

## Induction of Normal Prepubertal Behavior in Wolves with Restricted Rearing<sup>1</sup>

KEVIN B. MAC DONALD<sup>2</sup> AND BENSON E. GINSBURG

*Department of Biobehavioral Sciences, The University of Connecticut, Storrs, Connecticut 06268*

A series of studies in which wolves were born and reared in a population field as members of a variety of captive packs had been previously undertaken in our laboratory. Two females were each isolated from conspecifics at 4 weeks of age and individually reared as pets until 6 months of age in a household containing a domestic dog. One of these was included in the socialization procedures to conspecifics used in the present study. Another female (previous study) was taken from the mother on the second day after birth and bottle-raised until 9 weeks, when it was isolated from conspecifics until 10 months of age and then socialized (B. E. Ginsburg, in *Communicative Behavior and Evolution*, pp. 59-79, Academic Press, New York, 1976). In the present study, six wolf pups were subjected to a variety of regimes of rearing and handling beginning at 4 weeks of age. Two males were isolated from humans and conspecifics from 4 weeks to 6 months of age, with minimal human handling from weeks 4 to 6. One male was socialized to humans beginning at 4 weeks of age, but had no experience with conspecifics from 4 weeks to 6 months of age. Two females were pair-housed from 4 weeks of age to 6 months of age, with minimal human contact from weeks 4 to 6 and intensive socialization with humans thereafter. At 6 months of age, the animals, with the exception of one male isolate who died, were paired in a series of round-robin encounters lasting 1 day each and subsequently group-housed for 5 days. Videotapes of the interactions, obtained without humans present, revealed that after a variable period of adjustment the animals exhibited behaviors normally seen in wolves of this age on the first day of pairing. The group encounters also demonstrated that normal social behavior, including normal group structure, could develop within this time span. The animals, with the exception of the dominant male, reacted with appropriate submissive behavior to an adult female. The results are discussed with reference to the previous canid isolation literature, and it is concluded that normal social behavior in wolves is sufficiently well buffered from environmental effects to permit rapid recovery from aberrant conditions of rearing, under appropriate experimental circumstances.

<sup>1</sup> This research was supported by grant MH27591 from NIMH and by grants 0221-114 and 0221-245 from The University of Connecticut Research Foundation. The authors gratefully acknowledge the assistance of René Greenberg-Prouty, who independently scored the videotapes so that reliability assessments could be made.

<sup>2</sup> Present address: Department of Psychology, University of Illinois at Urbana-Champaign, Champaign, Illinois 61820.

The behavioral characteristics of wild animals constitute a favorite model for the study of genetically preprogrammed behavior. From the earliest period of *postpartum* development, such behavior cannot seriously misfire without endangering the survival of the variant. On this view, it would seem that there can be few degrees of freedom between the genotype and those behavioral phenotypes upon which survival depends.

There is, however, ontogenetic flexibility, and, as shown perhaps most clearly by classical imprinting studies, there is more than one way of achieving adaptive behavior. For Lorenz (1965), flexibility is achieved by intercalated sequences of genetically fixed and learned components, and the normative environment is one in which the learned components, which also depend upon genetic capacities, are adaptive. The greater behavioral flexibility seen in domestic animals and in our own species is partly attributed by ethologists to a degeneration of instincts due to relaxed selection (see, e.g., Eibl-Eibesfeldt, 1975, Chapter 18). This could lead to higher order adaptations—namely, a greater capacity for learning (our view), but this side of the coin is often underplayed by those holding strict nativist views.

In our comparative studies of canid behavior, we have seen something of this contrast between closely related wild and domestic forms. Our data, however, suggest an alternative interpretation that can be highly generalized: namely, that there are genetic equilibrium points for various aspects of biologically based behavior that may be attained in a number of ways and that there are varying degrees of freedom between what is encoded in the genotype and what is expressed in the context of life experience. Given such variability, there is still a genetically buffered biologic tendency to approach the equilibrium point—as illustrated by the data compiled by Clarke and Clarke (1976), Kagan and Klein (1973), and many others, including data to be presented in this paper. This concept predicts two outcomes: (1) for the normally programmed individual, even intensely abnormal experiences can be overcome using a variety of compensating techniques; and (2) for the abnormally programmed individual undergoing species-typical development, an aberrant equilibrium point will be reached, and ameliorative techniques will be much less effective. Such techniques may be analogized to the aberrant rearing of normal individuals. In each case, they will tend to approach their phenotypic equilibrium point. In the abnormally programmed individual, the readout of the genetic program must be changed in order for a normal profile to be achieved. Thus, on the one hand, the remarkable recoveries from the effects of early deprivation, and, on the other, the difficulties of achieving lasting “cures” in behavioral disorders that are biologically based unless the underlying mechanism(s) can be altered or their abnormal consequences averted by compensatory techniques at the

level of genetically influenced mechanisms, such as those used with PKU.

In the studies reported in this paper, isolation rearing of wolf cubs was used to induce aberrant behavior. This was followed after 6 months by programmed social encounters, resulting in the production of essentially normal behavior.

Isolation experiments have long been used as an analytic tool with which to study the development of social behavior. Within the context of canid research, the design of such experiments has been greatly affected by current views on canid development. Dog and wolf puppies are born with eyes and ears closed, and it is only at about 3 weeks of age, the beginning of the period of socialization as described by Scott and Fuller (1965) for the domestic dog, that the first signs of social behavior are seen. Between 3 and 4 weeks of age, play behavior is still restricted by poor perceptual and motor development (Fox, 1971a), and it is only after 4 weeks of age that a broad repertoire of behaviors develops. As a result, many canid “isolation” experiments described in the literature are begun between 3 and 4 weeks of age and are continued until after the 12th week and usually to at least the 16th week of life. By this time, in normally reared puppies, the great majority of social behaviors are present and attachments to other animals, people, and places have been formed (Scott & Fuller, 1965).

*Review of isolation literature.* Fuller (1967) found that visual and physical isolation from conspecifics and humans affected the intensity of contacts with humans, objects, and other dogs more than the number of contacts as assessed in 7-min arena tests conducted 4 times weekly from Weeks 16 to 20. Some animals were completely unaffected, and the results were interpreted as suggesting that isolation effects were not due to the withholding of “information” during a critical period but, rather, were the result of stress due to a new environment (the arena). Results said to support this interpretation were that animals handled gently prior to the arena tests were behaviorally much more like control animals than those not so handled. The tranquilizing drug chlorpromazine accentuated the beneficial effects of moderate amounts of handling, but did not improve the beneficial effects of relatively large amounts of handling and had a negative effect in the absence of handling (Fuller & Clark, 1966a). Breed differences were very important, with terriers improving rapidly to the levels of the normal animals without special handling of chlorpromazine (CPZ), and with beagles showing gradual improvement over the 5 weeks of testing to levels approaching those of control animals when given the handling and drug regime (Fuller & Clark, 1966a). In addition, a mere 20 min of distributed normal experience per week between 3 and 16 weeks was sufficient to produce dogs of both breeds that were indistinguishable from normal animals.

Fuller and Clark (1968) replicated these results in a subsequent series of experiments. They confirmed that wire-haired fox terriers improved rapidly after isolation, with beagles improving more slowly. The analysis of variance for the final testing block (Week 19) resulted in only 4 of 24 significant *F* ratios, and the authors conclude that after 20 testing periods spread over 5 weeks, few, if any, specific categories of response differentiated the breeds or isolates from pet-reared animals. However, pets were socially dominant to isolated animals as assessed by a towel competition test.

These results are remarkable, since the arena test is unlikely to provide an optimal condition for revealing normal social behavior. Animals previously unsocialized to humans were tested with humans present and given only 2-3 min per test, with the people, dogs, and toys used as stimuli. Thus, at the conclusion of testing at Week 19 or 20, an isolate had only 40 min of contact with a normal conspecific distributed over 5 weeks. In addition, isolation with a companion resulted in very poor performance when tested individually on the arena test despite normal social behavior between the isolates (Fuller & Clark, 1966b), indicating that social competence is not measured by performance on the arena test.

Fox (1971a) performed several experiments relative to these points. In one, dogs were reared with cats from 25 days to 16 weeks of age. When tested after isolation from their own species, the dogs showed deficits in reaction to their own species but recovered within 2 weeks, at which time socialization to other dogs was complete. In a second experiment by Fox, dogs were reared according to three separate paradigms. Some were hand-raised from 3 days of age and isolated at 3½ weeks; some were reared as a litter by the mother until 3½ weeks and subsequently isolated; the third group was reared with dogs until 8 weeks and then isolated. When tested at 12 weeks, the human-reared animals tended to be deficient in play behavior compared to the dogs raised by dogs until 8 weeks. However, recovery was rapid and deficits are described as occurring only early in the period of socialization. Some isolates became dominant to control animals within 3 weeks and deficits toward humans became less apparent. The dog-reared animals isolated at 3½ weeks were described as showing fewer deficits on emergence from isolation and as showing rapid recovery thereafter. These animals were said to be comparable to rhesus monkeys isolated for only the first 3 months of life, a treatment that has only transitory effects (Harlow, Dodsworth, & Harlow, 1965).

Fisher (1955) isolated four wire-haired fox terriers, three mixed-breed animals (wire-haired terrier crossed with cocker spaniel-basenji), and one sheltie from 18 days to 16 weeks of age. When tested, the isolated animals scored below normally reared littermates on the average for tests

with dogs and humans, but there was much variability and some isolates scored above normal littermate controls. On all tests, there was overlap with the normal controls. When the litters were reconstituted, the mixed-breed animals adjusted well. The two isolated terriers were the objects of severe aggression by their littermates and were the most subordinate animals. (Severe aggression against subordinates is common in these pedigrees of wire-haired fox terrier litters, and it is rare for litters of more than three to survive without one animal being maimed or even killed.) When the isolated terriers were grouped together, there was little aggression. The author hypothesized that the poor long-term adjustment of the terriers was due not to isolation during a critical period but to aversive post-isolation contact by the terrier littermates. The isolates of all breeds, however, are described as less aggressive than normal animals and often held a subordinate position in the group. These animals also initiated less interactions with other animals than the normals did.

In addition to the studies based on the timetable of normal behavioral development in the dog, several studies were done by researchers at McGill University using a longer period of restriction. These studies were focused mainly on the effects of early restriction on cognitive processes, but some observations of social behavior were made. Melzack and Thompson (1956) isolated 10 Scottish terriers visually and physically from other animals and from people from 4 weeks to 7½ months of age. In addition, 4 Scottish terriers were housed singly but allowed to look into the laboratory, and 7 were housed with 1 or 2 other animals and could see the ceiling of the laboratory. The restricted animals were subordinate to the pet-reared controls on a food competition test and reacted to other dogs either with great excitement or indifference. Diffuse emotional excitement also characterized their reactions to humans when tested up to 2½ months after isolation. One year later, however, there was no statistical difference between pets and restricted animals in response to humans, although the restricted dogs still showed diffuse excitement. Thompson and Heron (1954) found that Scottish terriers isolated to 8 months of age remained somewhat abnormal in response to humans, typically withdrawing after eagerly licking the human. No data are given in either study on long-range effects of the isolation on social behavior with other dogs, but Melzack and Thompson conclude that "restriction of social and perceptual experience retards the emergence of normal adult social behavior in dogs, whether towards members of their own or other species. With opportunities to gain such experience, however, most dogs reared in moderate isolation at least, can overcome to a significant degree the adverse effects of restriction on their social responses to man."

These studies do not support the view that dogs isolated during the period when social behavior normally develops are socially incompetent,

lack species-typical behavior, or continue stereotyped behavior after isolation. They support the view that isolation during this interval of development affects dominance within the litter, although Fox's (1971a) results do not confirm this. Fisher (1955) found that isolates retained a tendency to initiate interactions less often than normal animals. These data have not always been interpreted in this manner. For example, Fox (1971a) concludes on the basis of his isolation study that innate behavior patterns, if not reinforced, will undergo regression or modification under conditions of deprivation (p. 254). The effects of longer periods of social isolation on behavior with other dogs are less clear because of a lack of follow-up, but the results of Melzack and Thompson (1956) do indicate considerable improvement without special "therapy."

The isolation literature on rhesus monkeys is more widely known and presents quite a different picture. Monkeys are conventionally isolated from birth for periods ranging up to 12 months of age. Upon release, 6-month isolates are described as inactive, fearful, and withdrawn, almost completely nonexploratory and nonsocial and unable to avoid aggression from other animals (Harlow et al., 1965). Little improvement is shown by these animals unless "therapy" is given. Deficits in normal social behavior produced in isolate-reared monkeys can be substantially reversed if these animals are paired with normal 3-month-old monkeys. Isolates receiving this therapy show considerable improvement in their social behavior, but some deficits persist (Cumins & Suomi, 1976; Novak, 1979). The 3-month-old "therapists" are not aggressive in their interactions, but they do engage readily in social play and clinging and can thus act as behavioral pacemakers for the older monkeys.

Separation of young rhesus monkeys from parents has been shown to result in some long-range effects (Spencer-Booth & Hinde, 1971; Stevenson-Hinde, Zunz, & Stillwell-Barnes, 1980), but, in general, there is no gross impairment of social behavior. The age of separation (between 2 and 9 months of age) has little effect on the response to separation (Mineka & Suomi, 1978), and single-housing has more of an adverse effect than pair-housing (Suomi, Collins, & Harlow, 1973). These experiments bear some resemblance to canid isolation experiments, since animals in canid isolation experiments are typically not isolated from birth, although some investigators (e.g., Fox 1971a) used this technique. However, separation distress does not typically occur in canid isolation experiments, presumably because the response cannot be elicited until about 4 weeks of age in dogs (Scott, personal communication). Moreover, no attempt is made in the monkey separation experiments to isolate the animals after separation throughout the period of behavioral development. This has clearly been the case with many canid isolation experiments. The experiments were usually designed so that isolation would occur during the time in development when normal social behavior is first exhibited.

Thus, the literature indicates that the development of social behavior in dogs is more highly buffered from environmental effects than is the case in the rhesus monkey. There is some evidence that this is the case with wolves as well. Ginsburg (1976) isolated a wolf from other wolves (but not from humans) from birth to 9 weeks of age. The animal was then put into visual and physical isolation until 10 months of age. At this time, the animal exhibited the various species-typical behavioral components, but did not pattern them correctly and did not respond appropriately to other wolves. Attempts to restructure its behavior began immediately after isolation. When placed under supervised restraint with other wolves accustomed to strangers and rewarded for appropriate responses, the animal began to restructure its behavior effectively within 4 or 5 days. This indicates that Ginsburg's wolf suffered from an experiential deficit, as did Suomi's monkeys, but that in the case of the wolf, the deficit was in the organization of behaviors already possessed and in learning to interpret the behavior of other wolves as well as to react with the appropriate behavior.

The present experiment is conceived as an extension with six animals of the work of Ginsburg described above.

## METHODS

The wolf cubs from the litter available for this study, consisting of three males and three females, were subjected to a variety of environments, each lacking the normal range of social contacts for young wolves. Unlike previous isolation experiments involving canids, isolation facilities used after the animals were 6 weeks of age were relatively large, consisting of two  $2.4 \times 1.8 \times 2.1$ -m arenas separated by an opaque partition with a remotely operated door, which allowed for caretaking activities to take place while maintaining isolation. The various regimes of rearing (see Table 1) were instituted when the animals were 4 weeks old, at which time they were housed in metabolism cages (described below). At 6 weeks of age, they were housed in the larger pens. From birth to 4 weeks of age, the animals were kept with the mother with minimal human contact.

One male (M3) was housed singly from 27 days of age to 6 months of age. From Days 27 to 43, he was housed in a standard kennel run measuring  $1.1 \times 1.7$  m. After Day 43, he was housed in the  $2.4 \times 1.8 \times 2.1$ -m pen described above. This animal received social contact daily from humans, especially from one of the experimenters (Mac Donald), but had no visual or physical contact with the other animals.

Two other males (M1 and M2) were also housed singly for the same period (4 weeks to 6 months of age). These animals received no contact from other animals or humans, except from Days 27 to 43 when they were removed twice daily from the metabolism cage for caretaking. The

TABLE 1  
Experimental Design of the Isolation Experiment

	Days 1-27	Days 28-42	Days 43-208	Days 209-218	Days 221-225	Days 232-236	Days 237-239
M1	With mother	Isolated, open front cage; minimal handling	Isolation; died on day 137				
M2	With mother	Isolated, open front cage; minimal handling	Isolation	Round-robin pairings	Group housing	Pairings with adult female	Group with adult female
M3	With mother	Isolated, open front cage; socialized with humans	Isolated from conspecifics; socialized with humans	Round-robin pairings	Group housing	Pairings with adult female	Group with adult female
Fem1	With mother	Paired with Fem2 in open front cage; minimal handling	Paired with Fem2; socialized with humans	Round-robin pairings	Group housing	Pairings with adult female	Group with adult female
Fem2	With mother	Paired with Fem1 in open front cage; minimal handling	Paired with Fem1; socialized with humans	Round-robin pairings	Group housing	Pairings with adult female	Group with adult female
Fem3	With mother	Raised as pet; contact with Scottish deerhound		Round-robin pairings	Group housing	Pairings with adult female	Group with adult female

metabolism cages measured  $0.76 \times 0.91$  m, with open fronts through which people but no wolves were visible. After Day 43, they were housed in the  $2.4 \times 1.8 \times 2.1$ -m pens.

M1 died at approximately 20 weeks of age, so that only his behavior during isolation was analyzed. This animal adjusted very poorly to isolation, exhibiting severe separation distress. He ate very poorly and actively sought human contact both during Weeks 4 to 6 when he was regularly handled by humans and during direct observations between Weeks 7 and 20. On Day 85, isolation was broken because the animal refused food. He was easily socialized to humans and began gaining weight rapidly. Isolation was reimposed on Day 106. However, he again stopped eating and he was allowed interaction with humans beginning on Day 111. He made rapid progress after this time, but died suddenly on Day 138. The cause of death was unknown, but a postmortem diagnosis of rickets was made, undoubtedly due to his poor appetite. The results suggest a failure to thrive in the absence of social contact for this animal, who sought positive interactions from the time of his first contact with humans. This behavior contrasted with the behavior of M3, Fem1, and Fem2, who remained fearful of humans throughout the experiment, and suggests that the personality profile, or temperament, is established by this time in the wolf and is a powerful interactant with any environmental manipulations that ensue.

Two females (Fem1 and Fem2) were housed together and socialized by the experimenters and other humans beginning at day 44. From Days 27 to 43, they were housed in a cage measuring  $1.2 \times 0.91$  m, with an open front through which people but no wolves were visible. After Day 43, they were housed in a  $2.4 \times 1.8 \times 2.1$ -m pen.

One female littermate (Fem3) was reared as a pet in the home of a female graduate student (not the authors'). This animal was exposed to daily contact with an adult female Scottish deerhound and had wide social experience similar to that of a pet dog.

*Observations during isolation.* A television camera with a wide-angle lens was suspended above the arena to be photographed and connected to a time-lapse video recorder. Approximately 9 hr of activity were recorded on a 1-hr videotape, with the machine taking  $6\frac{2}{3}$  pictures per second during this interval. The video recorder was turned on between 9:30 and 10:30 AM and allowed to run to the end of the tape (9 h). Between Days 54 and 180, 16 tapes were made of each animal. Tapes were analyzed by recording the behavior that occurred within epochs of 3 ft, as determined by the counting device on the recorder. When played back, the tape consisted of 873 ft or 291 epochs, each epoch lasting 110 sec.

*Procedures after isolation.* At 6 months of age, the isolate and semi-isolate animals were introduced to each other in a  $6.1 \times 1.8$ -m arena separated into two sections by a wire mesh partition with a guillotine door. The arena had chain-link fencing on each end and plywood sides. Animals were placed on either side of the partition for 1 hr with no humans present. The partition was then raised, and the animals were allowed to interact freely for the remainder of the day and night (ap-

proximately 22 h). The first 9 hr of behavior were recorded on a time-lapse videotape recorder. Pairings were done in a round-robin in the order indicated in Table 2.

After the round-robin pairings, all the animals were placed together in the arena with the door between the two halves left open, and their interactions were filmed as described above for 1 week. The animals were then introduced singly in the same arena to an adult female wolf and allowed to remain with her for 1 day. The adult wolf used was socialized to human handling and to other animals and was known to be highly consistent in her reactions to young animals, typically behaving with indifference or mild hostility toward them. The test animals were then placed as a group in the arena with the adult female, and the behavior was recorded with the time-lapse videotape recorder described above for 3 days.

Each of two observers recorded the behavior of one animal on a 20-channel event recorder. Tests for observer reliability were made periodically for each of the paired encounters by having both observers independently record the behavior of the same animal. The event recorder rolls were then scored by dividing them into segments representing 15 min of elapsed time. The criterion for counting an instance of behavior is that it occurs at least once in a 10-sec epoch. This criterion allows behaviors lasting long periods of time (e.g., jaw wrestling, chasing) to be given more weight if they last beyond 10 sec.

Data from the group sessions were sampled. Sections from the beginning and end of the videotape, constituting approximately 2 hr of running time, were viewed and described with both viewers recording the behavior of the animals during discrete episodes. The onset and offset of the episode were determined by the viewers with the purpose of including significant behaviors in which the animals involved were clearly visible. Only those aspects of the animal's behavior that were common to the descriptions of the two independent observers were used for analysis, and a behavioral profile was constructed on this basis. In addition, the percent agreement between observers was calculated.

Data on pack-reared wolf cubs were obtained from the records of over 300 h of observation by six observers of a wolf litter left to develop with their parents in a population field from 25 days of age to almost 8 months

TABLE 2  
Order of First Round-Robin Pairings

Day 209	M2-Fem3	Day 214	Fem1-Fem3
Day 210	M2-M3	Day 215	Fem1-M3
Day 211	M2-Fem1	Day 216	M3-Fem3
Day 212	M2-Fem2	Day 217	M3-Fem2
Day 213	Fem1-Fem2	Day 218	Fem3-Fem2

of age. Observers sat in an observation hut and used a tape recorder and paper-and-pencil methods to give a running account of the proceedings. Samples of complex interactions were either videotaped or filmed. The wolf pack at this time consisted of six cubs, two adults (their parents), and five juveniles between 1 and 2 years of age from previous litters.

*Behaviors recorded after isolation.* The following is a list of nonvocal behaviors used in the analysis of the paired and group encounters.

1. *Approach.* One animal approaches another. This category was not used during play bouts in which repeated approaches were made but only to record the initiation of an interaction.

2. *Nose mouth.*

3. *Nose rear.*

4. *Nose inguinal region.*

5. *Standing over.* This was recorded if one animal was standing next to or directly over another animal who was lying down, whether or not there was any response from the other animal. Typically, one animal would simply approach another animal and stand near the other animal, followed by walking off or the initiation of some other interaction.

6. *Rubbing muzzles.* This was recorded when the sides of the muzzles were touched together.

7. *Bite neck.*

8. *Bite other part of body.*

9. *Feet on.* Recorded when one animal put its feet on the other animal's back. A separate category was made for putting feet on from the rear.

10. *Jump at.* During play fighting, one animal would jump at another, usually also attempting to bite it at the same time.

11. *Body block.* One animal turns its hip toward another animal and slams its body into the other.

12. *Snap.* The animal opens and closes its jaws and directs its bite at another animal without actually touching the other. This behavior was usually used defensively to ward off the advances of other animals.

13. *Jaw wrestle.* Animals entwine jaws or attempt to do so, often with the muzzles pointing up.

14. *Chase.*

15. *Play invitation.* The front part of the body is lowered, with tail wagging often observed. Typically, the animal will then run off, thereby initiating chasing, or initiate some form of wrestling.

16. *Pinning.* One animal grabs the other by the neck and holds it down.

17. *Following.*

18. *Submarine.* One animal puts its head under the other animal's belly and rises up.

19. *Pawing*.

20. *Romp*. An animal runs back and forth, tail waving, bounding, and sometimes jumping at the walls. Other animals sometimes join in this behavior, leading to bouts of chasing, but often only one animal is involved.

21. *Retreat*. The animal pulls its head back or its entire body back as the other animal snaps at or jumps at it.

22. *Chin in*. This submissive posture is scored when the animal pulls its chin in toward the body, often pulling the gums back horizontally (submissive grin).

23. *Regurgitation*.

24. *Grovel*. This submissive approach behavior was scored when the animal approached another animal with the shoulder touching or almost touching the ground.

25. *Solicit regurgitation*. This behavior involves nipping and pushing at the mouth and was only seen in the young animals interacting with the adult female.

26. *Stalk*. The animal lies or crouches rigidly, intently observing another animal, sometimes wagging the tail. The animal often then charges at the other animal.

27. *Threat*. Teeth are bared, often followed by snapping.

## RESULTS

*Data recorded during isolation.* Tables 3 and 4 show results of tabulating self-directed behaviors and behaviors involving inanimate objects for 16 videotapes of M2, M3, Fem1, and Fem2 and 11 tapes for M1. Self-directed behavior is defined as including grooming the front leg, grooming the rear leg, self-scratching, chasing the tail, and biting the rear leg. Behavior toward inanimate objects includes interactions with the rope, food dishes, can or bucket, pawing the water, playing with a bone (not chewing), and eating shavings or dry food. A one-way analysis of variance was performed on the data and a highly significant difference was found between the isolated males and the paired females ( $p < .01$ ) for both classes of behavior.

Although the differences could conceivably be due to sex differences, they are most reasonably explained as being due to the conditions of rearing, since data from the comparison litter reared with adults and juveniles observed over the first 8 months of life for over 300 hr revealed only two instances of tail chasing with a group consisting of six pups during this period. These data point to the conclusion that singly isolated animals will engage in abnormal levels of self-directed behavior and behavior with inanimate objects.

*Behavior after isolation.* The percent agreement between independent observers, calculated by dividing the total number of agreements by the

TABLE 3  
Frequencies of Self-Directed Behavior in 16 Consecutive 9-Hr Time-Lapse Recordings

	Tape:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
M1		50	57	44	10	—	—	18	57	26	40	26	19	—	—	—	—
M2		83	37	16	74	28	31	35	18	41	12	41	14	22	7	4	15
M3		64	24	19	21	21	34	23	39	15	38	49	16	26	59	41	29
Fem1		15	11	6	9	3	7	4	2	5	7	1	0	8	5	6	7
Fem2		10	1	3	7	4	3	10	1	1	3	5	0	7	3	2	6

TABLE 4  
Frequencies of Behavior Directed toward Inanimate Objects (as Defined in Text) in 16 Consecutive 9-Hr Time-Lapse Recordings\*

Tape:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
M1	18	64	16	1	—	—	20	27	8	7	8	19	—	—	—	—
M2	22	61	72	44	12	17	0	21	21	5	21	0	5	22	2	4
M3	0	17	20	20	4	19	24	23	49	7	15	28	7	16	0	1
Fem1	0	10	0	13	17	6	8	2	0	1	0	0	0	3	0	0
Fem2	4	4	0	6	5	3	5	1	0	2	0	0	0	2	0	0

\*M1 died prior to Tape 13 and was sick during Tapes 5 and 6.

number of agreements plus disagreements, ranged from 0.588 to 1.0 for the paired encounters, with only two behaviors showing reliabilities below 0.75 (Approach and Bite). For the group encounters, reliability ranged from 0.57 to 1.0, with only two behaviors having reliabilities below 0.75 (Approach and Snap).

Not all of the behaviors were seen immediately, but typically showed a pattern of gradual emergence during the paired encounters. For example, in the M3-M2 pairing (Table 5), nosing and approach behaviors predominate for the first 9 epochs (2½ hr). In the 10th epoch, instances of snapping, biting, putting feet on, and jumping at are recorded. It is only after 5 hr that really high levels of jumping at, biting, and snapping occur. Jaw wrestling and chasing are seen only after 3 hr; play invitation, after 5 hr; and pinning, after 6 hr.

It should be noted that high levels of fear behavior, involving tail tucking, running back and forth, drooling, and jumping up on the walls, occurred in all the animals except M3 at the beginning of the pairings (and group encounters) when humans were present. These behaviors subsided after the humans left. Fear of the testing arena was also shown by all animals, despite the fact that it was a near duplicate of the quarters in which the animals had been reared. For example, in the first pairing for M3 (that with M2), M3 exhibited a marked delay in crossing to the other side of the testing arena and scanned the walls and ceiling repeatedly, while crouching with his tail tucked. It was only after several hours and prolonged sniffing that he very cautiously entered the side opposite the one he started in.

The pairing of M2 with Fem3, the first pairing for both animals, resulted in no interaction for 1¼ hr, after which nosing and approach behaviors predominated. M2, the complete isolate, clearly initiated these behaviors. Jaw wrestling and snapping first appeared at 2 hr, chasing at 7 hr, jumping at, at 3½ hr, romping at 4¼ hr, and play invitation at 11 hr. The pairing between Fem1 and Fem3 (Table 6) resulted in considerable behavior in the first several epochs, including instances of jaw wrestling and biting. Nevertheless, it was not until 3½ hr that high levels of jaw wrestling occurred, as well as play invitation and jumping at. The one instance of chasing occurred at 3¾ hr. The pairing between M2 and Fem2 (Table 7) also resulted in considerable approaching and nosing behavior in the first hour. However, it was not until 3½ hr that jaw wrestling and jumping at occurred, with high levels of jaw wrestling occurring after 5 hr and of chasing at 6 hr. In the Fem3-Fem2 pairing, high levels of nosing, biting, and snapping occurred early, and jaw wrestling occurred within 2½ hr, as did threatening. Chasing was first seen at 4¼ hr, and high levels of jaw wrestling, chasing, and putting the feet on occurred at that time.

In the M2-Fem1 pairing, considerable interaction occurred during the first hour, including snapping, threatening, approaching, nosing, and paw-







TABLE 8

Totals of Various Behaviors Occurring during Group Encounters with the Pups Only

Behavior	M2	M3	Fem1	Fem2	Fem3
Bite neck	M3 0	M2 38	M2 0	M2 0	M2 3
	Fem1 0	Fem1 12	M3 0	M3 0	M3 11
	Fem2 0	Fem2 4	Fem2 2	Fem1 0	Fem1 3
	Fem3 0	Fem3 24	Fem3 0	Fem3 0	Fem2 0
Pin	M3 0	M2 29	M2 0	M2 0	M2 1
	Fem1 0	Fem1 9	M3 0	M3 0	M3 0
	Fem2 0	Fem2 2	Fem2 0	Fem1 0	Fem1 0
	Fem3 0	Fem3 13	Fem3 0	Fem3 0	Fem2 0
Bite (not neck)	M3 4	M2 6	M2 5	M2 0	M2 0
	Fem1 3	Fem1 3	M3 1	M3 1	M3 3
	Fem2 0	Fem2 1	Fem2 0	Fem1 2	Fem1 2
	Fem3 0	Fem3 1	Fem3 0	Fem3 0	Fem2 0
Nose	M3 4	M2 2	M2 2	M2 0	M2 2
	Fem1 4	Fem1 1	M3 5	M3 0	M3 4
	Fem2 0	Fem2 1	Fem2 1	Fem1 0	Fem1 0
	Fem3 3	Fem3 4	Fem3 2	Fem3 1	Fem2 0
Threat	M3 0	M2 1	M2 3	M2 0	M2 0
	Fem1 3	Fem1 0	M3 0	M3 0	M3 0
	Fem2 0	Fem2 0	Fem2 0	Fem1 0	Fem1 0
	Fem3 0	Fem3 0	Fem3 0	Fem3 0	Fem2 0
Snap at	M3 6	M2 3	M2 6	M2 0	M2 6
	Fem1 4	Fem1 3	M3 9	M3 4	M3 16
	Fem2 0	Fem2 2	Fem2 0	Fem1 0	Fem1 0
	Fem3 6	Fem3 5	Fem3 0	Fem3 0	Fem2 0
Jaw wrestle	M3 29	M2 32	M2 15	M2 3	M2 11
	Fem1 12	Fem1 13	M3 10	M3 9	M3 16
	Fem2 3	Fem2 7	Fem2 7	Fem1 6	Fem1 6
	Fem3 13	Fem3 35	Fem3 11	Fem3 10	Fem2 4
Put feet on	M3 4	M2 0	M2 4	M2 0	M2 1
	Fem1 1	Fem1 0	M3 2	M3 0	M3 0
	Fem2 0	Fem2 0	Fem2 2	Fem1 0	Fem1 0
	Fem3 0	Fem3 3	Fem3 0	Fem3 0	Fem2 0
Lick mouth	M3 1	M2 1	M2 2	M2 0	M2 0
	Fem1 0	Fem1 0	M3 0	M3 0	M3 0
	Fem2 0	Fem2 0	Fem2 0	Fem1 0	Fem1 0
	Fem3 0	Fem3 0	Fem3 1	Fem3 0	Fem2 6
Paw at	M3 2	M2 0	M2 0	M2 0	M2 0
	Fem1 0	Fem1 0	M3 0	M3 0	M3 0
	Fem2 0	Fem2 0	Fem2 0	Fem1 0	Fem1 0
	Fem3 1	Fem3 1	Fem3 0	Fem3 0	Fem2 0
Jump at	M3 0	M2 0	M2 0	M2 0	M2 0
	Fem1 0	Fem1 0	M3 0	M3 0	M3 8

TABLE 8

(continued)

Behavior	M2	M3	Fem1	Fem2	Fem3
	Fem2 0	Fem2 0	Fem2 0	Fem1 0	Fem1 4
	Fem3 1	Fem3 5	Fem3 0	Fem3 0	Fem2 1
Chase	M3 2	M2 8	M2 0	M2 0	M2 0
	Fem1 3	Fem1 5	M3 0	M3 0	M3 0
	Fem2 0	Fem2 0	Fem2 1	Fem1 0	Fem1 1
	Fem3 0	Fem3 3	Fem3 0	Fem3 0	Fem2 0
Stand over	M3 3	M2 4	M2 2	M2 1	M2 1
	Fem1 1	Fem1 0	M3 1	M3 1	M3 0
	Fem2 0	Fem2 1	Fem2 0	Fem1 0	Fem1 1
	Fem3 0	Fem3 1	Fem3 0	Fem3 1	Fem2 0
Submarine	M3 0	M2 0	M2 0	M2 0	M2 0
	Fem1 0	Fem1 0	M3 0	M3 0	M3 0
	Fem2 1	Fem2 0	Fem2 0	Fem1 0	Fem1 0
	Fem3 0	Fem3 0	Fem3 0	Fem3 0	Fem2 0
Group chase	1. All except Fem2 chase M3.				
	2. Fem1 runs off; M2 and M3 chase.				
	3. All chase Fem2.				
	4. All chase Fem2.				
	5. All chase M2, who has a bone.				
	6. All chase M3.				
	7. All chase M3.				
	8. All chase M3.				
	9. All chase M3.				
	10. All chase M3.				
	11. All chase M3.				
	12. All chase Fem1.				
	13. All chase Fem1.				
	14. All chase Fem1.				
	15. M2, Fem1, and Fem3 chase M3.				
	16. M2 and M3 chase Fem1.				
	17. M2 and M3 chase Fem1.				

<sup>a</sup> Numbers at right indicate the number of times the behavior occurred. Animal at top performs the behavior indicated at left to animal listed in the table.

complete set of round-robins. As in the paired encounters, M3 was a very dominant animal. Fem3 was the beta animal and was the only one to bite M3 on the neck and attempt to pin him. Fem1 did not jump at the other animals, but put her feet on the backs of others five times and engaged in much chasing and being chased.

There is good evidence here for a social structure. There was a clear hierarchy of dominance-aggressiveness within the group, with M3 dominant to the others, followed by Fem3, Fem2, Fem1, and M2, in that order. The animals engaged in many behaviors as a group. Especially

relevant are the group running and chasing sequences. These behaviors were very common in the pack-reared animals at this age and occurred in the present experiment despite very circumscribed spatial limitations. Fem2, who was recorded on the list of behaviors as interacting the least, was recorded as being a member of such a group on 16 occasions on Day 225. As a result, the list of behaviors in Table 8, which mainly indicates dyadic interactions within the group, does not indicate the large number of interacting animals on many occasions.

*Group behavior with the adult female.* The behavior of the pups with the adult female when all were grouped together is presented in Table 9. As in the individual encounters, the pups, with the exception of M3, behaved submissively and solicited regurgitation from the adult female.

TABLE 9  
Social Interactions of the Experimental Subjects with the Adult Female (T)

Behavior	M2	M3	Fem1	Fem2	Fem3	T*
Snap at						M2 (14) M3 (19) Fem1 (5) Fem2 (3) Fem3 (3)
Bite muzzle or head						M2 (4) M3 (1) Fem1 (2) Fem2 (1) Fem3
Bite neck						M2 (2) M3 (0) Fem1 (1) Fem2 (0) Fem3 (0)
Pin		T (1)				M2 (3) M3 (0) Fem1 (4) Fem2 (0) Fem3 (0)
Solicit regurgitation	>10	0	>10	>10	>10	
Regurgitate						2
Paw at adult	10	0	3	1		
Lie flat when approached by adult	5	0	2	1	1	
Crouch when approached by adult	4	0	2	1	2	
Threaten pups						8

\* Numbers in parentheses indicate number of times behavior occurred.

This occurred especially on the first day of the group encounter, and it occurred within the first hour. The adult snapped at the pups, threatened them, bit them on the muzzle, head, and neck, and pinned Fem1 and M2. She regurgitated twice on Day 239 and occasionally sniffed one of the pups. M3 did not behave submissively. On Day 237, he bit the adult's neck four times and once briefly held her down while holding the neck. He stood on her back once on Day 239. The adult bit M3 on the muzzle after emitting a brief threat following one of these episodes. After Day 237, M3 did not behave as aggressively, but never showed submissive behavior toward the adult and never solicited regurgitation.

The following behaviors were found in both the groups of isolated animals and pack-reared animals: face licking, putting feet on, standing over another animal, pinning another animal, biting another animal, putting chin over another animal, threatening another animal, pawing, chasing, jaw wrestling, or mouthing, and other wrestling. Play invitation, stalking, and body rubbing were noted in the paired encounters, as well as a high incidence of sniffing the mouth, rear, and inguinal region.

Both groups solicited regurgitation from the female adult, were regurgitated to, and adopted standard submissive poses when approaching adults, including lying flat and submissive pawing along with the submissive grin (Fox, 1971b). Because the adult that was placed with the pups showed hostility toward them and did not adjust completely to her new surroundings during the period of the experiment, it was not possible to assess other differences of behavior between the isolate and the pack-reared animals with respect to the adult.

There are no major types of behavior that are missing from the deprived-environment animals after a brief period of social experience. There were, however, very large individual differences between the pups as noted.

## DISCUSSION

Our data demonstrate that, within the limits of our procedures, restricted rearing conditions, including isolation from conspecifics, result in exaggeration of the personality profiles exhibited at 4 weeks, but do not result in animals unable or unwilling to interact appropriately with conspecifics, animals that are extraordinarily violent, socially incompetent, or ostracized from the group. A notable difference between normal pack-reared animals and our isolates and semi-isolates is that pinning occurred much more frequently in the latter when they were placed together. This, however, could as well have happened among normally reared strange cubs encountering each other initially as strangers. As mentioned, a dominance order and other aspects of typical social interactions and organization developed in the experimental animals, and, in general, the results demonstrate that the potential for normal social be-

havior in wolves, in most instances, is well buffered from prepubertal environmental effects.

1. After the end of the restricted rearing, there was complete disappearance of the stereotyped tail-chasing and self-biting behaviors typical of M3 and M2 during isolation. Animals did not direct their attention to inanimate objects or groom themselves for long periods of time. The disappearance of tail chasing and self-biting is particularly significant since it was the gradual lessening of various self-directed behaviors that marked recovery in Suomi's isolate-reared monkeys (Suomi & Harlow 1972). Indeed, the immediate disappearance of these behaviors upon reunion with the other restricted wolves contrasts with the tendency for continued stereotyped behavior exhibited at low levels by Suomi's monkeys at age 2½ yr, a full 2 yr after therapy was initiated (Cummins & Suomi, 1976).

2. Although there were clear individual differences in the pattern of behaviors and the types of behaviors observed, there were no behaviors missing in the isolate-reared wolves after the relatively brief period of socialization. Although Fem3 tended not to interact in the early stages of her social encounters, her interactions increased significantly with time and experience.

3. There was clear evidence of a normal social structure among the animals. M3 asserted his dominance over the others, and Fem3 clearly competed with him for dominance. M2 was the most submissive animal with Fem1 and Fem2 intermediate and with Fem2 dominant to Fem1. This social structure was apparent on the first day of the group-house condition and was achieved without severe fighting in animals that had not been raised as a group.

4. The animals, with the exception of M3, assumed appropriate submissive postures toward the adult female, solicited regurgitation, and were regurgitated to.

5. These data demonstrate that isolation-induced deficits in social behavior can be overcome using appropriate techniques. In addition to the induction of normal social behavior by these methods, the abnormal behaviors seen during isolation (stereotyped tail chasing and self-biting, social indifferences to other animals, bizarre or violent behavior, or extreme withdrawal) disappear.

There may be a threshold for minimal social stimulation, which, in rare instances (e.g., M1), is at a level that is incompatible with isolate rearing. Such a threshold could have a genetic set point.

The results are not directly comparable to the data for rhesus monkeys in an important way. Suomi, Harlow, and Novak (1974) interpret their successful therapy of isolate-reared monkeys in terms of a learning deficit. Suomi views these results as consistent with the view that social behavior in monkeys develops during a sensitive period and that isolation

during this period results in an animal that must receive intensive therapy during a postisolation period in which he learns the appropriate social behavior.

In the present case, the wolves exhibited substantially normal behavior within hours of exposure to social experience with the other restricted animals, and without the need of "therapy" from normally reared wolves or from chronologically younger "pacemakers." The deprived animals, when exposed to each other, were their own "therapists." They may be considered comparable to younger "pacemakers" in the sense that they were all deprived of normal social experience.

It is known that wolf cubs reared without adult tutors come to perform all the social behaviors and social roles of a normally reared pack (Rabb, Woolpy, & Ginsburg, 1967). These descriptions closely parallel the independent observations of Zimen (1981, see especially Chapter 9). This indicates that the propensity for social behavior in the wolf has a strongly genetic basis. The present results argue that this genetically based behavior is well buffered from environmental effects in the sense that these can be quickly overcome under appropriate conditions.

Theoretically, the results of Suomi and Harlow (1972) are interpretable within a model that stresses interaction between early experience and later environments. Such a model has been spelled out by Samaroff (1975) and is essentially followed by Clarke and Clarke (1976), Kagan, Kearsley, and Zelaza (1978), and Thomas and Chess (1977). Early experience is not viewed as a main effect, immune to later environments, but as a continuous causal interchange between organism and environment, both of which are viewed as plastic during development. However, Samaroff also proposes a biologically based righting mechanism such that normal levels of functioning are attained despite deprived early environments or gross physiological insults. This view is also held by Clarke and Clarke (1976) and Kagan et al. (1978) and is consistent with much data on development in humans, including cognitive and social development in deprived early environments (Kagan & Klein, 1973; Koluchova, 1976) and reproductive casualty (Samaroff, 1975). Such a view is best construed as a genetically based system well buffered from adverse environmental effects in the sense that it can recover from these. All of these views are consistent with our hypothesis of a genetically based system that will return to its equilibrium point if provided with appropriate circumstances and that is well buffered from adverse environmental effects in the sense that it can recover from these as demonstrated in all of these studies, including our own.

A behavioral system is well buffered from environmental effects if, given a wide range of environmental conditions, a narrow range of phenotypic outcomes is produced. In such cases, selection is viewed as resulting in a system with little chance of major phenotypic variation. It is not surprising that a basic competence to interact with conspecifics

should comprise such a system, especially in a species where normal social behavior is known to have a strongly genetic base. Buffering is, of course, a relative concept. Although social isolation of rhesus monkeys for the first 6 months of life has devastating results, normal social behavior in these animals does result from surrogate-peer rearing (Novak, personal communication). These animals had no contact with adults and only 1-2 hr per day contact with conspecifics, but they constitute a normal breeding colony. Clearly, normal social behavior in these animals does not depend on a very narrow range of environmental conditions.

It is important to stress the difference between these two viewpoints regarding early experience, which, although broadly consistent with each other and often held by the same writers, really rely on quite different types of data and lead to radically different views of development. Both views deemphasize the unique and irreversible role of early experience, but for quite different reasons. The interactionist views early experience as potentially important, but as being subject to being overridden by later experience. Data supporting this position show that some later environment interacts with the early experience to the point of reversing a deficit induced by deprivation or by other departures from normal rearing. A paradigm of such an effect would be the intensive therapy given by Suomi and Harlow (1972) and Novak (1979) to the isolate-reared monkeys. Our view is further supported by these results, which show that adverse early experience does not necessarily have long-range consequences, even without an especially therapeutic later environment. In the absence of a positively deleterious environment, development returns via a genetically based righting mechanism to normal pathways. The former view emphasizes the importance of the later environment; the latter emphasizes the importance of buffering against the effects of early environments even without intensive therapy. As Kagan and Klein (1973) phrase it, despite early adversity, "nature will win in the end." In our view, "nature" refers to the genetic equilibrium point typical for the species.

Despite the genetic buffering of the normative phenotype that occurs for species-typical adaptive behaviors, aberrant equilibrium points also occur, particularly under relaxed selection pressures or during times of rapid evolutionary change. Laboratory rats and mice, as well as domestic animals, may be examples of this, and results obtained from them would in this view, not apply to natural species. In the latter, genetic buffering for behavioral endpoints would be expected primarily in those species with well-developed social behavior, including our own, where a shift in genetic equilibrium points could result in familial psychoses.

Clearly, the present data are more congruent with the tendency to view certain aspects of development as well buffered from environmental effects. The postisolation treatment did not constitute intensive therapy.

Animals were merely placed together in a small arena. Normal prepubertal behavior was observed within hours of pairing and there was immediate cessation of stereotypic self-directed behavior. Nor is there evidence in these data for as circumscribed a sensitive period for social behavior in the wolf as there is in the monkey, based on the data of Suomi and Harlow.

These results are also congruent with the canid isolation literature reviewed above. Isolation in canids is viewed as not affecting competence nor the desire to interact socially; species-typical behavior is present, and stereotyped behavior is absent. The somewhat exaggerated personality profiles of M2 and M3 in this experiment are consistent with the view that isolation affects dominance-submission within the group, as was also found by Fuller (1967), Fuller and Clark (1968), Fisher (1955), and Melzack and Thompson (1956). Thus, the canid data do not argue that social behavior in these animals is completely immune from the effects of restricted socialization during development.

In conclusion, our data indicate that the development of social behavior in wolves is well buffered from environmental effects, including isolation from conspecifics, isolation from conspecifics with human socialization, and paired isolation. The data are considered within the context of a growing literature suggesting that certain basic cognitive and social competencies will be shown by an organism despite a wide range of environmental circumstances.

## REFERENCES

- Clarke, A. D. B., & Clarke, A. M. (1976). *Early Experience: Myth and Evidence*. New York: Free Press.
- Cummins, M. S., & Suomi, S. J. (1976). Long-term effects of social rehabilitation in rhesus monkeys. *Primates*, 17, 43-52.
- Eibl-Eibesfeldt, I. (1975). *Ethology: The Biology of Behavior* (2nd ed.). New York: Holt, Rinehart and Winston.
- Fisher, A. E. (1955). The effects of differential early treatment on the social and exploratory behavior of puppies. Ph.D. dissertation, Pennsylvania State University.
- Fox, M. L. (1971). *Integrative Development of Brain and Behavior in the Dog*. Chicago: Univ. of Chicago Press. (a)
- Fox, M. L. (1971). *Behaviour of Wolves, Dogs and Related Canids*. New York: Harper & Row. (b)
- Fuller, J. L. (1967). Experiential stress and later behavior: Emergence stress is postulated as the basis for behavioral deficits seen in dogs following isolation. *Science*, 158, 1645-1652.
- Fuller, J. L., & Clark, L. D. (1966). Effects of rearing with specific stimuli on post-isolation behavior of dogs. *Journal of Comparative & Physiological Psychology*, 61, 258-263. (a)
- Fuller, J. L., & Clark, L. D. (1966). Genetic and treatment factors underlying the post-isolation syndrome in dogs. *Journal of Comparative and Physiological Psychology*, 61, 251-257. (b)
- Fuller, J. L., & Clark, L. D. (1968). Genotype and behavioral vulnerability to isolation in dogs. *Journal of Comparative and Physiological Psychology*, 66, 151-156.

- Ginsburg, B. E. (1976). Evolution of communication patterns in animals. In E. C. Simmel and M. E. Hahn (Eds.), *Communicative Behavior and Evolution*, pp. 59-79. New York: Academic Press.
- Harlow, H. F., Dodsworth, R. O., & Harlow, M. K. (1965). Total social isolation in monkeys. *Proceedings of the National Academy of Sciences*, *54*, 90-96.
- Kagan, J., Kearsley, R., & Zelaza, P. (1978). *Infancy*. Cambridge, Mass.: Harvard Univ. Press.
- Kagan, J., & Klein, R. (1973). Cross cultural perspectives in early development. *American Psychologist*, *28*, 947-961.
- Koluchova, J. (1976). Further development of turns after severe deprivation. In A. M. Clarke and A. D. B. Clarke (Eds.), *Early Experience: Myth and Evidence*. New York: Free Press.
- Lorenz, K. (1965). *Evolution and Modification of Behavior*. Chicago: Univ. of Chicago Press.
- Melzack, R., & Thompson, W. R. (1956). The effects of early experience on social behavior. *Canadian Journal of Psychology*, *10*, 82-92.
- Mineka, S., & Suomi, S. (1978). Social separation in monkeys. *Psychological Bulletin*, *85*, 1376-1400.
- Novak, M. A. (1979). Social recovery of monkeys isolated for the first year of life: II. Long term assessment. *Developmental Psychology*, *15*, 50-61.
- Rabb, G. B., Woolpy, J., & Ginsburg, B. E. (1967). Social relationships in a captive wolf pack. *American Zoologist*, *7*, 305-311.
- Samaroff, A. J. (1975). Early influences on development: Fact or fancy? *Merrill-Palmer Quarterly*, *20*, 275-301.
- Scott, J. P., & Fuller, J. L. (1965). *Genetics and the Social Behavior of the Dog*. Chicago: Univ. of Chicago Press.
- Spencer-Booth, Y., & Hinde, R. A. (1971). Effects of brief separations from mothers during infancy on behavior of rhesus monkeys 6-24 months later. *Journal of Child Psychology and Psychiatry*, *12*, 157-172.
- Stevenson-Hinde, J., Zunz, M., & Stillwell-Barnes, R. (1980). Behavior of one-year old rhesus monkeys in a strange situation. *Animal Behaviour*, *28*, 266-277.
- Suomi, S. J., & Harlow, H. F. (1972). Social rehabilitation of isolate reared monkeys. *Developmental Psychology*, *6*, 487-496.
- Suomi, S. J., Collins, M. C., & Harlow, H. F. (1973). Effects of permanent separation from mother on infant monkeys. *Developmental Psychobiology*, *9*, 376-384.
- Suomi, S. J., Harlow, H. F., & Novak, M. A. (1974). Reversal of social deficits produced by isolation rearing in monkeys. *Journal of Human Evolution*, *3*, 527-534.
- Thomas, A., & Chess, S. (1977). *Temperament and Development*. New York: Brunner/Mazel.
- Thompson, W. R., & Heron, W. (1954). Exploratory behavior in normal and restricted dogs. *Journal of Comparative and Physiological Psychology*, *47*, 77-82.
- Zimen, E. (1981). *The Wolf, A Species in Danger*. (Translated from *Der Wolf: Mythos und Verhalten*, Vienna, Munich: Meyster Verlag, 1978). New York: Delacorte.