as Manny formed a playbond with Shadrach. The playbond between Manny and Shadrach developed more slowly than that between Petal and Shadrach (the latter occurring on the first day of group formation), but once it was formed a similar periodicity occurred, and it appeared that by the end of the study period Shadrach was beginning to alternate between a period of play with Manny, followed by a period of play with Petal.

Shadrach also became Manny's most frequent play partner, accounting for 49% of Manny's total play. Additionally, Manny, like Petal, engaged in infrequent non-kinship play prior to forming a playbond with Shadrach. Afterwards, however, Manny, like Petal, also began playing with other group members. Thus, it seemed that the siblings, Manny and Petal, were more reluctant to engage in non-family play than was Shadrach who had no siblings. Shadrach not only established early playbonds with Petal and Manny, but he also began to play frequently with the other mothers, Mimi and Pampy, during the month of October. Neither Petal nor Manny played frequently with another mother until 2 months later, at which time each established a playbond with one other mother, Petal with Carries, and Manny with Mimi.

Group play thus was initially coordinated to a considerable extent

around Shadrach, with most individuals playing either within their own family group or with Shadrach.

BIBLIOGRAPHY

Altmann, S. A. (1967). The structure of primate social communication. In Social Communication among Primates, S. A. Altmann (ed.), University of Chicago Press, Chicago.

Bingham, H. C. (1927). Parental play in chimpanzees. J. Mammal., 8, 77-89.

Fossy, D. (1975). Development of the mountain gorilla (Gorilla gorilla beringei) through the first thirty-six months. In Perspectives in Human Evolution, V. 5, D. Hamburg and J. Goodall (eds.), Holt, Rinehart and Winston, New York.

Hinde, R. A. and Spencer-Booth, Y. (1969). The effect of social companions on mother-infant relations in rhesus monkeys. In Primate Ethology, D. Morris (ed.), Anchor Books, Garden City, New York.

van Hooff, J. A. R. A. M. (1971). Aspects of social Behavior and Communication in Human and High Non-Human Primates. Bonder-Offset, Rotterdam.

_____ (1973). A structural analysis of the social behavior of a semi-captive group of chimpanzees. In Social Communication and Movement: Studies of Interaction and Expression in Man and Chimpanzee, M. von Cranach and I. Vine (eds.), Academic Press, New York.

Kaplan, J. (1972). Differences in the mother-infant relations of squirrel monkeys housed in social and restricted environments. Devel. Psycholbiol., 5, 43-52.

van Lawick-Goodall, J. (1968). The behavior of free-living chimpanzees in the Gombe Stream Reserve. Anim. Beh. Mong., 1, 1-311.

_____. Unpublished glossary of chimpanzee behavior.

McGrew, W. C. (1972). An Ethological Study of Children's Behaviors, Academic Press, New York.

Middgett, Palmer. Personal communication.

Nadler, R. D. (1974a). Determinents of variability of reproductive behavior of captive gorillas. Paper presented at the 5th Int. Cong. Primat., Nagoya.

_____ (1974b). Preparturitional behavior of a primiparous lowland gorilla. Primates, 15, 55-74.

Pavenstedt, E. (1967). The Drifters. Little-Brown, Boston.

Radl, S. L. (1973). Mother's Day is Over. Charterhouse, New York.

Rogers, R. K. and Davenport, C. M. (1970). Chimpanzee maternal behavior. In The Chimpanzee, V. 3, G. H. Bourne (ed.), Karger, Basel.

Rowell, T. E. (1968). The effect of temporary separation from their group on the mother-infant relationship of baboons. Folia Primat., 9, 114-122.

Savage, E. S., Temerlin, J. W. and Lemmon, W. B. (1973). Group formation among captive mother-infant chimpanzees (Pan troglodytes). Folia Primat., 20, 453-473.

Tomilin, M. I. and Yerkes, R. M. (1935). Chimpanzee twins: Behavioral relations and development. J. Genet. Psych., 46, 239-263.

Yerkes, R. M. And Tomilin, M. I. (1935). Mother-infant relations in chimpanzees. J. Comp. Psych., 20, 321-359.

Yorberg, B. (1973). The Changing Family. Columbia University Press, New York.

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