Postpubertal social isolation and male sexual behavior in rodents: Facilitation or inhibition is species dependent

DENYS deCATANZARO and BORIS B. GORZALKA
University of British Columbia, Vancouver, British Columbia V6T 1W5, Canada

Experiment 1 examined male Swiss-Webster, C57, and DBA mice that were housed individually or grouped for 2 weeks and subsequently presented with ovariectomized, estrogen-primed, progesterone-treated females. Within each strain, social isolates showed more mounts, intromissions, and ejaculations and shorter latencies to first mount and intromission. Experiment 2 involved a similar comparison of isolated and grouped male rats, hamsters, and gerbils. Isolation produced no major effect in hamsters but reduced performance in rats and gerbils. The results suggest that facilitation of sexual action patterns by isolation is characteristic of the mouse species. Response decrements with postpubertal isolation in the rat resemble effects of prepubertal isolation in this species. These species differences may parallel differences in physiology and social behavior.

In previous investigations (deCatanzaro & Gorzalka, 1979, Note 1; Gorzalka & deCatanzaro, 1979), it has been found that male CD-1 house mice housed postpubertally in social isolation show increased sexual performance relative to group-housed male mice. Social isolation increases several measures of sexual performance regardless of sexual experience or amount of housing space allotted per animal. This differential performance of isolated and grouped mice reverses when the housing conditions are reversed. Differences between grouped and isolated mice in male-female interactions correlate with differences in intermale interactions, where isolates show higher levels of aggression. Facilitation of sexual performance occurs in male mice after remarkably short (12-24-h) as well as long (4-week) periods of social isolation. Inhibition of performance in grouped animals does not relate to intermale mounting, but may depend upon the occurrence of intermale aggression among grouped male mice. Adrenalectomy prevents facilitation of male sexual behavior by isolation, suggesting pituitary-adrenal hormone involvement in the phenomenon.

The present study examined the strain and species generality of isolation/grouping differences in male sexual performance. Because of cross-species variation in social structure, various social arrangements may

differentially affect the behavior of members of different species. Furthermore, there are indications that physiological variables may be differentially affected by social isolation in different species (Bennett & Rosenzweig, 1971; Sahakian, Robbins, Morgan, & Iverson, 1975; Stolk, Conner, & Barchas, 1974), effects which may in turn produce differences in sexual performance. Previous investigation of isolation-induced facilitation of male sexual behavior was limited to CD-1 strain mice (deCatanzaro & Gorzalka, 1979, Note 1; Gorzalka & deCatanzaro, 1979). It is thus important to examine whether the phenomenon is characteristic of this strain, of mice in general, or of a number of species. Furthermore, differential sexual responsiveness to isolation or grouping can be compared to differential physiological responsiveness and social differences among species. Such a comparison might provide indirect information regarding the relationship of sexual behavior to social and physiological variables.

EXPERIMENT 1

There is considerable evidence that inbred strains of house mice (*Mus musculus*) may respond differentially to social isolation. Differences may occur in aggressiveness (Karczmar & Scudder, 1969; LeDouarec & Broussy, 1969), pituitary-adrenocortical and pituitary-gonadal response (see Brain, 1975), and neurochemistry (Karczmar & Scudder, 1969). Furthermore, the distribution and relative frequencies of sexual action patterns may vary among strains. Several researchers (Levine, Barsel, & Diakow, 1966; McGill, 1962; 1965; Mosig & Dewsbury, 1976) have provided descriptions of strain differences in sexual

This research was supported by National Research Council of Canada Grant AG277 and a Natural, Applied, and Health Sciences Grant from the University of British Columbia, both awarded to B. B. Gorzalka. The able assistance of Ellen Beaumont is gratefully acknowledged. Requests for reprints should be sent to B. B. Gorzalka, Department of Psychology, University of British Columbia, Vancouver, B. C. V6T 1W5, Canada.

performance. On this basis, it becomes necessary to establish whether or not a phenomenon found in one strain is characteristic of only that strain. The present experiment examined the effects of isolation and grouping upon the sexual performance of three commonly studied strains of mice.

Method

Subjects. Experimental animals consisted of 24 male C57BL/GCrIBR and 24 male DBA/2NCrIBR mice obtained from Canadian Breeding Farms, Montreal, Canada, and 24 male Swiss-Webster mice obtained from Biobreeding Laboratories, Ottawa, Canada. All animals were sexually naive. After receipt from the breeders at 55 days of age, the animals were housed in groups of 6 of homogeneous strain until commencement of the experimental housing conditions. Each group was in a cage measuring $28 \times 16 \times 11$ cm high and maintained under reversed 12-h-dark/12-h-light cycle at $21^\circ \pm 1^\circ\text{C}$. Animals were tested 5-8 h after the commencement of their dark phase in an illuminated room maintained at this same temperature.

Stimulus females. Stimulus animals consisted of 40 group-housed CD-1 females obtained from Canadian Breeding Farms. Females from a fourth strain were employed to avoid confounding of male strain differences with strain differences in female receptivity (see Gorzalka & Whalen, 1976). Stimulus females were prepared according to a procedure that ensures maximum sexual receptivity at the time of presentation to experimental males. This procedure was adapted from studies (Gorzalka & Whalen, 1974, 1976) showing increases in receptivity with successive weeks of hormone treatment and experience with males. The procedure involved, first, bilateral ovariectomy at approximately 60 days of age. Two weeks following surgery, an injection schedule began in which each female received $10 \mu\text{g}$ of estradiol benzoate in .05 cc of peanut oil SC, followed 48 h later by $500 \mu\text{g}$ of progesterone in .05 cc oil SC. This injection schedule was repeated weekly. For the first 5 weeks, stimulus females were presented in groups of six for 1 h to a group of six stimulus males 6 h following progesterone treatment. On the 6th week, females were presented to the experimental animals 6 h following progesterone. Females were used for no more than two successive hourly tests.

Procedure. At 60-65 days of age, 12 of the animals from each strain were rehoused in clean cages in groups of 6 while the remaining 12 animals were housed individually in clean cages. Each group of 6 was made up of animals that had been housed together since receipt from the breeder. The cages were made of polypropylene by Carworth Lab Cages. They were $28 \times 16 \times 11$ cm high, and were equipped with straight-wire tops containing a built-in feeder and water dispenser which, together, displaced 952 cm^3 . Each cage contained 1 liter of commercial bedding material (San-i-cel) and one 24×24 cm paper towel torn into several pieces. The cages were cleaned as required to maintain all conditions at an approximately equivalent level of cleanliness, but under no circumstances were they disturbed during the 3 days immediately preceding testing.

After 2 weeks in these conditions, a period previously established as sufficient to produce effects in CD-1 mice (deCatanzaro & Gorzalka, 1979), the animals were tested for sexual performance. This test consisted of a 1-h session during which each animal was presented with receptive females in a Plexiglas enclosure measuring $23 \times 12 \times 22$ cm high. A time-limited test was employed because, unlike procedures that use multiple criteria for commencement and termination of the observation of behavior, which eliminate the data from some animals (e.g., McGill, 1965; Mosig & Dewsbury, 1976), this procedure measures all animals in an equivalent manner. Furthermore, unlike procedures involving such a selection process, this procedure allows generalization of results to the entire population from which animals are sampled. Six animals were tested simul-

taneously in adjacent enclosures, with one animal from each treatment combination represented at each session. Internal walls of the enclosures were covered so that an animal could not see events in adjacent enclosures. After 5 min of adaptation to the chamber, a single receptive female was presented to each animal. At 10-min intervals, the females were rotated so that each treatment combination received each female for an equivalent amount of time. During sessions, the frequency, duration, and latency of mounts without intromission (mounts) and mounts with intromission and pelvic thrusting (intromissions), and the number and latency of ejaculations were measured. All latencies were measured from the commencement of the session. Responses were recorded via an Esterline-Angus event recorder by a trained observer who was unaware of the purpose of the experiment. Mounts, intromissions, and ejaculations were defined as described by McGill (1965).

Results and Discussion

Figure 1 shows the results for measures of duration of mounting, with or without intromission, and number of mounts, intromissions, and ejaculations. The duration-of-mounting measure reflects the fact that male sexual responses in mice vary in duration as well as in number. Table 1 reports remaining measures of copulatory performance. The measure of copulatory efficiency is adapted from Parrott (1975) and is calculated using all mounts and intromissions preceding the first ejaculation or the end of the session as follows: if $M + I > 0$, $CE = I/(M + I)$; if $M + I = 0$, $CE = 0$, where M = number of mounts, I = number of intromissions, CE = Copulatory efficiency. Individually housed mice of all strains showed substantially more mounts, intromissions, and time spent mounting than did same-strain group-housed mice. There were only a few ejaculations in any condition, but these were also more common in isolated than in group-housed mice. Latencies to

Figure 1. Mean performance of isolated and grouped Swiss-Webster (Swiss), C57BL/GCrIBR (C57), and DBA/2NCrIBR (DBA) male mice on measures of sexual behavior in the presence of receptive females. Lines above the bars indicate standard errors.

Table 1

Means and Standard Errors of Response Latencies (in Seconds) and Copulatory Efficiency, and Percent Responding in Experiment 1

Strain	n per Cage	Latency						Copulatory Efficiency		Percent Responding		
		M		I		E		Mean	SE	M	I	E
		Mean	SE	Mean	SE	Mean	SE					
Swiss	1	592	140	985	247	3234	224	.318	.036	100	100	25
	6	1088	327	1664	399	3226	258	.258	.053	92	83	17
C57	1	344	100	1265	354	3304	163	.256	.047	100	92	50
	6	1163	356	1881	375	3314	151	.214	.062	92	67	25
DBA	1	2105	471	2986	285	3600	0	.119	.048	50	42	0
	6	3315	285	3225	275	3600	0	.021	.021	8	8	0

Note—M = mount, I = intromission, E = ejaculation.

first mount and intromission were on the average shorter in isolated mice, while the percentage mounting, intromitting, and ejaculating was, in all cases, higher in isolated animals within each strain. DBA mice showed substantially less sexual activity than either C57 or Swiss-Webster mice; this may, in part, be due to their smaller relative size compared to CD-1 females.

Parallel two-factor (housing condition and strain) analyses of variance were conducted on all measures except percentages of responses. The isolation/grouping factor was significant in total duration [$F(1,66) = 7.54, p = .008$], number of mounts [$F(1,66) = 10.94, p = .002$], number of intromissions [$F(1,66) = 4.62, p = .033$], mount latency [$F(1,66) = 11.25, p = .001$], and intromission latency [$F(1,66) = 4.16, p = .043$]. There was not a significant effect of this factor in other measures. There was a significant effect of strain in all measures except ejaculation latency: duration [$F(2,66) = 16.10, p < .001$], mounts [$F(2,66) = 13.30, p < .001$], intromissions [$F(2,66) = 10.87, p < .001$], ejaculations [$F(2,66) = 6.03, p = .004$], mount latency [$F(2,66) = 25.87, p < .001$], intromission latency [$F(2,66) = 18.44, p < .001$], and copulatory efficiency [$F(2,66) = 12.03, p < .001$]. In all cases, Newman-Keuls tests ($p < .05$) indicated that the DBA mice showed lower performance than both the C57 and Swiss-Webster mice, but that these latter two strains did not differ. There were no significant Strain by Isolation/Grouping interactions.

While the measurement system employed here differs from that of other researchers (e.g., McGill, 1965; Mosig & Dewsbury, 1976), several permutations of the procedure produce the same results. For example, if postejaculatory mounts and intromissions are excluded from calculations, 1 mount would be removed from each of one grouped animal and one isolated animal, while 3 mounts and 4 intromissions would be removed from another isolated animal. Thus, terminating the tests after ejaculations would have produced essentially the same conclu-

sions. Moreover, during 8 weeks of repeated testing and a general increase in sexual responding, isolates in a previous study consistently showed more sexual behavior than group-housed mice (deCatanzaro & Gorzalka, 1979). Finally, the significant latency differences here indicate that this phenomenon is not an artifact of the test procedure.

These results suggest that facilitation of sexual behavior by isolation is characteristic of the species. Isolation affects several components of sexual behavior. An effect is evident in all measures, although a few may not reach statistical significance under these conditions. There is considerable variability among grouped animals; some show no sexual response whatsoever, others show performance comparable to that of isolates. In the Swiss-Webster and C57 mice, the major effect of isolation appeared to be an increase in the average amount of sexual behavior, with most grouped animals showing some response. In the DBA strain, the major effect of isolation was to increase the number of animals showing any response to females.

EXPERIMENT 2

House mice normally live in small demes composed of a dominant male, several females, and a few subordinate males (Reimer & Petras, 1967). Male mice may consequently adapt readily to individual housing but be relatively stressed under group-housing conditions, an interpretation that is supported by hormonal comparisons of isolated and grouped mice (see review by Brain, 1975). It has been hypothesized that stress may antagonize sexual behavior (Christian, 1971; Gray, 1971; Selve, 1961); the findings of Experiment 1 are consistent with this hypothesis.

Other rodent species differ from mice in social organization. The rat (*Rattus norvegicus*), for example, is a fairly social species with individuals living in large colonies that share nesting sites and feeding grounds (Barnett, 1975). The golden hamster (*Mesocricetus auratus*) is believed to be solitary in

its natural environment (Eibl-Eibesfeldt, 1953; Johnson, 1975). The Mongolian gerbil (*Meriones unguiculatus*) is reported to show small personal distances and aggregate peacefully in seminatural environments (Eisenberg, 1967; Thiessen & Yahr, 1977). These species may also respond differently to isolation and housing conditions with respect to levels of aggressiveness (cf. Blanchard & Blanchard, 1971; Conner, 1972; Edwards & Rowe, 1975; Scott, 1966; Thiessen & Yahr, 1977) and physiology (see Bennett & Rosenzweig, 1971). Moreover, the topography of male sexual behavior differs among these species (cf. Gorzalka & Mogenson, 1977; Kuehn & Zucker, 1968; Larsson, 1956; McGill, 1965). Because of these species differences, there is reason to suspect that male sexual behavior might respond differentially in different species to the isolation/grouping manipulation. Therefore, in order to test the generality of previous findings, male rats, gerbils, and hamsters were examined under conditions known to produce isolation/grouping differences in mice.

Method

Subjects. Twenty-four sexually naive male Long-Evans rats, obtained from Canadian Breeding Farms, Montreal Canada, were housed in groups of six in standard triple wire-mesh cages until commencement of the experimental housing conditions at about 120 days of age. Twenty-four sexually naive male golden hamsters, obtained from Charles River Laboratories, Newfield, N.J., were housed in groups of six in polycarbonate cages measuring 46 × 25 × 15 cm high equipped with large straight-wire tops, until commencement of experimental housing conditions at about 100 days of age. These cages each contained 2 liters of bedding material and one paper towel. Twenty-four sexually naive male gerbils, obtained from High Oak Ranch, Goodwood, Ontario, Canada, were housed in the manner described for hamsters until about 120 days of age. These ages were chosen because almost all males of these species should be sexually mature by these ages. All animals were housed under a reversed 12-h-dark/12-h-light cycle and kept in rooms maintained at 21° ± 1°C. The animals were tested 5-8 h after commencement of their dark phase in an illuminated room at this same temperature.

Stimulus females. Adult females of each species were obtained and group-housed. These were bilaterally ovariectomized at least 3 weeks prior to testing. On the 1st and 2nd days before testing, the females were given 5µg estradiol benzoate in .05 cc peanut oil SC. On the day of testing, the females were given 500µg progesterone in .05 cc oil SC 5 h prior to testing in the case of rats and hamsters and 9 h prior to testing in the case of gerbils. Females were used for no more than two successive hourly tests.

Procedure. Two weeks prior to testing with receptive conspecific females, the males were placed into two conditions, each of which contained 12 animals of each species: animals grouped in 6 and animals housed individually. All groups of 6 were simply placed in clean cages at this point, with each group being constituted by the same individuals that had been housed together since receipt from the breeders. Individually housed rats were each housed in standard laboratory single wire-mesh cages. Individually housed gerbils and hamsters were each housed in cages identical to those described for mice in Experiment 1. The animals were tested for 1 h in cylindrical Pyrex testing jars measuring 45 cm in height with a diameter of 29 cm. Each species was tested at separate times. Six animals, three isolates and three grouped

animals, were observed simultaneously. After 5 min adaptation to the jar, each animal was presented with a receptive conspecific female. The females were transferred to adjacent jars every 10 min so that grouped and isolated conditions received each female for identical lengths of time. During these sessions, the number and latencies of mounts, intromissions, and ejaculations were recorded via an Esterline-Angus event recorder. The sexual responses of rats were defined as described by Larsson (1956), those of hamsters as described by Gorzalka and Mogenson (1977), and those of gerbils as described by Kuehn and Zucker (1968).

Results and Discussion

Figure 2 gives the results for measures of mounts, intromissions, and ejaculations. Remaining measures

Figure 2. Mean performance of isolated and grouped male rats, hamsters, and gerbils on measures of sexual behavior in the presence of receptive conspecific females. Lines above the bars indicate standard errors.

Table 2

Means and Standard Errors of Response Latencies (in Seconds) and Copulatory Efficiency, and Percent Responding in Experiment 2

Species	n per Cage	Latency						Copulatory Efficiency		Percent Responding		
		M		I		E		Mean	SE	M	I	E
		Mean	SE	Mean	SE	Mean	SE					
Rats	1	1494	354	1801	378	2867	293	.338	.070	83	75	50
	6	838	370	1079	394	2216	351	.529	.076	92	92	66
Hamsters	1	207	68	418	130	1808	406	.660	.057	100	100	75
	6	99	23	192	48	1230	373	.620	.053	100	100	92
Gerbils	1	1635	410	3018	391	3600	0	.094	.070	82	18	0
	6	1276	388	2198	440	3600	0	.321	.112	83	50	0

Note—M = mount, I = intromission, E = ejaculation.

are given in Table 2. A duration-of-mounting measure is not reported since most mounts and intromissions tend to be very brief and of about the same duration within each of these species. More mounts, intromissions, and ejaculations were evident in grouped rats and more mounts and intromissions evident in grouped gerbils than in socially isolated conspecifics. There was little difference in performance between isolated and grouped hamsters, although there was a slight trend in the same direction as found in rats and gerbils. Gerbils showed relatively few mounts and intromissions and no ejaculations. One isolated gerbil died prior to testing.

An analysis of variance on the measure of mounts indicated a significant difference between grouped and isolated animals [$F(1,65) = 7.54, p = .007$]. Newman-Keuls tests ($p < .05$) on individual species indicated a significant difference between the grouped and isolated conditions in rats and gerbils but not hamsters. Analyses of variance indicated that the difference between grouped and isolated animals approached significance, but did not reach the accepted level, for intromissions [$F(1,65) = 3.75, p = .054$] and copulatory efficiency [$F(1,65) = 3.61, p = .059$], while a similar analysis of intromission latency was significant [$F(1,65) = 4.18, p = .042$]. The isolation/grouping factor was not significant in other measures. In all analyses there were also significant differences among species: mounts [$F(2,65) = 10.37, p < .001$], intromissions [$F(2,65) = 12.06, p < .001$], ejaculations [$F(2,65) = 14.96, p < .001$], mount latency [$F(2,65) = 9.68, p < .001$], intromission latency [$F(2,65) = 23.66, p < .001$], ejaculation latency [$F(2,65) = 24.41, p < .001$], and copulatory efficiency [$F(2,65) = 15.68, p < .001$]. None of the interaction factors were significant.

These results indicate that, contrary to findings with mice, postpubertal social isolation may decrease sexual performance in rats and gerbils and have little effect in hamsters. The low level of performance observed in gerbils may relate to the fact that adults of this species frequently form monogamous pairs (Thiessen & Yahr, 1977). This may limit interpretations of findings with this species.

GENERAL DISCUSSION

The present results indicate that the effects of isolation and group-housing upon male sexual behavior vary considerably across different rodent species. The results of Experiment 1 suggest that previous findings (deCatanzaro & Gorsalka, 1979) of facilitation of male sexual patterns in CD-1 mice by isolation can be generalized to other mouse strains. While the different strains investigated here showed markedly different levels of sexual behavior, within each of the three strains isolated animals showed performance that exceeded that of group animals. By contrast, in Experiment 2, isolated male rats, gerbils, and hamsters showed poorer performance than group-housed conspecifics. This latter effect was most marked in rats and gerbils and only slightly evident in hamsters.

In most cases, the measures of duration of mounting, mounts, intromissions, and some of the latency measures reached significance, while measures of ejaculation did not. It thus remains possible that specific components of the sexual response pattern, rather than the quantity of all responses, are sensitive to the presence or absence of conspecific males. However, in all cases where ejaculations occurred, this measure reflected a strong trend in the same direction as was found with other measures. The lack of significance in the ejaculation measure was usually due to a low number of such responses in all conditions, which reduced statistical power. In unpublished research, we have found that this problem is not overcome, with mice, when 3-h sessions are employed.

The finding in Experiment 2 of decreased sexual performance in isolated male rats and gerbils is consistent with many (but not all, e.g., Beach, 1958) previous investigations of copulatory behavior following isolation. The literature abounds with reports of deficits in copulatory behavior following isolation. For example, isolation has been reported to impair sexual performance in rats (Folman & Drori, 1965; Gerall, Ward, & Gerall, 1967; Gruendel & Arnold, 1974) and guinea pigs (Valenstein, Riss, &

Young, 1955). However, studies of this type have employed postweaning, prepubertal isolation. These deficits have been typically interpreted as evidence that contact between conspecifics prior to puberty is essential for normal adult sexual performance. In the present study, animals were isolated during adulthood after having been group-housed during development. The results of Experiment 2 open the possibility that isolation per se, rather than isolation during a critical period, produces deficits in adult sexual performance. Although these data do not rule out the potential importance of prepubertal social interactions, earlier studies may nevertheless have confounded the concept of critical periods with the intrinsic effects of isolation.

The species differences observed here are consistent with findings of other differences between these species in behavioral responses to social isolation. Aggressiveness is also increased in male mice by isolation (Scott, 1966), while isolation-induced aggression is either absent (Conner, 1972) or very mild and attenuated in rats (Blanchard & Blanchard, 1977) and less pronounced in hamsters (Edwards & Rowe, 1975) and gerbils (Edwards & Rowe, 1975; Thiessen & Yahr, 1977) than in mice. Moreover, these effects may relate to the natural social ecology of the different species. Although laboratory rats and mice have been bred under unnatural laboratory conditions through several generations, it is likely that many of their natural social predispositions survive (cf. Boice, 1977; Boreman & Price, 1972). Since, as discussed above, rats are naturally found in larger groupings than are mice, it is consistent that they adapt more readily to group housing. It may be that the suppression of sexual performance in mice in the presence of conspecific males relates to the population dynamics of natural house mice.

The species differences of the present study, at least those between mice and rats, are also consistent with differences between these species in their physiological response to social isolation. Isolated mice exhibit less pituitary-adrenocortical and more pituitary-gonadal activity than do grouped mice (Benton, Goldsmith, Gamal-El-Din, Brain, & Hucklebridge, 1978; Brain, 1975; Brain & Nowell, 1971; Christian, 1955; 1959; McKinney & Desjardins, 1973). Isolated mice may also show lower baseline levels and utilization rates of brain catecholamines, and lower utilization of serotonin than grouped mice, but greater utilization of these amines in stressful, and novel situations (Garattini, Giacalone, & Valzelli, 1969; Welch & Welch, 1969a, 1969b). There would appear to have been fewer investigations of the effects of isolation on physiological mechanisms in rats; those that exist indicate effects which are qualitatively different or relatively weaker (cf. Bennett & Rosenzweig, 1971; Sahakian et al., 1975;

Stolk et al., 1974). For example, isolation in rats may produce an increase in baseline turnover of catecholamines and minimal changes in serotonin metabolism relative to grouped subjects (Stolk et al., 1974). These differences in physiological response to isolation may be relevant in light of evidence that pituitary-adrenal hormones (Bertolini, Gessa, & Ferrari, 1975), pituitary-gonadal hormones (Gorzalka & Mogenson, 1977), and central catecholamines and serotonin (Gessa & Tagliamonte, 1975) may all influence male sexual behavior.

The present study suggests, then, that the modulation of male sexual behavior by isolation may be dependent on the social ecology of the species and the profile of physiological changes accompanying individual housing. One possibility is that physiological determinants of sexual behavior are constant across species but that social mechanisms affecting them are not. The pituitary-adrenal and neurochemical effects of group-housing in mice are consistent with the interpretation that grouping may produce some level of stress in this species (Brain, 1975). In more social species, such as the rat, isolation of previously grouped animals may constitute a stressor and thereby produce sexual performance deficits. Future research correlating physiological responses and social mechanisms might therefore help to explain behavioral effects of social isolation.

REFERENCE NOTE

1. deCatanzaro, D., & Gorzalka, B. B. *Facilitation of mating patterns in male mice: Brief periods of isolation or grouping*. Manuscript submitted for publication, 1979.

REFERENCES

- BARNETT, S. A. *The rat: A study in behavior*. Chicago: University of Chicago Press, 1975.
- BEACH, F. A. Normal sexual behavior in male rats isolated at fourteen days of age. *Journal of Comparative and Physiological Psychology*, 1958, **51**, 37-38.
- BENNETT, E. L., & ROSENZWEIG, M. R. Chemical alterations produced by environment and training. In A. Lathja (Ed.), *Handbook of neurochemistry* (Vol. VI). New York: Plenum, 1971.
- BENTON, D., GOLDSMITH, J. F., GAMAL-EL-DIN, L., BRAIN, P. F., & HUCKLEBRIDGE, F. H. Adrenal activity in isolated mice and mice of different social status. *Physiology & Behavior*, 1978, **20**, 459-464.
- BERTOLINI, A., GESSA, G. L., & FERRARI, W. Penile erection and ejaculation: A central effect of ACTH-like peptides in mammals. In M. Sandler & G. L. Gessa (Eds.), *Sexual behavior: Pharmacology and biochemistry*. New York: Raven Press, 1975.
- BLANCHARD, R. J., & BLANCHARD, D. C. Aggressive behavior in the rat. *Behavioral Biology*, 1977, **21**, 197-224.
- BOICE, R. Burrows of wild and albino rats: Effects of domestication, outdoor raising, age, experience, and maternal state. *Journal of Comparative and Physiological Psychology*, 1977, **91**, 649-661.
- BOREMAN, J., & PRICE, E. Social dominance in wild and domestic Norway rats (*Rattus norvegicus*). *Animal Behaviour*, 1972, **20**, 534-542.

- BRAIN, P. F. What does individual housing mean to a mouse? *Life Sciences*, 1975, **16**, 187-200.
- BRAIN, P. F., & NOWELL, N. W. Isolation versus grouping effects on adrenal and gonadal function in albino mice. 1. The male. *General and Comparative Endocrinology*, 1971, **16**, 149-154.
- CHRISTIAN, J. J. Effects of population size on the adrenal glands and reproductive organs of male mice in populations of fixed size. *American Journal of Physiology*, 1955, **182**, 292-300.
- CHRISTIAN, J. J. The roles of endocrine and behavioral factors in the growth of mammalian populations. In A. Gorbman (Ed.), *Comparative endocrinology*. New York: Wiley, 1959.
- CHRISTIAN, J. J. Population density and reproductive efficiency. *Biology of Reproduction*, 1971, **4**, 248-294.
- CONNER, R. L. Hormones, biogenic amines, and aggression. In S. Levine (Ed.), *Hormones and behavior*. New York: Academic Press, 1972.
- DECATANZARO, D., & GORZALKA, B. B. Isolation-induced facilitation of male sexual behavior in mice. *Journal of Comparative and Physiological Psychology*, 1979, **93**, 211-222.
- EDWARDS, D. A., & ROWE, F. A. Neural and endocrine control of aggressive behavior. In B. E. Eleftheriou & R. L. Sprott (Eds.), *Hormonal correlations of behavior*. New York: Plenum, 1975.
- EIBL-EIBESFELDT, I. Zur Ethologie des Hamsters (*Cricetus cricetus* L.). *Zeitschrift für Tierpsychologie*, 1953, **10**, 204-254.
- EISENBERG, J. F. A comparative study in rodent ethology with emphasis on evolution of social behavior: 1. *Proceedings of the U.S. National Museum*, 1967, **122**, 1-51.
- FOLMAN, Y., & DRORI, D. Normal and aberrant copulatory behavior in male rats (*R. norvegicus*) reared in isolation. *Animal Behavior*, 1965, **13**, 427-429.
- GARATTINI, S., GIACALONE, E., & VALZELLI, L. Biochemical changes during isolation-induced aggressiveness in mice. In S. Garattini & E. B. Sigg (Eds.), *Aggressive behavior*. Amsterdam: Excerpta Medica Foundation, 1969.
- GERALL, H. D., WARD, I. L., & GERALL, A. A. Disruption of the male rat's sexual behavior induced by social isolation. *Animal Behaviour*, 1967, **15**, 54-58.
- GESSA, G. L., & TAGLIAMONTE, A. Role of brain serotonin and dopamine in male sexual behavior. In M. Sandler & G. L. Gessa (Eds.), *Sexual behavior: Pharmacology and biochemistry*. New York: Raven Press, 1975.
- GORZALKA, B. B., & DECATANZARO, D. Pituitary-adrenal effects on sexual behavior in isolated and group-housed mice. *Physiology & Behavior*, 1979, **22**, 939-945.
- GORZALKA, B. B., & MOGENSEN, G. J. Sexual behavior. In G. J. Mogenson, *The neurobiology of behavior: An introduction*. Hillsdale, N.J.: Erlbaum, 1977.
- GORZALKA, B. B., & WHALEN, R. E. Genetic regulation of hormone action: Selective effects of progesterone and dihydroprogesterone (5α -pregnane-3, 20-dione) on sexual receptivity in mice. *Steroids*, 1974, **23**, 499-505.
- GORZALKA, B. B., & WHALEN, R. E. Effects of genotype on differential behavioral responsiveness to progesterone and 5α -dihydroprogesterone in mice. *Behavior Genetics*, 1976, **6**, 7-15.
- GRAY, J. A. *The psychology of fear and stress*. New York: McGraw-Hill, 1971.
- GRUENDEL, A. D., & ARNOLD, W. J. Influence of preadolescent experiential factors on the development of sexual behavior in albino rats. *Journal of Comparative and Physiological Psychology*, 1974, **86**, 172-178.
- JOHNSON, R. The use of space in caged golden hamsters. *Zeitschrift für Tierpsychologie*, 1975, **37**, 213-221.
- KARCZMAR, A. G., & SCUDDER, C. L. Aggressive and neurochemical changes in different strains and genera of mice. In S. Garattini & E. B. Sigg (Eds.), *Aggressive behavior*. Amsterdam: Excerpta Medica Foundation, 1969.
- KUEHN, R. E., & ZUCKER, I. Reproductive behavior of the Mongolian gerbil (*Meriones unguiculatus*). *Journal of Comparative and Physiological Psychology*, 1968, **66**, 747-752.
- LARSSON, K. Conditioning and sexual behavior in the male albino rat. *Acta Psychologica Gothoburgensia*, 1956, **1**, 1-269.
- LEDOUAREC, J. C., & BROUSSY, L. Dissociation of the aggressive behavior in mice produced by certain drugs. In S. Garattini & E. B. Sigg (Eds.), *Aggressive behavior*. Amsterdam: Excerpta Medica Foundation, 1969.
- LEVINE, L., BARSEL, G. E., & DIAKOW, C. A. Mating behavior of two inbred strains of mice. *Animal Behaviour*, 1966, **14**, 1-6.
- MCGILL, T. E. Sexual behavior in three inbred strains of mice. *Behavior*, 1962, **19**, 341-350.
- MCGILL, T. E. Studies of the sexual behavior of male laboratory mice: Effects of genotype, recovery of sex drive, and theory. In F. A. Beach (Ed.), *Sex and behavior*. New York: Wiley, 1965.
- McKINNEY, T. D., & DESJARDINS, C. Intermale stimuli and testicular function in adult and immature house mice. *Biology of Reproduction*, 1973, **9**, 370-378.
- MOSIG, D. W., & DEWSBURY, D. A. Studies of the copulatory behavior of house mice (*Mus musculus*). *Behavioral Biology*, 1976, **16**, 463-473.
- PARROTT, R. F. Aromatizable and 5α -reduced androgens: Differentiation between central and peripheral effects on male rat sexual behavior. *Hormones and Behavior*, 1975, **6**, 99-108.
- REIMER, J. D., & PETRAS, M. L. Breeding structure of the house mouse, *Mus musculus*, in a population cage. *Journal of Mammalogy*, 1967, **48**, 88-99.
- SAHAKIAN, B. J., ROBBINS, T. W., MORGAN, M. J., & IVERSON, S. D. The effects of psychomotor stimulants on stereotypy and locomotor activity in socially-deprived and control rats. *Brain Research*, 1975, **84**, 195-205.
- SCOTT, J. G. Agonistic behavior of rats and mice: A review. *American Zoologist*, 1966, **6**, 681-701.
- SELYE, H. Stress and sex. In A. Ellis & A. Abarbanel (Eds.), *The encyclopedia of sexual behavior*. New York: Hawthorn Books, 1961.
- STOLK, J. M., CONNER, R. L., & BARCHAS, J. D. Social environment and brain biogenic amine metabolism in rats. *Journal of Comparative and Physiological Psychology*, 1974, **87**, 203-207.
- THIESSEN, D., & YAHR, P. *The gerbil in behavioral investigations*. Austin, Texas: University of Texas Press, 1977.
- VALENSTEIN, E. S., RISS, W., & YOUNG, W. C. Experiential and genetic factors in the organization of sexual behavior in male guinea pigs. *Journal of Comparative and Physiological Psychology*, 1955, **48**, 397-403.
- WELCH, B. L., & WELCH, A. S. Aggression and the biogenic amine neurohumors. In S. Garattini & E. B. Sigg (Eds.), *Aggressive behavior*. Amsterdam: Excerpta Medica Foundation, 1969. (a)
- WELCH, B. L., & WELCH, A. S. Fighting: Preferential lowering of norepinephrine and dopamine in the brainstem, concomitant with a depletion of epinephrine from the adrenal medulla. *Communications in Behavioral Biology*, 1969, **3**, 125-130. (b)

(Received for publication February 2, 1979;
revision accepted April 23, 1979.)