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**The Integration of Biology and Behavior in the
Socialization of *Macaca sylvana* of Gibraltar**

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(Original pagination has been retained. The proper name for this species is now recognized as *Macaca sylvanus*.)

Socialization operates on the total organism within a specific context. The processes of socialization are ongoing and may be termed "maturation within the social milieu." These processes can effect or develop the proper behaviors only in the measure that the organism is receptive to them. This receptivity is directly a function of a concatenation of personal events at a particular moment.

These events are simply summarized as biological development. The inherent qualities of protoplasm-irritability, reproduction, energy utilization, and so on--are specifically organized as the zygote becomes embryo becomes fetus within the limits of the genotype. The particular form this organization takes within the range of possibilities available is influenced by its exogenous and endogenous environments. These range from the state of the mother nutritionally, emotionally, and endocrinologically, and the nature of the maternal feedback system to the particular nature of the zygote's cells and the genic system that affects them. The more differentiated the tissue, the greater the organization of the systems, and thus the more susceptible the organism to a wider range of diversified influences. Susceptibility refers to sensitive periods--the moment(s) at which the matter, or target structure, has developed sufficiently to respond by growth, differentiation, and so on, to a given influence--exogenous or endogenous.

The neonate emerges with a repertoire of abilities and a range of potentialities as Coghill (1929), Carmichael (1928), Kuo (1967), and others have illustrated with their researches. For example, Carmichael (1928), in studying the fetal guinea pig, observed ontogenetic motor development similar to that which Coghill found in the salamander, and Kuo in the chick. The first movements occur as thrusts from the heart's beating. Body movements, as in the bird embryo, are myogenic and originate anteriorly and progress caudally. It is of great importance to note that these movements are myogenic and not neurally inspired. The myelination of the nervous system permits increasing integration of movements, which in turn allows for new coordinations within the limits of the morphological potentials (monkeys cannot fly; dogs cannot grasp).

Seen from this, the epigenetic view (Kuo, 1967), the conjecture of fully

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developed patterns of behavior, which are inherited (Lorenz, e.g., 1965; Tinbergen, 1951) or located in the central nervous system (Delgado, 1965; Moyer, n.d.), present in the embryo and merely awaiting the proper releasing mechanism for their full manifestation, is superfluous and reminiscent of the ancient homunculus and other preformationist theories. As Schneirla (1965), Maier and Schneirla (1964), Marler (1966), Tavolga (1970), and especially Lehrman (1970) have recently shown, the old nature-nurture or exogenous-endogenous dichotomization of behavior is not intrinsic to animals. Behavior is the inventory of all that an animal does, and there is a unity of the organism within its context. Kuo (1967, pp. 84-85) has argued that this ancient dualism is an artifact of western European logic stemming from the Hegelian dialectic.

Modern philosophical, social and biological thinkers of the Western World seem to have been unable to free themselves from the bondage of ... thesis and antithesis: mind versus body, nature versus nurture, innateness versus learning, and so on. Since the time of Sherrington, Pavlov and Watson we have had: reflex versus habit (chain reflexes), reflex versus instinct, instinct versus habit, and conditioned versus unconditioned reflexes, and similar dichotomies.

The recrudescence of dichotomization is evident in recent primatology, particularly in the writings of Struhsaker (1968) and Gartlan and Brain (1968). Gartlan and Brain evoke nurture, or more modernly, environment, as the major influence in the behavior of a primate group, whereas Struhsaker argues that the genotype transcends any particular milieu for any given group of a species, so that behavior is consistent throughout. Although Aldrich-Blake (1970) has attempted to reconcile these views by attempting a synthesis of the extremes, the tendency is for ecologically oriented scholars to oppose ethnologically oriented ones. Perhaps our desire to formulate theoretical frameworks has outstripped our descriptive knowledge.

The purpose of this article is to describe and analyze the biological processes of socialization in *Macaca sylvana* of Gibraltar, with emphasis on the biological developments that precede, follow, and integrate with the social ones.

CONDITIONS OF THE STUDY

Two troops of *M. sylvana* range freely on Gibraltar. They are the charges of the Gibraltar regiment of the British army and are provisioned to approximately one-third of their nutritional needs. The provisioning is not only to supplement their natural diet but also to limit to some extent their foraging in the built-up areas. The natural habitat of these two troops

includes rock faces, vegetational growth including shrub trees and bushes, and terraces made primarily of concrete. The Middle Hill (MH) troop may range from the summit of the rock at 1,350 feet to approximately 200 feet, while the Queen's Gate (QG) troop tend to restrict themselves to approximately 1,040 feet to 520 feet. Although free-ranging, both troops are tame; that is, they permit approach from humans, hand-feeding, and, in the case of the QG troop, will jump on people. Members of both troops do not permit humans to touch them, and will threaten and occasionally bite if such a gesture is made.

The presence of humans, whether tourists, residents, or military personnel, is a daily event. The extent of this contact is greater for the QG troop, which is maintained as a tourist attraction. The MH troop, which roams over a larger area, receives less contact, as they frequent inaccessible areas and remain in the forest growth, partially out of view, even when they are in their "tourist location." The monkeys are tended by an officer of the Gibraltar regiment and are the responsibility of this regiment. Effects of disease and injury are, therefore, attenuated. The number of animals is controlled, both in absolute size and sex ratio, surplus animals being sent to toes. This factor no doubt accounts for the great longevity of the animals, mitigating against the natural predation of disease, injury, and fighting.

Observations were made almost daily, generally from 7:00 A.M., when the animals first appeared from their sleeping shelters in the rock face, until they returned to their sleeping places at 8:00 or 9:00 P.M., depending on the seasonal setting of the sun, with a break at some time during the forenoon. It was possible to accumulate 462 contact hours, 278 hours with the MH and 184 with the QG troop, during the period April 28 to July 30, 1970. Four people were engaged in observation, and the contact hours represent the total period of continuous observation irrespective of the number of field workers present at any one time. Observation distance ranged from 2 or 3 feet to 400 yards for which 8 x 40, 9.5" binoculars were employed. Still and motion pictures were taken and vocalizations recorded. Further observations in October 1970, and December 1970 through January 1971 were made and have been drawn upon for this report.

GROUP COMPOSITION¹

At the end of the 1970 birth season, the troops together numbered thirty-three animals, both troops having a male to female adult ratio of 1 to 5.

¹See Table 1, p. 58.

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The animals would not tolerate more than one adult male, and in the past, when a male was in his fifth year, fighting broke out with the leader until solitarization or injuries or the threat of these forced the army to remove the loser (Holmes, p.c.²).

In the Gibraltar macaques, the onset of behavioral patterns was closely linked with age. Analysis is based on the natural division into age-grades, which are described below. The following are the categories for the animals :

Infant 1	Birth to three months
Infant 2	Three months to one year
Juvenile	One year to three years
Subadult female	Three years to four years
Subadult male	Three years to five years
Adult female	Four years
Adult male	Five years

INFANT 1: BIRTH TO THREE MONTHS

Neonate pelage is dark brown dorsally, and yellowish ventrally. Fingernails are almond shaped and black, but the skin of the feet, hands, face, perineum, and tail are light pink. The eyes are dark. The genital region is swollen at birth, undoubtedly as the result of maternal hormonal influence, but recedes after forty-eight hours. Birth blotches may be present on the face as dark red patches randomly positioned. The umbilicus, approximately one to two feet long, is left to dry out and break off. The ischial callosities are barely distinct from the perineal region; they appear as soft, wrinkled, pinkish translucent tissue within the smoother pink area. The tail is visible and approximately two to three centimeters long. As the individual matures the tail becomes proportionately smaller until in the adult it is not longer noticeable. The cheiridia are prehensile from birth, although the infant can only cling with its hands, which is probably why the mother supports the infant in the ventral clinging position as she moves about. Between the third and fourth day the feet have developed sufficiently for clinging but still appear weak, as the legs often dangle. Support is given less frequently, although the mother continues to signal the infant 1 that she is prepared to move by pressing its back. The infant 1 vocalizes from the first day of life--its first vocalization a high-pitched cry similar to the English sound "eeee." The infant 1 is capable of turning its head laterally, ventrally, and dorsally; but the latter two movements are uncontrolled, and the head wobbles as the movement is

²p.c.: personal communication

accomplished. Movement to the teat is undirected, but sucking itself is coordinated.

The eyes seem to focus twenty-four hours after birth, although no test of this could be made. The impression was received by the manner in which the neonates oriented their heads, especially when seeking the teat; that is, they would look for it, sight upon it, and move their heads directly toward it, the dorsal neck muscles only permitting a strong wobble. The newborn infant in *M. sylvana*, as among most cercopithecoids, attracts the attention of the entire troop. There was a marked difference between the MH and QG troops in whether or not other females with or without infants in arms were permitted to approach. In QG troop, other females were permitted to sniffle and touch the neonate, although they were not allowed to take the infant 1 from its mother until it was approximately six to eight days old. In the MH troop other females were not usually permitted to come close until the infant 1 was over ten days old, and even then the other females were not allowed to take the infant 1 from its mother, although such attempts were made. Often a struggle ensued, with the mother pulling on the forepart of the infant 1 while the other female pulled on the hind parts, the mother usually threatening the other female at the same time, and the other female making the "teeth-chattering" grimace (Hooff, 1967; abbreviated in this article as "chatter") in return to the threat. This facial expression is an open-mouth gesture with lips and cheeks contracted, mandible opening and closing rapidly, teeth contacting teeth, and, in some animals, tongue flicking against teeth, producing a clicking sound. The head³ male, however, was permitted to approach and even take the neonate from its mother on the first day (MH, four instances) and certainly by the third day (MH, one instance) and fourth day (QG, two instances). This behavior is extremely important to the development of basic social behaviors. The head male who is the putative biological father (Holmes, p.c.) sniffs, licks, caresses, pats, and holds the infant i. While inspecting it, he looks into its face and chatters. The mother, who sits close by the head male, occasionally grooming him as he holds the infant 1, joins in chattering to it. Each time the infant 1 makes a sucking motion, both parents immediately chatter to it. By the third day at the earliest, and fifth generally, the infant 1 is capable of returning weak chatter movements when it is chattered to, but invariably just moves closer to the animal chattering to it. That is, it returns sucking motions with an added component of pulling back the lips and opening and closing the mouth. Thus a preexisting action movement, already

³ This term seems preferable to "dominant," "control," or "leader," as these terms include functions that are not unique to this animal.



Figure 1. A two-day-old infant in its mother's lap.



Figure 2. The head male (MH) encourages the infant to walk toward him.



Figure 3. The subadult male retains the infant 1 while the leader male (left) and the mother (right) stay close-by.

included in the repertoire by birth, is conditioned into a purely social gesture. The importance of this lies in the use of the chatter, which functions as a distance-decreasing mechanism (Marler, 1968). It is (1) an approach gesture; (2) a pacifying and appeasement gesture; and (3) an invitation or encouragement to follow or be picked up. It is used when one animal is at a distance from another and moving in his direction. If a mild threat is given upon its approach, the animal will again chatter. If an animal surprises another by coming up from a place obscured from view, he will chatter. If two or more animals are wrestling in play, and one gives a high-pitched vocalization, the other(s) will chatter.

On as early as the sixth day of life, but no later than the eighth day, in the case of the MH troop, or fourth to eighth days, in the case of the QG troop, the infant begins to walk. It has already been climbing over its mother's and the head male's bodies since as early as the third day, mostly by means of its hands and arms. On four occasions the MH head male was the initiator of the infant's beginning to walk: he placed the animal on the ground, moving backward away from it to a distance of approximately two feet, lowering his head, and looking at the infant and chattering to it. The infant would return the chatter and make crawling motions toward him. That is, each arm was alternately extended, the digits flexed, the legs and feet digits flexed, and a pulling-hopping motion employed. As the infant approached within six inches to a foot, and if no other animal except the mother was nearby, the head male would again move away and repeat the chatter. If other animals began to close in, he would pick up the infant, and move away from the crowd, making a mild threat gesture to them.

It is interesting that encouraging the infant to walk occurred after the infant recognized the chatter and was beginning to be able to use it, and before the infant's locomotor development permitted the action. Walking was initiated in the infant's FIRST week by the head male in MH but not in QG, although the leader male in the latter troop did encourage infants to walk in the manner described after they had begun to do so on their own.

Significantly, at one and one-half months, the MH infants seemed capable of locomotor feats such as jumping, climbing, and leaping across two feet of space, with greater facility than did age-mates in QG. They differed in certain behavioral traits as well, particularly in greater apparent independence from their mothers and from male care. This was manifested by the fact that the MH infants could go farther away from surveillant animals and remain away longer than their QG age-mates. The age and personality differences of the leader males that fostered these differences are discussed below in the section on adult males.

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From the fourteenth to the twentieth days after birth, the subadult males came to predominate as an influence in the infant's life. Three- and four-year-old males tended to follow the head male when he had the infant 1 from as early as the sixth day. After the infant had been walking for a few days, however, neither the head male nor the mother would interfere when a subadult attempted to pick up the infant 1. The FIRST time this occurred, the head male and the mother would follow the subadult very closely and remain within a few feet of him. They relaxed their vigilance after a few days, especially after another female gave birth. First the leader male, then the mother would permit the subadult to take the infant as much as fifteen to twenty yards away. The distance increased to approximately 200 yards (during troop movements) when the infant reached a month old.

At first the infant 1 would give high-pitched vocalizations when the subadult took it. The subadult would chatter to it and eventually the infant 1 would leave the proximity of its mother or the head male in response to the subadult's chatter. Although it was during the time that the infant 1 was tended to by the head male that it learned to climb and be transported on the back, it was under the subadult's care that this behavior developed.

Like walking, the dorsal transport was initiated by the head male. This behavior began just after the infant 1 had begun regularly to walk toward the head male in response to the chatter. As the infant 1 approached him the leader male would turn sideways to the infant 1 and drop one shoulder so that the infant 1 in effect had no surface to touch other than the shoulder; the infant then climbed up. At first the infant 1 would lie horizontally across the back, or obliquely to the vertical axis, but within a few days it would consistently ride with its hands cephalad and its feet caudad. The infant's mother similarly would offer her shoulder, usually the day after the head male had just done so, but she tended to continue to carry the infant 1 ventrally (when she had possession of it) until after it reached approximately one and one-half to two months of age. As the infant grew larger the invitation for dorsal transport included a total body crouch or lowering of the hindquarters toward the infant 1 while chattering in its direction. At one and one-half to two months the infant 1 might solicit dorsal transport by touching the other animal's hindquarters or shoulder.

The subadult male stayed with the infant 1 as it made the maturational transition from adult surveillance to peer group membership--a period of approximately two and one-half to three months. As already mentioned, this association began once the infant could chatter and had developed

basic locomotor skills, that is, walking, running, and climbing. The active role of the subadult in "male care" (Deag and Crook, 1970) was to "baby-sit"; that is, (1) to convey the infant 1 over any walking distance greater than approximately five feet, or over any jumping distance greater than one foot; (2) to remove the infant 1 from negative situations (physical danger, as in falling; threat of aggression, for example, from a female; or over strenuous play of the infant 2); and (3) to provide the context within which the next stage of socialization takes place. The subadult seemed to convey the infant 1 always in respect first to the head male, then to its mother, irrespective of the distance from them. The subadult typically watched these individuals and if they should move into an area obscured from view, the subadult would often move in that direction until visual contact was restored. The subadult would often bring the infant 1 to the head male, chatter to the male, and with him to the infant 1. He then would either leave the infant with the head male or go off with it again. If the mother approached him, the subadult would either permit her to take the infant or would move off again with it. If the mother pursued, he would relinquish the infant to her.

The physical contact with the infant 1 was reduced as a function of the infant's growth: the older it became, the less the subadult would pick it up or offer his shoulder for dorsal transport; but the subadult's vigilance persisted until approximately six months (Holmes, p.c.). That is, as the one- to two-month-old infant clambered through the trees and over railings and rocks, or walked over uneven terrain, the subadult would be within one to three feet. The subadult would often follow along a branch, with one arm curved over and around the infant 1, his hand beneath it or his body over it, as if in readiness to grab it should it fall. The socialization of the infant 1 at this stage (fifteen days to three months) occurred largely within the framework of this relationship, but was not confined to it. The infant 1 would be with the subadult for a large part of the daylight hours, ranging from approximately three to four hours a day at one month to a peak of about eight hours at two and one-half months, this decreasing again at about three months to approximately four to five hours.

A subadult-infant association was not a fixed one. Like most of the relationships among *M. sylvana*, age, season, breeding status, temperament, and so on, affected the duration, intensity, and even the nature of the relationship. That is, as the infant 1 matured, it was passed from subadult male to subadult male. For example, Paris (three years old) took Rosemary when she was fifteen days old; when she was one and one-half months, Ben (four years old) took her, as Paris was occupied with Dorothy. By the time Olga was born, Eliot (three years old), the subadult male who

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had come from the QG troop, was no longer being threatened away from infant Is, and while he accompanied Rosemary, Ben got Dorothy, and Paris was making the first approaches toward taking Olga from Mark.

During these months contact with the juveniles and infant 2s increased in proportion to the infant I's age, from almost no contact at all at fifteen days, to about two hours per day broken into smaller time units at two months, to approximately four hours similarly broken down at three months. While the actual contact remained of short duration until about three months of age, the infant 1 was close to the juveniles, held or carried by the subadult or within a few inches to about five feet from him. The orientation toward the juveniles and infant 2s was reinforced by the rejecting behavior of the head male toward the infant 1. At anywhere from as late as one month of age to only, but not less than fifteen days, depending on the advent of new infants into the group, when the infant 1 would run up to the head male, or when the subadult surrogate would bring the infant 1 to the head male, instead of chattering to it, holding it, or carrying it, the head male immediately returned it to its mother, who then released it. The subadult, who had followed the head male, would then chatter to the infant 1 to follow or get onto its back. If the head male was holding a younger infant when an older infant approached, the head male might mildly threaten the older infant or the subadult who was bringing it toward him.

The increased association of the infant Is (fifteen days to three months) with the juveniles and infant 2s coincided with the period of greatest development of locomotor and manipulative skills. This was also the time when the infant 1 was physically capable of imitating the younger animals. It was during this period that the infant began to test and, after one and one-half months, eat solid foods. Although many nonfood objects were brought to the mouth (rocks, dirt, paper), the infant 1 tended to put to his mouth those foods that he saw other animals take. Juveniles and infant 2s typically gathered foods (like flower heads, stems and, in the dry season, pulp of twigs) that are softer than those taken by subadults (like leaves and, in the dry season, tubers and roots dug up from six to ten inches in the ground). Although there was, of course, an overlap in the diets (such as seeds from various sources, figs, fruits, and so on), the infant 1 would try both the harder and softer foods, and was observed to reject, for example, thick leaves in favor of a diet closer to that taken by infant 2s and juveniles. No doubt this feeding behavior was related to masticatory muscle and tooth development, milk teeth being fully erupted by five months, first molars by ten to twelve months (Fitzgerald, 1950). Juvenile and infant 2 play with the infant Is differed from that with age-mates in that the animal appeared to restrain himself, that is, he did not fully use his strength as he would in playing with members of his peer group. If the infant 1 should squeal dur-

ing these bouts, the subadult would interfere, picking it up and/or giving a mild threat to or chasing away the juvenile or infant 2.

Gradually during its association with subadults and younger animals, the infant 1 would learn the appropriate responses for specific vocalizations in given contexts. This process seemed to be a conditioning one, a function of the differential behaviors of the subadult male, such as his picking or scooping up the infant in response to a negative vocalization (warning bark, threat, and so on) or his lack of a particular response to a positive vocalization (greeting call, contentment noise, play sounds, and so forth).

INFANT 2: THREE MONTHS TO ONE YEAR

At three months pelage has uniformly lightened with the fine lanugo hairs being gradually replaced by shorter ones. Eye color is beginning to lighten, and the infant 2 appears to have trebled in length from its size at birth.

All locomotor movements are coordinated by three months; the animal can walk without the lateral wobble characteristic of this motion at one and two months. Digits of cheiridia are extended instead of flexed in locomotion. Leaping and manipulation are, however, still clumsy, perhaps because depth vision essential for these has not yet developed, but the legs have gained muscular strength, so that even though a leap may miss its mark it is executed correctly. By approximately three months the male genitalia are distinguishable from the rear as a thick amorphous sac, yellowish-white in color.

In the Gibraltar groups, weaning in the nutritional sense began at about three months, with the mother responding more slowly to the infant's signals (for example, squealing, nuzzling) to be taken to the teat. Reorientation away from the head male and the mother began even earlier.

Encouraged away from its mother from about the tenth day by the head male, the infant 2 would increasingly be brought into contact with other members of the troop in a descending age pyramid, until finally by the third month, the infant 2 frequented a play group of peers. This integration into the troop was effected by the action of the older animals until the infant was about three months, when he actively sought contact with age-peers, older infant 2s, and juveniles. The infant 2s active contact included jumping, pulling, wrestling, and so forth, with the older animals. Bodily contact with the mother through this grade diminished from approximately twelve to fifteen hours per twenty-four-hour day at three months to approximately eight to ten hours per twenty-four-hour day at six months. Socialization, then, at this stage had three qualities: (1) it took place primarily within the context of the younger animals; (2) the animal was the recipient; and (3) the animal was the initiator. The study period did not cover the critical

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time between the third and eighth months. This developmental period--which covers the complete change from long dark pelage to the short, fuzzy, tawny gray of the older infant 2s, complete nutritional weaning, the refinement of locomotion and manipulation, as well as the refinement of response to vocalizations--must await future work and analysis. Some general statements, however, may be put forward.

The first two qualities of interaction, listed above, have been discussed in an earlier section. The active participation characterized the young infant 2. The tentative approaches to infant 1s, which had previously been rebuked by mild threats or retreat of the younger animals' mothers, were now permitted. The behaviors of touching, pulling, hitting, and climbing, which had been reinforced in the context of the subadults, juveniles, and older infants close to their first birthday, were transferred to this group of age-mates. The approach to peers may be attributed to "curiosity" however defined, to low intensity approach stimulus (Schneirla, 1959), or to contact resulting from random exploration. It is, of course, impossible to assess without experimentation what the young infant perceives of the subtlety of interrelationships in his society, or when a perception previously gained becomes a cognition or influence.

Peer contact at this stage was characterized by surveillance, primarily by subadults, head male and mother coequally, and juveniles, in that order. As the individuals of the infant 2 peer group developed in size and strength, distinguished primarily by the change in pelage, interference with the playing group diminished. That is, squeals and vocalizations would generally receive less rapid response than the cries of an animal one or two months younger. Booth (1962) has discussed the significance of the neonate pelage to the troop. It is, judging by older animals' response, a mark or signal of psychophysiological changes intimating, perhaps, the increasing ability of the infant 2 to take care of itself. This was evident when an infant of this age group would remove itself from a play situation that was too physically strenuous, leap across spaces that were two and one-half feet wide without assistance, climb and descend twenty-to-thirty-foot trees, and so forth.

Beyond the age of six months the faces deepen in color, but are not yet fully pigmented. The eyes are lighter than those of the infant 1. The ischial callosities have only just begun to differentiate into the adult patterns (see below). Cheiridia (hands and feet) are fully pigmented. The tail is visible as a stub one-half to one centimeter long. Pelage has lightened to a tawny gray, and the hair is quite short and gives the appearance of fuzziness. The face is round and there is yet no development in the superciliary region.

Sexes can be told apart from the rear, as the scrotum is no longer amor-

phous and gives the appearance of a sac with two chambers. The scrotum is large enough to be evident but not obvious. The penis is clearly visible ventrally, and flaccid; it seems to be approximately two to two and one-half centimeters long.

Vocalizations are still high pitched, though lower than those of the infant 1.

In the Gibraltar troops infant 1s were observed to make tentative grooming motions at one month, and by nine months the infant 2s groomed regularly. Although executed correctly, that is, with chatter gesture and hand, finger, and mouth movements described for Cercopithecidae in general, the activity was initiated less frequently than by other age groups. Each grooming bout was sustained for a very short period, never in excess of five minutes (see Table 2, p. 59). With four males and one female in this age group, it is not possible to say whether or not there was any sex difference in the amount of time spent grooming. Infant 2s groomed and were groomed most by adult females, but received grooming more from subadult males than from the head male, although they groomed the head male more frequently than they did the subadult males.

Bouts of grooming with peers, juveniles, and younger infants easily turned into play sessions, with either groomer or groomed initiating. An infant 2 groomer involved with an older animal (subadult or adult) was easily drawn away from this activity by his peers or juveniles. Infant 2s preferred to play with peers or juveniles rather than with subadults, who often initiated or joined these play groups. "Preferred" refers to both the relative duration of a play bout and the fact that when a subadult joined younger play groups, the younger animals would move away from the subadult and continue group play activity or do something else (individual play, groom, feed, and so on). The significance of this is that the tendency to frequent peer groups was maximal in infant 2s and juveniles and, largely because of sex differences in behavior, diminished thereafter until, by the adult stage, there were no discrete groups, only individuals.

The infant 2 was still occasionally transported dorsally by the subadult males. Either the subadult or the infant 2 might initiate contact for this--the subadult looking behind and perhaps lowering his hindquarters, and the infant 2 by grasping the subadult from the rear at about the level of his pelvis. When the subadult did not lower his hindquarters, the infant 2's head would only reach to just above the subadult's back, so that the infant 2 was obliged to climb up; he did this generally by placing a foot about the level of the popliteal cavity, so that the infant 2's penis was at about the level of the subadult's callosities. As the infant 2 completed the movement onto the subadult's back he might thrust his pelvis as in copulation. Whether or not he did this because in climbing upon the subadult he was

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stimulated by contact is difficult to assess, as copulatory mounting arises at approximately the same age in *Cercopithecus* that do not generally carry dorsally. Nevertheless, in *Macaca sylvana*, the proper mount seems to develop from a precursor movement, just as the chatter develops from precursor sucking motions. In this context it is significant that the subadult female who does not carry infant 1s is solicited for dorsal transport by the infant 2s, and this transport is often accompanied by pelvic thrusting.

In summary, the critical biological development in the infant 2 age group is the change of pelage that inaugurates qualitatively different interactions, characterized by increasing independence of the infant. Sexual dimorphism has not yet appeared and behavior is basically homogeneous throughout the peer group, with the important exception that the one female spent more time sitting with, or grooming, the adult females, especially her mother.

JUVENILE: ONE YEAR TO THREE YEARS

The juvenile group is a transitional one. In many respects, the juvenile could be considered an "infant 3" on the basis of size, degree of sexual dimorphism, and play-group mates. In terms of participation in surveillance behavior, sexual behavior, and types of association with older animals, however, they have certain affinities with subadults that warrant the designation "juvenile."

The juvenile, by his second birthday, appears approximately a third longer than the first year old. This seems to be a behaviorally critical time, but in external development there is little morphological contrast to the first year old. The fur is beginning to change to the adult condition; that is, it is somewhat longer and gives less appearance of fuzziness. The light pinkish facial coloration has given way to brown. Freckles, white spots, and so on, which distinguish one adult animal from another, have begun to appear. Eye color is dark hazel to light brown. The ischial callosities have differentiated, the male pattern being an ovoid continuous shape, whereas the female pattern is one of two distinct, nearly triangular forms, whose apex is central. The difference is easily noted and enables rapid identification. The scrotum is visible from the rear, but extends only approximately one inch toward the knee. The female perineal region appears as a circular mass distinct from the callosities region. In the groups studied there was as yet no sex difference in size, but some differentiation in behavior was manifest that perhaps reflected sex hormone development. Vocalizations had deepened, and the "eeee" fear sound was replaced by "ahnh" with the exception of one male juvenile who retained the infant sound because it

would bring the head male or subadult to or near him. This lasted until two months before his birthday⁴.

The juvenile male would mount subadult males and females and give pelvic thrusts with greater frequency than would the infant 2, but the juvenile male still elicited dorsal transport from the head male or from the subadult males (see Table 3, p. 60). That is, while this behavior was transforming into sexual behavior, it retained the quality of its infantile function. The juvenile female (QG troop) did not mount other animals. While all juveniles groomed more frequently than did infant 2s (see Table 2), the females sustained the bouts at least three to five minutes longer but received less grooming and as a corollary were decreasingly involved in play. When not involved in grooming or play, the juvenile female might be sitting close to an adult female, or feeding and sitting by herself. The juvenile female tended to begin the solitary existence that characterized subadult females (see below). She spent much of the day sitting or wandering by herself, whereas the male was more integrated and more likely to be groomed, playing, or simply associating with others. The juvenile female was more likely to be repulsed from contacting infant 1s or 2s, and infant 2s were more likely to avoid play invitations. The juvenile could displace the infant 2 from food (both natural and provisioned), play, place, and grooming, but it would be more exposed to censure from the subadults and full adults. This punishment took the form of being threatened, chased, grabbed, pulled, or a combination of these, with the juvenile responding by a distress vocalization, appeasement chatter, submissive crouch, or moving off. The distress vocalizations might bring another subadult or adult to the juvenile, and this older animal might intercede with the punisher (threatening, and so forth) or might make contact with the juvenile (embracing, chattering, grooming).

Although each animal is given a name at birth by the British army, unless the animal is with its mother it cannot be told apart from age-mates until three years of age or later, because the freckles, pelage patterns, behavior characteristics, and so forth, that distinguish one from another are not sufficiently developed until that time. It was therefore impossible to tell whether any intercession by an older animal was effected because of a

⁴ Similar behavior had been observed in *C. aethiops* and *C. neglectus* at Tigon Primate Research Centre, Kenya, where an animal caged with its biological parents would retain the vocalization of a younger animal. Responses of older animals were protective toward it. When, in each case, the animal was moved to a different cage with age-mates, the vocalizations appropriate to its age group were then utilized. It is as if the animal in question were manipulating a behavioral response. Lack of response by the age-mates seemed to have extinguished this behavior.

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particular genetic, familial, or other special bond. (See MacRoberts, 1970, for a different view.) It is perhaps more likely that a mother would intercede for her offspring, and a subadult male intercede for the infant he had carried for a month, but this does not clarify the head male's intercessions (all the offspring were his) nor the subadult female's intercession (she very seldom carried infants) or clarify which animal the subadult would intercede for, as the two older subadults both carried two infants during the course of this study. Intercession was an important element of socialization, as it established the boundaries for permissible behavior in given contexts and conditioned the animal to appropriate behaviors vis-ii-vis younger animals. Furthermore it was instructive as a means by which the juvenile came to learn the personalities of the older animals. The juvenile began to relate to the older animals in terms of their idiosyncrasies rather than in terms of functional categories such as "male-care," protection, and so on. For example, the juvenile had to learn that this female (Joan, the youngest, MH troop) was more apt to grab if an infant 2 squealed than was another female (Bridget), or that one subadult male (Paris) was more apt to chase than was another (Ben), who would only mildly threaten.

Juveniles participated in troop life on a different level. For example, if a dog, hawk, or other threat appeared, the juvenile might give the warning bark. Interestingly, the response to a juvenile warning signal was observed to be investigation of the situation rather than immediate flight or defense posture. That is, the adults and subadults would look in the direction the juvenile was looking, and then respond. As discussed from the point of view of the infant, the juvenile was involved with the care and socialization of younger animals. At first threatened away by the mother, leader male, or subadult in the male-care role, the juvenile was increasingly allowed to contact the infant as it matured. When the infant was approximately three months old, the juvenile might offer dorsal transport, engage the infant in play, and so on. Similar behaviors extended from the juvenile to the infant 2.

The juveniles never initiated troop movements. The direction having been established (see below), the juveniles would walk with or follow the subadults. They might also walk along with an infant 2, who in turn might be accompanying a female, walking with a subadult male, or walking in a peer group. As the subadult males were more directly involved in troop movement, the routes must have been memorized sometime between the late infant 2 stage or during the juvenile stage. The routes taken did not vary; there were two down to the Moorish Castle area and back to Caroline's Battery, and two up to Middle Hill, with use depending on season.

SUBADULT MALE: THREE TO FIVE YEARS OLD

A substantial change is apparent between an animal beginning its second year (older juvenile) and one beginning its third year (subadult). The latter is twice the size of the second year old, and this is particularly visible in the limbs, which have quite nearly attained their adult length. The face has lengthened, particularly in the nasal area, more so than in the older juveniles. The facial characteristics are apparent; spots, blotches, and pigmented areas, which permit recognition of individuals, are now present. The fur is quite long, coarse and dry, and more interspersed with brown. Ischial callosities are fully differentiated, and the scrotum extends from approximately one inch to almost two inches toward the knee. Males have a characteristic walk, an undulating, almost salamander-like motion. The body is still slim, full bulk not being achieved till beyond the seventh year (Holmes, p.c.). Vocalizations are quite deep and the repertoire has expanded to include the true warning bark--a deep-throated staccato "rowr" akin to a dog's bark in rhythm and sound.

The influence of sex hormones on the behavior of the subadult male may be deduced from the difference in the nature of its sexual experimentation as compared to those of the juvenile or infant 1. Direct stimulation of genitalia was sought from others, the self, or objects. Mounting occurred with increased frequency, and was distinct from dorsal transport in the posture assumed, which was close to the fully adult one. Occasionally, however, both feet grasped the distal portion of the femur, or both feet might be on the pelvis, or one foot up and one down. Subadult males mounted subadult females occasionally, and other subadult males and the leader male frequently, but they were not observed to mount adult females probably because this would lead to a fight with the leader male (Holmes, p.c.). Animals of both sexes, from juvenile to infant 1, were held in the correct posture and thrust against, although a correct mount could not occur because of the younger animal's size. Two such episodes were observed to result in ejaculation after the younger animal was released. Masturbation, while less frequent in the summer months than during the breeding season of September to December (Holmes, p.c.), did occur, and ranged from rubbing the genitalia against a stone to autogrooming an erect penis, often culminating in ejaculation. Grooming, particularly of the ventral and femoral areas, frequently caused an erection, the penis appearing to be approximately two inches long.

Play was less acrobatic and included more wrestling and chasing, occupying fewer of the daylight hours than did grooming or sexual behavior as compared with the younger animals. The two instances recorded of subadult male play with the leader male are significant because neither was

more than two minutes long, and both took the form of wrestling and bumping, with the leader male crouching low to the ground with a chatter face. In these instances, the subadult males were restrained in their movements. That is, muscular tension and jerky movements characterized the interaction that in each case terminated in a chatter embrace. This controlled play is in contrast to bouts between peers or with younger animals. Subadult males were never observed to play with either subadult or adult females. While total play time decreased at this age, grooming increased. Subadult males groomed adult females more frequently than they did subadult females, but groomed the leader male almost twice as frequently as both female groups combined. The subadult male could approach neonates when the leader male held them, and attempts to gain proximity to them by means of grooming him contributed to the high frequency.

Subadult male contact with the subadult females changed radically during the course of the study and progressed from virtually total disregard of them to infrequent bouts of grooming, and more infrequent mountings. Toward the end of the study period, however, subadult females were permitted to stay near the subadult males when they had, or were close to, the infant Is. Interactions with the adult females also changed. While the subadult males could still be displaced by the adult females at the end of the study, the frequency decreased, and the behavior was more often met with resistance in the form of mild threat. Furthermore, subadults gave way to certain adult females and displaced certain others. For example, they were more likely to stand their ground against Joan, the youngest female, than against Caroline, a ten year old. Subadults would intercede for infants and juveniles when these were chased by adult females--by threatening or chasing the female--and look at or for the head male as if to see whether he would intervene on behalf of the females. The adult male did not respond to this behavior toward the females.

Aggressive incidents among subadult males themselves were slightly more frequent than those among younger animals. These incidents took the form of wrestling and chasing, as did play, but were accompanied by threat gestures and vocalizations. The subadult males scrapped primarily over the taking or keeping of an infant 1 or 2, which contact began after the infant could stand alone and had been chattered to and encouraged to walk. Thus this kind of contact could begin as early as the seventh to the twelfth day of the infant's life. Only two of the subadult males were permitted to care for infants. The third and youngest male (Eliot) had come from the QG troop. His exclusion from contact with the young infants may reflect the fact that, although he first appeared at MH in February 1970 (Holmes, p.c.), he was not yet a fully integrated member of the troop; when the in-

fants were two and one-half to three months old, he was permitted the male-care role.

When the infant Is were less than a month old, the subadults would return to the head male with them, give and receive a chatter or chatter-embrace, and then depart again. After that age, the head male would often threaten the subadults away. This behavior seemed to have a double function: (1) it was effective in reorienting the infant toward younger animals; and (2) it acted to reinforce the subadults' leadership behavior. That is, the subadults' responsibility for the infant grew the more he was rebuffed. The fact that at times the subadults were found more than two miles from the troop also attested to their growing independence.

The subadult males took an active role in troop movement. Like the adult females and head male, they could indicate time and direction of movement by moving in the desired direction and sitting on a high point with the body facing the direction. Whether or not they then "led" the movement, they usually moved in the vanguard. If the head male led the movement, they might be a considerable distance (up to 200 yards) from the infant's mother, though close to the head male. The subadult males further assumed troop responsibility by "standing guard," that is, when people, dogs, and cats approached or a warning bark was given indicating something that might not be visible, the subadult males would sit near or facing the danger. If a female threatened some such intruder, the subadult males, themselves threatening, would rush toward the thing being threatened.

To summarize, the subadult male's socialization at this stage was less a learning of new skills or practicing of old ones than a transformation of those already learned with the addition of increased independence and responsibility. He retained an ambivalent position vis-à-vis the adults, that is, like a juvenile he approached them for chatter-embrace, to be groomed, to groom, and so forth. While difficult to objectify, the subadult's body posture reflected this ambivalence. Many approaches to adults were submissive, with all muscles tense and the body in a slight crouch. At the same time, however, the subadult male began to assert himself toward the adults, by, among other things, threatening, particularly when intervening on behalf of a younger animal. His assertions would be met with more and more deference, which undoubtedly reinforced this behavior. The leader male was influential in this acquisition of independence and leadership by not interfering when the subadults were threatening females, and by rebuffing them when they returned infant Is to him.

**SUBADULT FEMALE:
THREE TO FOUR AND ONE-HALF YEARS OLD⁵**

The females are generally smaller than the males of the same age; this difference does not occur before this stage. Their faces, too, are smaller and rounder, though similarly marked with blotches, freckles, and so forth. The ischial callosities are by now two distinct triangular forms, and the perineal region, which is pigmented, has enlarged to a diameter of approximately five centimeters; there is no other sign of sexual development. In other physical respects they very much resemble the subadult males. The Gibraltar subadult females walked with a straight-through movement and very little undulation of pelvic or pectoral girdles. The interaction of subadult females with the other animals was characterized by timidity and infrequency. These females were typically solitary, wandering or eating by themselves. Their primary contact with other animals was in grooming, although they were never observed to touch each other or the head male. Unlike the subadult males the females could be displaced by all adults and subadult males.

Subadult females played with the infant Is and 2s, but with no other group. Play consisted primarily of wrestling and chasing and was generally solicited by the subadult female.

The contact pattern between the subadult female and the infant 2s or juveniles was perhaps significant in the subadult female's socialization, as in many respects it simulated mother-infant relationships. The subadult females solicited contact from the infants in play and grooming. They attempted to hold them, although the young ones would break away; and they offered dorsal transport, which was sometimes accepted as such, but which frequently became a sexual mount. Subadult females were attracted, as were all other troop members, to the neonates, and would even try to grab them. They were consistently rebuffed by adult females, the head male, and subadult males when they approached the infant Is. Toward the close of the study, however, they were allowed greater proximity to the neonates and were even permitted to touch them for moments at a time. Whether this represents a recognition of the maturation of the subadult female or personality factors in the adult females who had babies at this time can only be known from subsequent study. Sexual behavior began to change as the females approached their fourth birthday. Previously mounted only by infant 1s and 2s, as they approached their birthdays the subadult males began to mount them. Although the

⁵ Four and one-half years is given as the upper limit for this age group, as females are considered to be adult after parturition, which has occurred as early as four years of age.

action was accompanied by pelvic thrusts, there was no intromission. The adult male was not observed to take any sexual interest in females of this age group during the first study period, which terminated before the breeding season. Unlike the subadult males, the females were never seen to mount each other or to engage in any form of autoeroticism. Both females had their first sexual swelling by October, 1970, which differed from those of the adult females in color and form. Two distinct swellings were visible: one around the anus, and one apparently involving the labia. The skin of the uppermost swelling appeared taut while that of the lower area was looser. Unlike that in the adult females, the color was gray, white, and pink. Adult female swellings involve the entire perineal area and are larger and blacker. These swellings were present in December, 1970, and in the case of the slightly older female, resulted in an infant born at the beginning of June, 1971. This infant died on its fifth day, apparently due to her mother's insufficient milk production.

Subadult females, like adult females, gave the warning bark, often after an older animal had done so. They did not lead troop movements and usually took a place in the middle of the migration, often following an adult female, or accompanied by a younger animal.

It is very difficult to understand what was involved in the social processes of subadult female maturation. Since subadult females were solitary for the greater part of the day, learning would not seem to be a function of association. Perhaps the hormonal changes occurring at this time are in themselves causative of changes in behavior, or are influential in conjunction with the subadult female's perception and subsequent identification of herself as a female. In order to avoid anthropomorphism, this kind of question should be studied in the laboratory rather than under field conditions. What is known from analyzing the British army records, and from the instance herein reported, is that subadult females can conceive as early as three and one-half years. Inasmuch as the social status of a female adult is largely a function of having an infant, such a subadult female would be socially recognized as an adult by just over four years of age.

In summary, subadult females appeared to be isolated from the rest of the group even though they groomed and were groomed as much as some other age groups, because they did not seek each other's company, and when their invitations to play were accepted, the play was shorter in duration than was play on the part of the subadult males. They were almost totally ignored by the leader male, except when they threatened or disturbed one of the young. The isolation seems to be part of the overall limitation of the female's role in the socialization of the young, as elaborated in the next section on adult females. As the subadult female becomes sexually viable, the frequency of contact with males increases--first with the subadult males

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and then, in full estrus, assumedly with the leader male. But it is probably having an infant that fully integrates the female into the troop, as a function of troop interest in the neonate.

ADULT FEMALE: FOUR AND ONE-HALF YEARS AND ABOVE

Adult animals are included in this discussion both because they illustrate the end point of socialization and because biological development, even though catabolic, does not cease with maturity; behavior changes throughout the life span of the animal according to its previous experiences.

Adult females are characterized by bulk, by distinctive markings about the face and head, and by the perineal prominence. The facial markings include individualistic pigmentation of the face, particularly around the eyes, where freckles and nonpigmented spots may be variably distributed. The superciliary area is especially well marked, as a function of the increase in bone and fur. The perineum swells in the breeding and birth seasons, and may become so large that the tightened epidermis cracks or tears (QG troop), leaving large gaping areas with no epidermal covering. Outside of these seasons, the perineum remains prominent and is usually darkly pigmented except for the longitudinal section lining the vaginal and anal orifices. The fur at the sacrocaudal juncture forms an arcuate pattern as a result of the swelling, and is useful in identifying a seated female at a distance. After parity the teats remain distended, sometimes to a length of approximately an inch. They are variably pigmented, with black, white, and pink areas forming bands or spots. During lactation the breast tissue is quite distended, primarily below the level of the teat. The distance between them is approximately three to three and one-half inches. The infant suckles from one teat at a time.

Adult females of the groups studied, perhaps as a function of their bulk, did not leap from tree to tree as did the younger animals. They could execute acrobatic feats, and were observed to make jumps of ten to fifteen feet. They seldom did this, however, and tended instead to lower themselves down from heights to cross the ground, particularly if carrying an infant.

For females taken as a group, the period of solitarization terminates with maturity. Adult females were not observed to engage in any form of play, to the extent that they would (unlike *Cercopithecus* females) reject overtures or inclusion in play with threats or cuffs. During the summer study period the adult females spent approximately 85 percent of fourteen daylight hours grooming or being groomed (see Table 2). Typically, grooming bouts were not only more frequent, but of longer duration than those

of other age groups. Association was not, however, restricted to grooming, as females would sit, feed, and sleep with other troop members. This generalization does not hold for all the females, however, as personality factors seemed to affect the nature and amount of interaction with other individuals. Wilma and Joan of the MH troop and Fiona of the QG troop, for example, tended to be more solitary throughout the study than did the other females. Caroline and Bridget (MH) tended to frequent each other's company, as did Venus and Rose (QG). Charlotte (MH) could move freely from female to female even when that female had just given birth. The factors involved in the differences in conduct are hard to define, although "personality" or "temperament" identify the nature of the factor. Wilma, for example, was very submissive, to the extent that she would retreat from contact offers. Joan was very energetic, and would rush or move quite quickly toward other animals, which would often result in her being threatened or in the other animal's moving away.

Adult females participated in troop protection, but the amount of their participation seemed to depend largely on group composition. That is, in the MH troop whose head male was fifteen years of age, and which contained two subadult males and one more in the process of integrating into the troop, the function of troop protection appeared relegated, for the most part, to the males, although the females had some share. In the QG troop, however, the leader male of which was only five years of age, and which was losing its only subadult male, the adult females adopted the role of guardian in standing watch, warning of danger, interceding for the young, and so forth.

Troop movements were primarily initiated by the head male or adult females. An adult female would stand or sit in an open area or on a high point where she was clearly visible, or she might begin walking slowly in a particular direction. Some subadults and/or infants would come next; the leader male would then follow. When he went off, the remainder of the troop would move on in the chosen direction. Even when not leading, however, the adult females exercised strong control in troop movement. If one did not follow the troop, the adult male might call to her or return to the female in question and then lead off again. If she still did not follow, he might return, and the troop would follow him back. There was no indication of how the troop discriminated between the male's returning to urge the female to follow, and his leading the troop back. Adult females were observed to aggress toward all members of the troop (including infant Is) with the single exception of the head male. They were the subject of aggression primarily from each other, and secondarily from the adult male. The most frequent causes of strife were attempts at contacting the infant Is and proximity to the head male. Most aggression took the form of chasing

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and vocalizing, although aggravated situations would turn into true fights, characterized by grabbing, pulling, and biting, unless the leader male intervened. Most of the aggression from the head male was in the form of intervention, the male threatening or chasing a female who was aggressing toward some other troop member. Occasionally his intervention developed into grabbing at the female, or even biting. Generally a look and mild threat from him, or even his presence alone, was sufficient to reduce tension.

As stated earlier, data from British army records indicate that females may be impregnated for the first time at three and one-half years, although sometimes they will not necessarily conceive or successfully carry until six years of age. Females observed to be pregnant during the study have subsequently been noticed by the Officer-in-Charge to be no longer carrying. As the fetus will have been aborted in the bushes, verification is inadequate. During the summer of the 1970 study, one female (QG) lost her fetus from prolapsed uterus (M. Sutton, p.c.), and another, who had been pregnant early in the study, appeared no longer to be carrying by the middle of the summer study period (Holmes, p.c.).

It is assumed that all females are impregnated only by the head male (Holmes, p.c.), as the mounting of adult females in the breeding season by the subadult males incites aggression from the head male. Copulations occur throughout the year, but probably are not "true" copulations (Carpenter, 1942), because none of the copulations observed (thirty-five in MH, nine in QG) was seen to culminate in ejaculation. Episodes involving ejaculation may have occurred, however, outside the area of observation. In three instances, one in MH and two in QG, copulations took place just before, on the day of, or just after a birth, and seemed perhaps to function more as reinforcement of ties or "reassurance" than as reproductive sex.

The female, as described in the section on infant 1s and 2s, has a limited role in socialization of the young. The female might, however, act as a negative force, as, for example, did Bridget (MH), and Deirdre and Tessa (QG), who retarded contact with their respective head males by removing their infants a distance from him, so that encouragement of chattering, walking, climbing, and so on, took place later than with the other neonates. It seemed that these infants' development in locomotor and manipulative skills particularly took place more slowly. Dorothy (Bridget's infant), for example, was not any more capable at locomotor tasks (jumping distances, and so on) at one and one-half months than was Olga (Charlotte's infant), then aged only two weeks. Nevertheless, the female serves primarily to reinforce learning. That is, consistently the day after the male has encouraged the infant 1 to walk, or to climb dorsally, the female does the same. There were no observations of any female doing these sorts of activities before the male had done so. As the female would relinquish

the infant first to the male and then for greater periods of time to the sub-adult males, her contact with her own newborn was severely reduced after the sixth day or so. The infant is returned to its mother when it squeals a great deal, perhaps because it is then hungry. Assumedly, the infant sleeps with its mother until it is past six months, although it was impossible to observe this directly. Her function in the troop then, other than the obvious reproductive one, was reflected by the grooming frequencies, and would seem to be primarily as social adhesive. The male was the focus of the troop, but it was through the female that the infant was imprinted to its troop, since the female's body is the first environment of the infant, and since from the first day of its life the female sniffs, licks, grooms, and generally touches it. Perhaps because of its biological need of her as a young animal, and through the grooming association thereafter, it is through her that this connection with the troop is predominantly reinforced. (See Koford, 1963; Sade, 1965.)

ADULT MALE: FIVE YEARS AND ABOVE

A male is biologically an adult at five years of age, as he can reproduce at that time, although there is one report (Fitzgerald, 1950) of a male (Mick) fathering offspring at three and one-half years. The gradual process of developing bulk begins slowly after age three and accelerates within the fifth year. The canines, which have erupted by two years (Fitzgerald, 1950), descend below the occlusal plane, and the scrotum becomes larger and more pendulous, extending approximately three and one-half inches toward the knee. The superciliary region develops heavily after the fifth year, so that the fur may dangle forward. Spots and other characteristic marks are fully developed on the face, to which may be added fight scars. The fur is slightly darker than in the adult female, coarse, dry, and very long; it is quite full around the head and shoulders, appearing like a mantle. Between the fifth and seventh years, greater bulk is achieved, and this increase in girth continues to nine years. An adult male may eventually weigh approximately sixty to seventy pounds (Holmes, p.c.), and his canines may reach a length of approximately one inch from the gum. The adult male has lost the swagger, the undulating walk of the subadult male, and moves with a deliberate even motion. Like the female, and perhaps for the same reason, the adult male seldom leaps; he is cautious in climbing, and has been observed to test a branch or twig before placing his weight on it.

The attainment of leadership in Gibraltar is largely manipulated by the Officer-in-Charge. That is, when a young male approaches five years of age, a decision is made as to whether the incumbent leader can and should

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go on, or should be removed to a zoo in favor of the younger animal. The present leader of the QG troop was taken from the MH troop and put in the position at just under five years to fill a vacuum, as the former head male had died and the next possible male, then about thirteen years of age, had previously joined the MH group. This older male at first shared the troop with the incumbent, then eleven years old (Holmes, p.c.). After the thirteen year old (Mark) had been caged so that a hand injury could be tended, the two males began to fight, and the fighting became so serious that the younger one (Harold) was removed and put in a cage. Mark was thus chosen as leader of the MH troop, the choice having been made in his favor largely because Harold had once killed an infant, and on another occasion so molested a female that she thrust her infant away from her. The present QG leader (Sam), now fully five years old, has begun to fill his role. At times, however, he joins the subadults and infants in games, and the adult females have been observed to assume and share the leader role for the period. The head male is responsible for the protection of the troop as a whole and particularly of the younger infants. Although he does not necessarily initiate troop movements, he controls them by following (or not following) the initiator. The manner of leading troop movements has been described under the section on adult females.

The adult male functions as the "control" animal, as described by Bernstein (1966, 1968). In Gibraltar the adult male restrained individuals from aggression or broke up fights that had gotten beyond the threatening stage. He spent most of the day observing the surroundings and surveying the troop, this even while grooming or being groomed. He was apparently alert, even when dozing, as the slightest noise would cause him to sit up or move toward the noise to investigate. He played an important role in the socialization process as described in the section on infant Is. The nature and "definition" of the role was apparently a function of the head male and his age. An adult male may live until seventeen or twenty years of age (Holmes, p.c.), and much of what he does would seem to be the result of experiences gained. Mark (MH), for example, aged fifteen years, differed greatly from Sam, the five-year-old leader of QC. For example, Mark seldom played with the younger animals, whereas Sam frequently did. Mark seldom did more in punishment of an infant than threaten, and Sam would chase, grab, or bite. Both males immediately became alert when an animal made a distress call, but Mark waited longer to move in that direction, at first just turning his head toward the sound and looking. As he responded to some situations and not others, it was as if he were evaluating the nature of the situation. The first and second year olds in Sam's group approached a newborn infant within the first four days of its life. Mark would threaten off such approaches. until the

infant was at least five to six days old. Although both males conditioned the infant to chatter, and both males took the infant within the first few days of its life, Mark would encourage the infant to walk before it had the motor coordination to do so. In distinct contrast to this, in Sam's group the infants began to walk largely on their own initiative, undoubtedly largely because their mothers often removed them from contact with Sam. Interestingly enough, infants of one and one-half months in Mark's group seemed to have better locomotor coordination than did corresponding infants in Sam's; that is, they moved forward with less lateral wobble and could climb and jump without falling over.

If "respect" is operationally defined as speed of reaction to another individual combined with intensity of stimulus necessary to elicit this reaction, Sam received less respect from his females than did Mark, as Sam had to engage in physical contact or combat instead of mildly threatening them before they would respond, move, and so on.

In summary, the adult male's role in socialization is: (1) to encourage the infant to develop motor abilities that permit social interaction; (2) to reorient the infant, as it matures, away from himself and toward other troop members; (3) to reinforce socially acceptable behaviors appropriate to the age group by not interfering, or by giving positive reward (chatter, embrace, and so on); and (4) to extinguish or negate inappropriate behaviors by punishment (threat, chase, and so forth). Furthermore, in his functions as leader male of the troop the adult male acts as (1) major or sole breeder, (2) control animal, and (3) focus of the troop.

DISCUSSION

The major features of each age-grade's role in socialization are summarized herein. The adult female is the first environment for the neonate, and thus the context for the most important biological maturation. The infant first sees and makes its first oriented movements within her arms. However, since the leader male takes the neonate from as early as the first day of life, it is the leader male who is the preeminent influence in socialization of the infant until it is approximately two weeks of age. The leader male encourages biological maturation by reinforcing the infant's mouth sucking movements until they become the social chatter gesture, and by encouraging the infant in locomotor skills and to take the dorsal transport position. These basic body movements are of prime importance for all future social contact. The leader male reorients the infant away from its mother, himself, and other adults, by permitting subadult males to first snatch the infant, and later to take it away for greater and greater distances. It is while the infant is under the care of the subadult males that it in-

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creasingly contacts juveniles and later age-mates. From contact with subadult males and juveniles, as well as from this social context, the infant learns, as he develops motor skills, all the necessary information to become a functioning member of the troop. The information ranges from what to eat to available routes from one area to another. Subadult females play a very small role in socialization of the infants, as this age group is largely isolated from other troop members, and as they are rebuffed by all adults and subadult males when they make overtures. The adult females are more important in socializing juveniles and subadults than in socializing infants. Their relationship to the infants is primarily as feeder, and later groomer, that is, a relationship of comfort and support. Although they do defend and protect the infants, this is more the task of subadult males. Females influence the older animals primarily by rebuffing them as they approach infants, play with juveniles too roughly, or come for food the female herself is approaching. But what they learn from these females seems more to be how to respond to the personalities and temperaments of the individual animals.

What has been described is a population as it appeared at a particular point in time. It is interesting that notes on the Gibraltar monkeys made in the late 1940s indicate that certain biological and social features were different. At the time the notes were made, there were two strains of monkeys and their mixed descendants: one, smaller in number, descended from macaques on Gibraltar prior to World War II; the other, descended from African imports made to secure the population. A major difference between the 1940 monkeys and the present ones is relevant to this discussion. Infant socialization was apparently not as limited to the male context, as females, particularly sibling females, were at that time permitted to touch and hold each other's infants (Fitzgerald, 1950). The change in tradition and transformation in role definition implicit in this fact serves to stress the point of the plasticity of social relations even within a circumscribed deme (or population). In other terms, while the infant needs contact for "normal" development, as deprivation studies have shown (Harlow, 1962), there is no prescription as to which individual must occupy the contacting role. The personality of the head male is a large factor in this, particularly when he remains the leader for a prolonged period and thereby has access to several generations. In a sense then, there may be a "tradition drift" (Burton and Bick, in press), processually akin to genetic drift. The QG troop may serve as an example. As Sam gains bulk, completes his canine development, and gains experience, assuredly the adult females in his group will respond to him differently. The new infants maturing at that time will therefore be exposed to relationships substantially different from those described above. It may be that he will,

for example, take infants from their mothers when they are younger, and thus the acceleration in motor development seen in MH troop may become a feature in QG. The females' responsibility for the troop may be circumscribed as Sam takes on more responsibility himself, such as standing guard duty more frequently, and so on.

The difference just described illustrates the fact that there is flux in a population. This article is intended to delineate the extent to which biology, environment, tradition, and social relations alter and interaffect each other, giving rise to new forms. To see behavior as genetically fixed, or wholly environmentally determined, would be to ignore the basis of evolution.

TABLES

The following tables are included to represent tendencies in, but not the entirety of, the activities quantified. In most cases such overall representation is impossible, even over extended contact periods as was the case in Gibraltar. The animals are highly mobile, and the duration of an activity cannot always be ascertained or calculated, because although the activity may begin in direct view, it may continue or terminate behind a bush or in a tree, where visibility is, at best, limited. For example, infant 2s and juveniles spend most of the day, probably 90 percent, playing. Yet a frequency chart for play of this age group would not suggest this, and it is because when these young animals play, they range over the total area the troop is in, much of it bush. The factor of selection must also be admitted. Even with three observers posted at different places in order to maximize observation and obtain a check on the data, some kinds of actions will be noted and not others--the most unusual behavior, for instance, will be recorded and the most ordinary neglected, as reflected in the relatively low frequency of mother-infant grooming. This problem, which existed under positive observation conditions, is probably exacerbated by poor viewing conditions as with forest monkeys. Frequency charts are extracted from the context in which the activity occurred, and most activities are tightly interrelated with others. In one block of time, five or more activities may go on, interrelated or giving rise to each other, but each activity would be entered on a different chart, with the effect that the quantification itself does not adequately convey the texture of that which is analyzed.

TABLE 1. Group Composition: April 28 to September 23, 1970

	Infant 1s		Infant 2s		Juveniles		Subadults		Adults		Total
	Male	Fem	Male	Fem	Male	Fem	Male	Fem	Male	Fem	
Middle Hill	0	4	4	1	2	0	2(1*)	2	1	5	22
Queen's Gate	0	2	0	0	1	1	1(0*)	1	1	5	11
Total	0	6	4	1	3	1	3	3	2	10	33

*Subadult male moved from Queen's Gate to Middle Hill during the study period.

Table 2. Grooming

groomer	GROOMED							TOTAL
	Infant 1	Infant 2	Juvenile	Subadult		Adult		
				M	F	M	F	
Infant 1								
Infant 2			1 <i>.06%</i>	14.5 <i>.91%</i>	2 <i>.13%</i>	19 <i>.19%</i>	32.5 <i>2.04%</i>	69 <i>4.34%</i>
Juvenile			18 <i>1.13</i>	18 <i>1.13</i>	1 <i>.06</i>	23 <i>1.44</i>	72.5 <i>4.55</i>	132.4 <i>8.31</i>
Sub: Male		28 <i>1.76%</i>	15.5 <i>.97</i>	11 <i>1.69</i>	5 <i>.31</i>	134 <i>8.41</i>	83 <i>6.59</i>	350.8 <i>22.01</i>
Sub: Fem		9 <i>.56%</i>	29 <i>1.82</i>	1 <i>.06</i>			145.5 <i>9.13</i>	184.5 <i>11.57</i>
Ad: Male		15 <i>.94</i>	1 <i>.06</i>				279 <i>17.50</i>	274 <i>17.19</i>
Ad: Female	9 <i>.56%</i>	140.5 <i>8.81</i>	25(13/.82)* <i>1.57</i>	39 <i>2.45</i>	80.5 <i>5.05</i>	90.5 <i>5.68</i>	205.5 <i>12.89</i>	578 <i>36.26</i>
Total	9 <i>.56%</i>	202.5 <i>12.70</i>	102.5 <i>6.43</i>	83.4 <i>5.23</i>	89.5 <i>5.61</i>	330.4 <i>20.73</i>	783.1 <i>49.13</i>	1594

NOTE: Arabic numbers equal grooming time in minutes; italicized Arabic numbers equal percentage of total grooming time of Groomed animal.

* Sex of adult unknown

TABLE 3. Development of Sexual Motions

	Frequency of Dorsal (Transport) mount with thrust				Frequency of Pelvic Mount			
	Subadult		Adult		Subadult		Adult	
	Male	Female	Male	Female	Male	Fem	Male	Fem
<i>Infant 1</i>	0	0	0	0	0	0	0	0
<i>Infant 2</i>	8	0	0	0	4	2	0	2
<i>Juvenile</i>	15	0	0	0	7	1	0	0
<i>Subadult male</i>	0	0	0	0	11	2	11	0

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