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Social inhibition of infanticide in male house mice

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Although a variety of behavioural mechanisms are known to inhibit infanticide in male house mice, the potential for social subordination to inhibit infanticide has not been widely investigated. Sixty male CF-1 stock house mice (*Mus domesticus*) were grouped five per cage from weaning until 5 months of age. Each male was then isolated and tested for infanticide at 1-day and 25-days after being singly housed. Only 13% were infanticidal after 1-day of isolation, but after 25-days of isolation, 44% were infanticidal ($P < 0.0001$). Thus, being group-housed with other males inhibits infanticide in most CF-1 male mice. From an ecological perspective, the cage-by-cage data suggest that subordination is a behavioural counterstrategy by which a dominant breeding male can inhibit his rivals from killing pups, thus maintaining social stability and reproductive success in a typical house mouse microdeme.

KEY WORDS: infanticide, subordination, dominance, house mouse, *Mus*, group-housing, aggression.

Infanticide — defined as the killing of conspecific young — is a violent, but adaptive reproductive strategy found in a variety of mammals, particularly rodents (e.g., HAUSFATER & HRDY 1984). Male house mice (*Mus domesticus* and *M. musculus*), for example, frequently attack and kill alien young whenever they encounter them. An effective infanticidal strategy must also provide, however, for multiple/redundant mechanisms to inhibit pup-killing behaviour at the appropriate time. Consequently, cohabitation with a female, ejaculation during mating, or the birth of pups in a male's home cage are several of the multiple behavioural mechanisms known to effectively inhibit infanticide and prevent male house mice from killing their own sired offspring (e.g., SOROKER & TERKEL 1988, PALANZA & PARMIGIANI in press, PERRIGO & VOM SAAL in press). However, another potential inhibitory mechanism that has received less attention is the possibility that social subordination can also inhibit infanticide; specifically, defeat by a dominant male in an aggressive encounter appears to dramatically reduce infanticidal behaviour in subordinated male mice (HUCK et al. 1982, VOM SAAL & HOWARD 1982) and gerbils (ELWOOD & OSTERMEYER 1984).

We examined this hypothesis by raising male CF-1 stock house mice (*M. domesticus*) in groups of five males per cage before assessing their behaviour toward pups. Since male house mice begin to exhibit aggression toward each other at about 40 days of age (BARKLEY & GOLDMAN 1977), our standard laboratory husbandry in previous experiments has always consisted of singly housing CF-1 males on or before 50 days of age. When singly housed, virgin CF-1 males always show the same proportion of behaviours toward pups regardless of whether tested at 3 or 6 months of age; thus, in any large sample of adult CF-1 males about 50% are always infanticidal and 50% are noninfanticidal (replicated many times; see PERRIGO et al. 1991). For the purpose of this particular experiment, however, 12 cages of CF-1 males were randomly grouped five per cage at weaning (23 days of age) and remained so until 5 months of age, at which time all males were separated, singly housed, and tested for infanticide.

We postulated three potential outcomes to this experiment: *hypothesis 1* group-housing would represent a pathological condition of overcrowding and/or fighting in which virtually all males would be infanticidal (cf. CALHOUN 1962); *hypothesis 2* group-housing would have no effect upon infanticide and about 50% of the males would be infanticidal (see above); or, *hypothesis 3* group-housing would inhibit infanticide and result in each cage having either one or no infanticidal males. This last outcome was predicted here, since group-housed male house mice routinely establish a dominance hierarchy with one dominant male subordinating the other males in his cage. Likewise, the probability of either one or no infanticidal males in each cage depended on two factors: first, whether or not the dominant male was himself infanticidal; and second, that some group-housed male mice can live in mutual tolerance of each other and form stable hierarchies with little or no fighting (e.g., PARMIGIANI et al. 1981).

METHODS

Animal housing. All CF-1 males, whether grouped five per cage or singly housed, were kept in 28 × 18 × 12 cm polypropylene cages with aspen wood-shaving bedding and maintained at L:D 12:12 at 20-22 °C. Purina Mouse Chow and water were provided ad lib.

Assessment of infanticide. One day after group-housed males were separated, each newly isolated, 5-month old male was tested for infanticide using a "screen-protected" pup as described in PERRIGO et al. (1989). A 1-3 day old neonate was slid into a small tube made of 1.5-mm^2 wire mesh window screen and then placed in the male's home cage. An infanticidal CF-1 male typically attacked and bit at the screen, but without injuring the neonate. However, if the male showed no intent to harm the screen-protected pup after several minutes of observation, an unprotected pup was placed in his cage for 30 min to verify whether he was truly noninfanticidal. Since about 90% of infanticidal males will attack a screen-protected pup, this is a reliable and humane test procedure for assessing the pup-killing behaviour of CF-1 stock males (this methodology, however, is not as reliable in other house mouse stocks; see ELWOOD et al. 1990). Each isolated male was also retested 25 days later using the same procedure.

RESULTS

As shown in Fig. 1, only eight out of 60 males (13%) were infanticidal after 1 day of isolation. One male was infanticidal in six of the 12 cages while there were no infanticidal males in five of the 12 cages. In one of the 12 cages there were two

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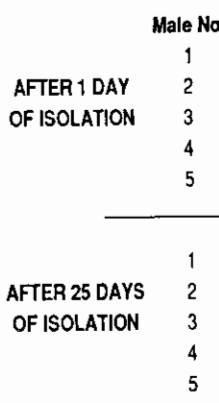

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infanticidal males. When retested after 25 days of isolation, however, a significant proportion of males changed their behaviour toward pups: 26 out of 59 males (44%) were now infanticidal (McNemar test for significance of changes, $\chi^2 = 16.05$, df = 1, $P < 0.0001$; SOKAL & ROHLF 1969). Two other points should be noted here: first, all eight infanticidal males were still infanticidal when retested 25 days later, so 18 out of 51 (35%) noninfanticidal males changed their behaviour toward pups; and second, the proportion of infanticidal males (44%) after 25 days of isolation was statistically identical to the proportion of infanticidal males expected if CF-1 males had been isolated by 50 days of age and then tested several months later (45-55% infanticidal in all previous experiments).

DISCUSSION

When viewed in toto, Fig. 1 confirms that group housing in a small cage with four other adult males is not a sociopathological condition which promotes infanticidal behaviour. In fact, being housed with other males clearly inhibited infanticide in most CF-1 males. Furthermore, the inhibition caused by this social condition was eliminated within 25 days of being singly housed and the new proportion of infanticidal versus noninfanticidal males from each cage grouping was no different than an expected 50/50 random distribution. While the proportion of infanticide and the magnitude of intermale aggression varies widely among the various wild and laboratory stocks of house mice used in the study of agonistic behaviour (e.g., BROOKS & SCHWARZKOPF 1983, PARMIGIANI 1989, BRAIN & PARMIGIANI 1990), the above results are still consistent with much of the previous research on the behav-

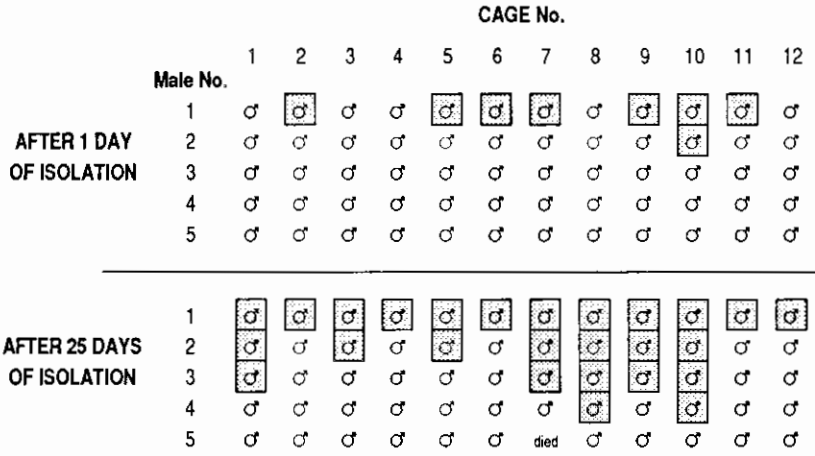

Fig. 1. — The propowrtion of infanticidal (shaded ♂ box) versus noninfanticidal CF-1 male house mice who were grouped five per cage and then tested for their behaviour toward a pup at either 1-day or 25-days after being ungrouped and singly housed. All testing was done in random cage and male order. For graphical purposes, however, the within-cage data are arrayed here to best visualize the overall proportions of behaviour within each of the caging subgroups.

iour and physiology of group-housed versus singly housed male mice. Specifically, isolated (singly housed) male house mice typically exhibit territoriality and aggression levels similar to that of dominant males (BRAIN & BENTON 1977, PARMIGIANI et al. 1981). It must be emphasized, however, that our results do not specifically eliminate the possibility that merely grouping five animals per cage (regardless of sex) would also result in the suppression of infanticide, nor did we attempt to identify the dominant male in each cage. Nevertheless, the cage-by-cage data displayed in Fig. 1 matches remarkably well with the results predicted by *hypothesis 3* above.

Female rodents have evolved counterstrategies which either inhibit infanticidal males from killing their litters (MENNELLA & MOLTZ 1988) or enable them to cut their reproductive losses early in pregnancy when threatened by infanticidal males (e.g., the "Bruce effect"; see ELWOOD & KENNEDY 1990). Interestingly, our data here suggest that male mice have also evolved a counterstrategy for inhibiting other males from killing pups. In natural situations, for example, house mice often form small social units in which a dominant male controls a breeding harem of several females (e.g., DEFRIES & MCCLEARN 1972). Non-breeding, satellite males may also be present in these microdemes. Through defeat and subordination the dominant male would obviously benefit by safeguarding his own offspring from attack. On the other hand, subordinate males may also be non-dispersers who were born in the same microdeme, possibly even sired by the dominant male. Under these social conditions, subordinated males would be beneficially inhibited from killing their close relatives, including their full- or half-siblings in recently born litters. Stability and reproductive success could thus be preserved in these social units as long as the dominant breeding male can subordinate his rivals.

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