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FEMALE AGGRESSION IN ALBINO ICR MICE: DEVELOPMENT, SOCIAL EXPERIENCE, AND THE EFFECTS OF SELECTIVE BREEDING *(MUS MUSCULUS)*

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ABSTRACT: Social experience has been shown to mask or eliminate heritable effects on aggressive behavior in male mice. This work assesses the impact of social experience in females from lines of mice selectively bred for differential male aggressiveness. These results confirm the earlier report of cross-sex similarity in aggressive behavior after selection directed only at male behaviors (Hood & Cairns, 1988). Repeated test experience increased aggressive behavior of S_0 females. In addition, a genetic-developmental interaction was found, with enhanced aggressiveness in mature vs. young high-aggressive line females. Repeated test experience in 4 daily trials with mature S_{15} females obscured the clear line differences in attack frequency obtained on the first trial. In particular, a few highly aggressive individuals emerged among the group-reared low-aggressive line females. Isolation housing did not alter female aggressiveness. These findings are discussed in regard to conceptions of genetic-experiential-developmental interactions, and the role of female social behavior in microevolutionary processes.

How genetic and experiential factors influencing aggressive behavior are fused in ontogeny has been the focus of recent investigations of mice selectively bred for differential male aggressiveness (Cairns, MacCombie & Hood, 1983). A central concern in this analysis has been the role of contextual and developmental factors in sex and line differentiation. Previous research demonstrates that, when sex-appropriate developmental and contextual assessment conditions are employed, the behavioral phenotype of males and females shows similar responsiveness to selection pressure based only on the behavior of males (Hood & Cairns, 1988). The present research extends those findings to determine whether female line differentiation is maintained after continued selective breeding based on male behavior, and to assess the influence of social experience on the development of line differences in female aggressive behavior.

The developmental impact of social experience in male aggressiveness has been demonstrated in these lines of mice. Isolated male mice

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show heightened aggressiveness at puberty (for example, Cairns, Hood, & Midlam, 1985; Cairns & Nakelski, 1971), and either repeated testing (Cairns, MacCombie, & Hood, 1983) or group rearing (Cairns & Hood, 1983; Hood & Cairns, in press; Lagerspetz & Lagerspetz, 1971) is sufficient to mask or eliminate selective breeding effects on intermale aggressiveness.

The evidence on social experience effects in female aggressiveness derives from research on a variety of lines and strains of mice, and the results are not so consistent. In wild-type mice selectively bred for differential female aggressiveness (Hyde & Sawyer, 1980), isolation-reared females score higher than group-reared females on a variety of social-investigatory measures, and line differences are maintained in both isolation and group-rearing conditions. (Also see Weltman, Sackler, Schwartz, & Owens, 1968). However, studies by Gray (1979, Gray, Whitsett & Ziesenis, 1978) indicate that in ICR female mice, isolation housing decreases aggressive behavior. Two investigations of selective breeding effects in mice failed to show any attacks at all by isolation-reared females (Cairns, MacCombie, & Hood 1983; Lagerspetz & Lagerspetz, 1975).

To clarify the developmental-genetic analysis of female aggressiveness, pilot work was implemented with the S_5 generation of selectively bred ICR mice. Thirteen females from the low-aggressive line and 17 from the high-aggressive line were reared in isolation and tested at maturity, age 200 days, in a dyadic test. Not one of the females attacked their same-age, same-sex test partner. In the S_6 generation, females were reared in small groups and tested longitudinally in the home cage with a same-age, same-sex intruder at seven points in the life-span. In this procedure, females from the high-aggressive line exhibited vigorous and repeated attacks against the intruder, in tests at maturity (Hood & Cairns, 1988). The comparison of these two outcomes suggests that females will attack and will show line differentiation, but only when they are tested at maturity, after being reared in a social context. The implication that female aggressiveness increases at midlife suggests that females show a developmental pattern rather unlike the male pattern of increased aggression at puberty. However, inferences about sex-related differences in the developmental function of aggressive behavior are limited by the experimental design employed in this work. Necessarily, the effects of maturation and the effects of test experience are confounded in the longitudinal design.

The research presented in this article is designed to separate maturation and experience effects by comparing same-age naive and longitudinal groups of selectively-bred females, tested at two points in development (Experiment I), and by testing mature females on 4 successive days (Experiment II). In the short-term longitudinal design of Experiment II, the effects of test experience are independent of age. The ubiquity of genotype-environment interaction is also examined in

Experiment II: the effects of a social rearing context on female aggression are assessed by comparing isolation-reared and group-reared females from the three male-selected lines, high-aggressive, low-aggressive, and control. By testing females from the 6th and the 15th generations of selective breeding, the generality of the previous findings of cross-sex similarity in response to selection (Hood & Cairns, 1988) will be evaluated in advanced generations.

EXPERIMENT I

Effects of Test Experience in Group-Reared Young and Mature Females from Selectively Bred Lines

This work assess the development of female aggressive behavior in three social contexts: one which maximizes social experience with dissimilar conspecifics by housing animals in genetically diverse groups and introducing strange females to the group at intervals; one which offers undisturbed social cohabitation with genetically diverse conspecifics; and one in which genetically similar females co-reside without disturbance. The comparison of genetically diverse and genetically uniform social contexts was designed to reveal genotype-environment interaction in regard to social structure in small groups. For example, we have observed in males that long-term housing with a high-aggressive line male may stimulate uncharacteristically intense aggressive retaliation by low-aggressive line males (Hood & Cairns, in press). Social processes among females may operate in a parallel, opposite, or unrelated manner.

Animals

Females (N = 270) from outbred albino ICR (Institute for Cancer Research) stock in the sixth generation of a selective breeding program at the University of North Carolina at Chapel Hill to establish high-aggressive, low-aggressive, and control lines of mice (Cairns, MacCombie, & Hood, 1983) were studied. In the bidirectional selective breeding procedure, male aggressiveness was assessed in each generation in standard 10-minute dyadic tests at 45 (± 2) days of age, after males had been housed alone since weaning (day 21). Males most likely to attack were mated with sisters of other high-aggressive males to produce the high-aggressive line in each generation, and males with no aggressive behavior were mated with sisters of other nonaggressive males to produce the low-aggressive line. The control line was bred from non-selected animals, derived from the same foundation stock. Line differentiation was rapid and distinct by the S_4 generation. Although female

aggressiveness was not considered in selective breeding, the selection of males produced changes in female aggressiveness that were essentially parallel and equal in magnitude to changes in male aggressiveness, when sex-appropriate test were employed (Hood & Cairns, 1988).

Housing and Rearing. Females were reared in litters of 10 or fewer pups, 5 males and 5 females, culled at day 3 after birth. They were randomly assigned at weaning (day 21) to one of two group-rearing conditions: genetically similar groups with three group members from the same line, or genetically heterogeneous group with three group members from different lines. In each condition, females were housed in standard mouse compartments, 28 x 18 x 13 cm. with two other same-age females, and all were dye-marked for individual identification. 261 females were assigned to 87 groups, 53 same-line groups (20 from the high-aggressive line, 20 from the low aggressive line, 13 from the control line), and 37 different line groups, each group containing one female from each of the three lines.

Test partners were 103 same-age, naive ICR females from unselected stock, reared in groups of 3 to 5 females.

Water and lab chow were continuously available, and all groups were maintained in the same colony room, with a 12:12 reversed light cycle, and constant temperature (22° C ± 2). Cages were changed weekly, except during the week before behavior assessments.

Test Procedures. Groups of females were tested for aggressive behavior in 10-minute intruder trials. During the dark portion of the photoperiod, at least 1 hour after dark onset, the subjects' cage was placed on an observation table in the colony room, under dim red illumination, with water bottle and food removed and wire top in place. After a 3-minute pause, a novel same-age ICR female was placed into the group's home cage. Attacks by each cage resident were coded by an observer, who was blind with regard to the line of the subjects. The coding method used in this series is a continuous time-sampling procedure; attack frequency is the number of 5-second intervals of the 10-minute trial, in which an attack occurred, by a particular animal. Attacks were coded only when a subject forcefully pounced upon a conspecific with biting and wrestling. Other aggressive behaviors, such as bites, feints (lateral display) and lunges (striking with the forepaws) were not included in these scores. Interrater reliability was high (r = .95 to .98). If no attack occurred, the maximum latency score was assigned (600 sec.). After the 10-minute observation period, the intruder was removed, weighed, and placed into a holding case.

Different-line groups were assigned to one of three test schedules. Sixteen groups were tested in a longitudinal series at days 30, 46, 90, 210, 270, and 500 (Hood & Cairns, 1988). Here we report the day 90 results for

16 groups, and day 270 test results for the 13 longitudinal groups that were intact at that age. Ten naive groups were tested at day 90 only, and 11 naive groups were tested at day 270 only.

Same-line groups were tested at day 90 only (26 groups, 10 from the high-aggressive line, 6 from the control line, and 10 from the low-aggressive line), or at day 270 only (27 groups, 10 from the high-aggressive lines, 7 from the control line, and 10 from the low-aggressive line).

RESULTS

The influence of developmental stage and the manipulation of testing and rearing conditions on aggressive expression is conditioned by the genetic background of these female subjects. In a 3 x 3 x 2 (line by test by age) analysis of variance, selective breeding line and age interact in attack frequency ($F(2,294) = 3.67$, $p = .03$) and latency ($F(2,294) = 3.55$, $p = .03$). Selective breeding line interacts with the factor of test condition for attack frequency ($F(4,294) = 2.34$, $p = .05$) and for latency ($F(4,294) = 3.38$, $p = .01$). Main effects of line and test condition are significant for frequency ($F(2,294) = 7.14$, $p < .001$ for line; $F(2,294) = 12.46$, $p = .0001$ for test) and for latency ($F(2,294) = 11.68$, $p < .001$ for line; $F(2,294) = 15.05$, $p < .001$ for test). The main effect of age is significant for attack frequency ($F(1,294) = 3.70$, $p = .05$), and not for latency ($F(1,294) = 2.74$, $p = .09$). The three-way interaction is not significant ($p < .25$).

In order to specify the ways in which line interacts with test condition and with age, two sets of post hoc pair-wise comparisons were made. For the line-by-test interaction, there was no prediction of direction of effects between same-line and different-line naive groups. Accordingly, Tukey's (HSD) method of comparing means was applied (Table 1): in every comparison but one, the high-aggressive line females are different from the other two lines, which are not different from each other. The exception is in naive different-line groups: line differences in frequency are not significant, although latency scores are.

The effect of test conditions distinguishes the longitudinal groups from the two naive groups, which are not different: this holds for each of the three lines, in frequency scores. In comparisons of latency scores, test conditions do not change control line scores, but for high- and low-aggressive line females, each of the three test conditions is different from the other two.

Does aggressive behavior change during development? Yes, but only for the high-aggressive line females. To test the hypothesis that female aggressiveness is increased at mid-life (Day 270) relative to the post-pubertal period (Day 90), Newman-Keuls method of comparing ordered

TABLE 1
Aggressive Behavior by S_6 Female Mice Reared with Same-Line or Different-Line Social Partners

Line	*Day 90*		*N Attacking* / *N Total* (%)	*Day 270*		*N Attacking* / *N Total* (%)
	Attack Frequency	*Attack Latency*		*Attack Frequency*	*Attack Latency*	
High Aggressive Line						
Same-line	0.27	591.67	1/30 (3%)	1.70	540.00	5/30 (17%)
Different-line (naive)	0.40	549.50	1/10 (10%)	0.91	493.64	2/11 (18%)
Different-line (longitudinal)	2.73	457.81	4/16 (25%)	7.92	307.69	7/13 (54%)
Control Line						
Same-line	0	600	0/18	0	600	0/21
Different-line (naive)	0	600	0/10	0	600	0/11
Different-line (longitudinal)	0.93	577.81	2/16 (12%)	2.08	556.54	1/13 (8%)
Low Aggressive Line						
Same-line	0	600	0/30	0	600	0/30
Different-line (naive)	0.30	554.00	0/10 (10%)	0	600	0/11
Different-line (longitudinal)	1.67	530.00	2/16 (12%)	0.50	549.58	2/13 (15%)

Note: Different-line groups each contain one female from each line. Longitudinal groups at Day 90 and Day 270 are the same groups, retested.

means was employed. High-aggressive-line females show increased aggressiveness at maturity, and females from the control- and low-aggressive line do not change over age. Comparisons of line differences at each age show the high-aggressive line to be different from the two other lines, which are not different from each other. The exception is in the comparisons of Day 90 females: high-line groups are different from control line, but not different from low-line groups, for frequency of attack.

In summary, the effects of breeding for differential male aggressiveness were found to alter female aggressive behavior in patterns that

reflect both genetic/developmental interdependencies (the line-by-age interaction), and genetic/experiential interdependencies (the line-by-test interaction). In each case, effects are in the predicted directions, with high-aggressive line females, older females, and previously tested females showing enhanced aggressive behavior.

There remains one confounding factor in these results: the day 90 and 270 assessments differ both in the number of trials administered to the longitudinal groups (3 vs. 5) and in the developmental stage of subjects at the time of comparison. Longitudinal subjects in the younger groups may have been too immature to fight, or alternatively, subjects in the older groups may have learned to fight in their 2 extra trials. To clarify the relative contribution of experiential and developmental factors, females in the S_{15} generation were repeatedly tested at age 200 days, in a short-term longitudinal design utilizing massed, or daily trials.

EXPERIMENT II

Effects of Test Experience in Group- and Isolation-Reared Females from Selectively Bred Lines

An alternative approach to longitudinal designs for understanding the influence of social experience is to eliminate contact with conspecifics by rearing animals in isolation. Pilot work with females of these lines suggests that isolation housing will abolish aggressiveness, although the same procedure augments aggressiveness in males from the high-aggressive line (Hood & Cairns, in press). This extreme manipulation produces a genotype-environment interaction in selectively bred males. The inconsistent outcomes of previous studies of isolation vs. group rearing effects on males aggressiveness may reflect unspecified genotype-environment interactions of the different species, strains, or lines of the subjects employed (Hood & Cairns, in press; also see Henderson, 1970; Lagerspetz & Lagerspetz, 1971; Levin, Vandenbergh, & Cole, 1974; Siegfried, Alleva, Oliverio, & Puglisi-Allegra, 1981; Valzelli, Bernasconi, & Gomba, 1974; in females, Scott, Bradt, & Collins, 1986). In another case, some species of mice show female aggressiveness to be less evident than male (Ebert, 1976), while female aggressiveness is equal to or greater than male aggressiveness in other species (Ayer & Whitsett, 1980; McCarty & Southwick, 1979). Similarly, the increase in aggressive behavior over repeated trials observed in isolation-reared male mice (Brain & Poole, 1974), but not in group-reared males (Goldsmith, Brain, & Benton, 1976; Svare & Leshner, 1973), may be genotype dependent (Bannerjee, 1971; Cairns, MacCombie, & Hood, 1983). This study applies massed repeated trials to isolation- and group-reared females, to

identify the components of social experience that may influence fighting in females.

Animals

Females, approximately 200 days old, (N = 130) from the 15th generation of selectively bred ICR mice (Cairns, MacCombie, & Hood, 1983) were studied. In the 11th generation, a parallel colony was established at The Pennsylvania State University from the NC lines. Subjects for this research were females from the 15th generation, bred at Penn State. The conditions for selection, rearing, testing, and coding have remained reasonably constant over the many generations of these selection experiments.

The test partners were 95 same-age females from a non-Swiss albino stock, retired breeders purchased from Harlan Sprague-Dawley, one month before the beginning of the test series.

Housing and Rearing. Subjects were reared in litters of 6-10 animals and weaned at 21 days, at which time females were randomly assigned to either isolation or group rearing. Isolated animals were housed singly in a standard opaque mouse compartment, 28 x 18 x 13 cm. The compartments were kept beside each other on several layers of a laboratory rack, exposing them to airborne odors and noises of the laboratory colony, though no physical contact with other members of their species was permitted following weaning. Thirty-one animals, 13 from the high-aggressive line, and 9 from each of the other lines, were assigned to isolation rearing.

The group rearing condition involved the placement of siblings of the same age and sex into a standard mouse cage, allowing for continuous conspecific contact and interaction. A group consisted of two to five females from the same line. Variation in group sizes reflects losses due to deaths with no additions to a group. Nine groups were formed from each of the three lines.

All animals were marked for individual identification with black dye (Clairol brand) three days prior to testing. Isolation and group rearing cages were maintained in the same colony room, and test partners were housed in the same colony room for six days prior to testing. The test partners were housed in small groups (3-5) in standard mouse cages in the colony room. Otherwise, conditions were identical to those in Experiment I.

Test Procedures. Group-reared and isolation-reared females from each of the three lines were tested daily on four successive days. All testing was conducted in the colony room during the dark portion of the photoperiod. In each 10-minute intruder trial the isolate or group-

reared subjects remained in their home cage, and the female intruder was placed into the subject's cage. Individual intruders were not used more than one time on any test day, and test partners were assigned to different resident groups on each test day. Behavior coding was carried out by the method described above (Experiment I). Again, interrater reliability was high (r = .97 for frequency; r = .98 for latency to first attack).

The analytic strategy follows the recommendation of Hertzog and Rovine (1985) for analysis of variance with repeated measures. In all of the analyses presented below, heterogeneity of variance is acceptable (Huynh-Feldt's Epsilon $>$.75), and mixed-model analyses were reported.

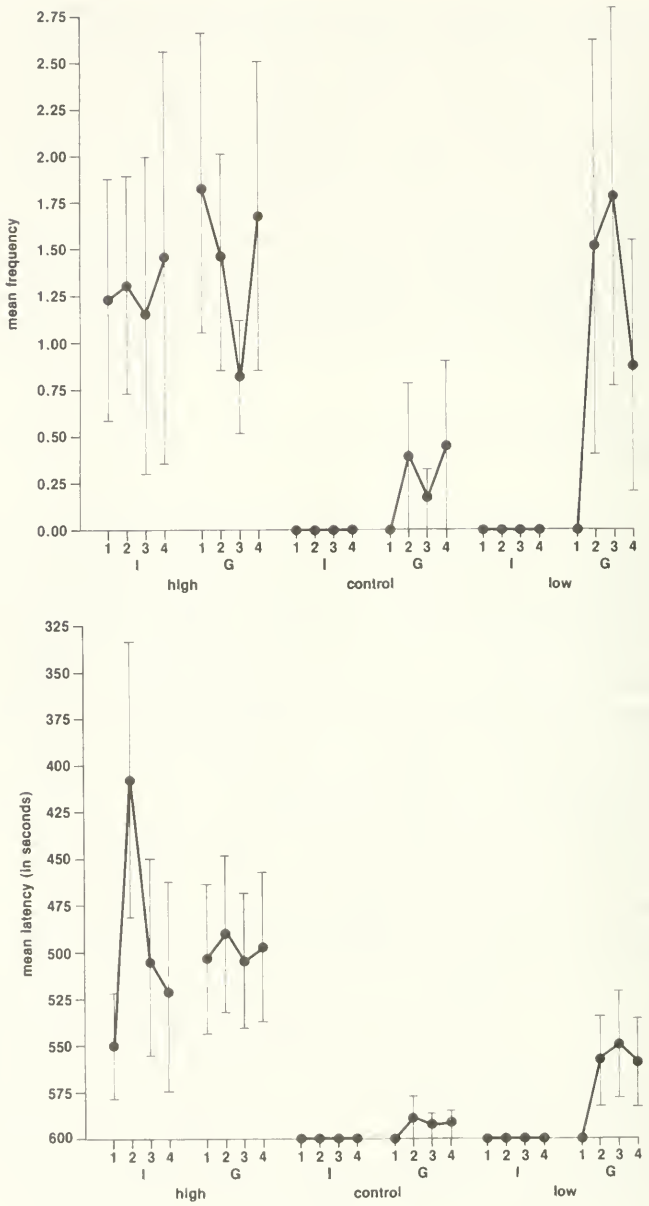
RESULTS

In a 3 x 2 (line by group) repeated-measures analysis of variance including 4 trials as the repeated factor, line differences were robust for latency to first attack ($F(2,124) = 10.99, p < .0001$). Aggressive behavior by females from lines of mice selectively bred for differential male aggression showed clear line differentiation, with high-aggressive-line females attacking fastest at each test occation (Figures 1a & 1b).

All other factors in the global analysis were not significant: the effect of line on attack frequency ($F(2,124) = 2.25, p = .11$), the effect of group vs. isolation housing (for frequency, $F(1,124) = 0.92, p = .34$), the effect of repeated trials (for latency, $F(3,372) = 1.53, p = .21$), and all interactions.

An alternative to the global F-test for assessing experience effects is to compare the results of independent analyses of naive groups (Trial 1) and experienced groups (here, Trials 2-4). This procedure is conservative in that it does not utilize the more precise error term generated by a repeated-measures analysis. Considering each trial independently, frequency scores showed significant line differences on the first trial ($F(2,124) = 5.11, p < .01$) with high-aggressive females attacking most: line differences were not significant on the second, third, and fourth trials. After the first trial, the increased attacks by a few group-reared low-aggressive line animals were sufficient to obliterate line differences. Latency scores showed significant line effects on each occasion.

An additional method of analysis yielded paralled results. In nonparametric analyses of variance of ranked scores on each trial separately, the effect of line is significant at each occasion (χ^2's = 20.79, 13.34, 10.46, 7.81, p's = .001 to .02 for frequency; χ^2's = 20.79, 14.62, 11.71, 8.60, p's = .0001 to .01 for latency). However, inspection of the mean scores in Figure 1 suggests that the control line differs from the high- and low-aggressive lines, after the first trial. The effect of isolation vs. group housing is not significant on any trial.



Figures 1a & 1b. Attack frequency and latency — MEAN and SEM — by females from three lines of mice selectively bred for high levels of male aggressiveness, low levels of male aggressiveness, and a control line. In each line, females were reared in isolation (I) or in small groups (G), and tested on four successive days with a same age (about 200 days) female intruder placed into the home cage.

TABLE 2
Aggressive Behavior by S_{15} Female Mice:
Effects of Isolation vs. Group Rearing and Repeated Test Experience

	N Attacking [a] / % / *N Total*	*N Attacking* *Maximum frequency* *Minimum latency (sec)* [b]			
		Trial 1	*Trial 2*	*Trial 3*	*Trial 4*
High-Aggressive Line					
Isolate Reared	7/13 (54%)	4	5	3	2
		8	6	11	14
		285	5	5	25
Group Reared	13/28 (46%)	5	6	7	6
		16	12	5	15
		20	10	30	10
Control Line					
Isolate Reared	0/9	0	0	0	0
Group Reared	1/38 (3%)	0	1	1	1
		—	15	6	17
		—	185	360	330
Low Aggressive Line					
Isolate Reared	0/9	0	0	0	0
Group Reared	5/33 (15%)	0	3	3	2
		—	34	23	22
		—	15	20	70

a. The number of animals that attacked on at least 1 of 4 trials.
b. Maximum latency score is 600 sec. Minimum frequency score is 0.

A key to understanding this pattern of findings is the wide range of individual differences in attacks over trials (Table 2). Among the group-reared low-aggressive line females, a few highly aggressive individuals emerged after the initial trial, and attacked at extremely high frequencies: in comparisons that include only scores from animals that attacked at least once in the four trials, the trial-by-line interaction was significant (F (3,51) = 3.34, p = .03), with low-line females *more* aggressive than high-line females in the third trial ($F(1,17) = 6.99, p = .02$). This increase in low-line female aggressiveness after repeated test experience offers a comparison to the increased aggressiveness of low-aggressive line males in life-span longitudinal tests (Cairns, MacCombie, & Hood, 1983). These convergent outcomes in females and males underscore the potential influence of repeated test experience in unleashing aggressive behavior by some low-aggressive line animals.

DISCUSSION

Three questions are addressed by the research reported here, and one is clearly settled: line differences in female aggressiveness persist after 15 generations of selection for male behavior. Latency scores are more powerful than frequency scores in discriminating among females from the selected lines, in both generations. Intensification of line differences in female aggressive behavior by the intervening 9 generations of male selection (S_6 vs. S_{15}) is not evident by these measures. (The same-line group scores in Table 1 are comparable to scores in Figure 1, Trial 1 only).

Social experience effects were investigated in three aspects of the two experiments: in comparisons of longitudinal vs. naive groups (Experiment I), in comparisons of social- vs. isolation-reared females and in comparisons of behaviors during repeated trials administered in a daily testing regimen (Experiment I). Longitudinal test experience spaced over the life span augments the expression of aggression in all three selectively-bred lines in Experiment I. The effects of massed test experience in Experiment II were not as clear: among mature S_{15} females, increased aggression over 4 daily trials was found for low-aggressive line animals, when each occasion was analyzed separately. However, these changes were not reflected in the simultaneous analysis of all effects. Similarly, the effect of social vs. isolation rearing is nonsignificant in the global test, but the fact that only group-housed females showed increased aggressiveness over massed trials suggests that isolation rearing may alter female social reactivity in some lines of mice.

Why are the effects of repeated test experience significant in Experiment I, but not in Experiment II? Three possible explanations arise from the differences of design in these two investigations. It may be that massed trials simply are not comparable to spaced trials, as employed in the life-span longitudinal design of Experiment I. Alternatively, the use of subjects that are under continued selection pressure in each generation (S_6 vs. S_{15}) affords the possibility that the phenotypic range of reaction has been shifted. Even after the direct effects of selection on aggressiveness are at asymptote, changes due to selection pressure may yet continue in correlated behavioral systems, as demonstrated by Gariépy, Hood, & Cairns (1988). Finally, the use of ICR strain test partners, each for one test only (Experiment I) vs. non-Swiss albino strain test partners, each tested repeatedly, (Experiment II) may be crucial in interpreting the different outcomes (Hood & Batcheller, in preparation). Attacks by intruders were never observed, but other behaviors or odors may have changed over repeated trials.

The interdependence of genetic-developmental factors, such as sex and line, with experiential factors, such as exposure to social stimula-

tion, may be of general significance for other species. (For a discussion of similar genotype-environment interactions in primates, see Sackett, 1982). The social dynamic that emerges from laboratory and field studies of mice is one in which aggressive adult females are primary agents in the dispersal of juveniles (Ayer & Whitsett, 1980; Fordham, 1971; Healey, 1967; Sadlier, 1965). For example, Savidge (1974) found that in the field, the dispersal of young mice is related to the level of aggressiveness of individual adult females. This regulatory social process may be influenced by familial factors, as demonstrated by studies of live-trapped wild mice (Fairborn, 1978) and voles (Hilborn, 1975). Recruitment of female outsiders into mouse demes may be restricted by the selective aggression of colony females (Chovnick, Yasukawa, Monder, & Christian, 1987; Haug, Spetz, Ouss-Schlegel, Benton, & Brain, 1986; Yasukawa, Monder, Leff, & Christian, 1985). The exclusion of strange females protects colony females from pregnancy block, which can be induced by strange females as well as by strange males (Yamazaki, Beauchamp, Wysocki, Bard, Thomas, & Boyse, 1983), and protects colony young from infanticide (in particular, see the field studies of ground squirrels by Sherman, 1980).

Two themes from the research presented here are in harmony with this view of female roles and social structure: female mice do attack same-sex intruders (also see Hood, 1984), and females from families with highly aggressive males are most likely to fight. This suggests that familial patterns of aggression may be influenced by selection pressures directed at either sex, in interaction with specific and predictable social experiences.

Two additional findings from this research point to characteristics of female aggressiveness that appear to be distinct from male patterns. The ontogenetic pattern of aggressiveness in females shows a peak at maturity, whereas in males there is a sharp onset of aggressiveness earlier in ontogeny, at puberty (Cairns, Hood, & Midlam, 1985; Hood & Cairns, 1988). In addition, the effects of isolation versus social rearing are modest or nonexistent in females of these lines, but quite pronounced in males (Hood & Cairns, in press). However, the exceptions to this conclusion are notable: the few low-aggressive line females that do fight after the initial test experience are markedly mean, and not one of them is isolation-reared. To the extent that there is sex-differentiation of aggressive patterns, fighting among females may serve a sex-differentiated social function in rodent societies (also see Benton & Brain, 1979). If the effect of social experience with intruders is to produce a few effective female fighters in an otherwise pacific group, then, at a population level, gene flow among demes may be modulated in part by interfemale aggressive behavior in response to periodic emigration pressure. Field studies coordinated with laboratory investigations (Schneirla, 1950) will be most useful in refining and testing these hypotheses.

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