Signaling and Priming Communication: Independent Roles in the Reproductive Isolation of Spatially-Separated Populations of Rodents

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Summary. This research concerned the relative potential for signaling and priming incompatibilities to promote reproductive isolation in rodents. Signaling is defined here as involving behavioral responses, while priming involves endocrine responses. Compatibility of both types of communications was tested between two widely separated and markedly diverging populations of deermice, and between equally separated but much less divergent populations of house mice. Signaling compatibility was assessed by comparing the amount of aggression toward young females by adult males when the two sexes were of the same vs the different stock of the same species. Priming compatibility was tested by measuring the relative amounts of uterine growth induced in young females by exposure to adult males.

No signaling or priming incompatibilities were detected during cross-testing of the house mouse stocks. A degree of developing reproductive isolation was observed between the two deermouse populations, however, and this isolation was reinforced by independently occurring incompatibilities of both the signaling and the priming type. The signaling incompatibility was particularly dramatic, manifesting itself in the killing of young females by adult males.

The present results provide the first demonstration of a priming incompatibility supporting reproductive isolation in diverging populations of a mammal. Furthermore, our results suggest that signaling and priming systems are independently subject to evolutionary change even when both systems probably operate through the same sensory modality.

Introduction

Whether conveyed via visual, auditory, tactile or olfactory pathways, the social cues that influence mating in mammals may be categorized functionally as either signals or primers (e.g., Wilson and Bossert 1963; Bronson 1968). Signaling cues, defined as those with a potential for exerting an immediate effect on a recipient's behavior, always form the basis for mate recognition. Cues emanating from one animal also may trigger neuroendocrine activity in another animal, thereby physiologically priming the latter for a fertile mating. In house mice, for example, unidentified chemical signals found in an individual's urine convey olfactory information relevant to its species, sex, stage of maturation and reproductive state, while unidentified chemical primers, also found in urine, modulate the release of the gonadotropic hormones in members of the opposite sex (reviewed by Bronson 1971, 1979; Vandenbergh 1975).

It is widely accepted now that signaling systems are important mediators of reproductive isolation in mammalian populations. In contrast, nothing is known about the role of priming factors in this regard. A major concern of the present research was with this last possibility. Specifically, we compared the relative compatibility of signaling and priming communication between two geographically separated populations of each of two common rodents, the deermouse (Peromyscus maniculatus) and the house mouse (Mus musculus). The two test populations of each species were separated by roughly 3,000 km. While the house mouse remains relatively impervious to geographical divergence in North America, the deermouse, however, displays a history of rapid evolutionary divergence. Our two test populations of deermice thus represented different subspecies, P. m. borealis and P. m. pallescens. Preliminary mating and pregnancy tests established that these two deermouse populations were partially isolated reproductively whereas our two house mouse populations showed no obvious signs of reproductive incompatibility.
Materials and Methods

Compatibility of communication was assessed by comparing the results of both brief and prolonged interactions between males and females of the same or different populations of the same species. Three such experiments were conducted: (a) signaling recognition was tested by observing the aggressive reactions of an adult male to an anesthetized prepubertal female for a 5 min period, followed by a 24 h test of aggression in which the same test males were cohabited with active, awake females; (b) primer recognition was tested by measuring uterine growth in a prepubertal female cohahited with an adult male for several days; and, finally, (c) to obtain a gross indication of the degree of reproductive isolation existing between our test populations, the potential for pregnancy was assessed among all combinations of sexes and stocks of the same species over a 35-day period of pairing. The origin of the experimental stocks, their maintenance, and those procedures common to all three experiments will be considered in this section, while the specific methodology of each experiment will be presented along with its results.

Animals. The progenitors of our stock of P. m. borealis, a robust woodland race of deermice, were trapped in 1979 near Fairview in northern Alberta by Mr. James Lopez, who also trapped the ancestors of our P. m. pallescens stock, a smaller prairie dwelling race, near Austin, Texas in the same year. The ancestors of one stock of house mice were trapped in barns in the Austin area in 1979 while the others were trapped that same year in granaries near Calgary, Alberta, by Dr. Paul Anderson. Thus, the two deermouse populations are separated by about 3,200 km and the two house mouse populations by about 2,700 km.

Maintenance and General Procedures. The four breeding colonies were housed in separate animal rooms at 21 ± 1°C. Alberta deermice were maintained on an 18L:6D light cycle and Texas deermice were held on a 10L:14D light cycle. Both house mouse colonies were kept on a 14:10 L:D cycle. Of these four stocks, however, only the reproduction of P. m. borealis is photoperiodically controlled (Bronson 1979; Lopez 1981). All animals used in the present research were second to fourth generation offspring housed in 18 x 29 x 13 cm polypropylene cages with pine shaving bedding and Wayne Breeder Blox mouse food ad lib. Experimental animals were weaned at 21-22 days of age; females were grouped 4-6 per cage until used at either 23-29 or 60-80 days of age, whereas males were isolated at weaning and not used until a minimum of 80 days of age.

Results

Signaling Compatibility During 5 min and 24 h Tests

Prepubertal females (23-24 days of age) were anesthetized with Nembutal and placed belly-down at one end of the home cage of an adult male of either the same or the different stock of the same species. Preliminary experiments revealed excessive behavioral variation if both sexes were awake and interacting, and, in addition, communication during brief encounters is primarily olfactory based in both species (Bronson 1981); hence, the anesthetization of one sex seemed reasonable. The male’s reactions were observed for 5 min after which the anesthetized female was replaced with an awake female of the same stock. After 24 h each cage was quietly checked for shared vs. separate nesting. Females then were killed, skinned, and examined for bite marks on the inside of the pelt. The design of this experiment was a 2 x 2 factorial for each species with 11 male deermice and 12 male house mice tested in each cell. All testing occurred between 08.00-11.00 h.

Several measures were quantified during the 5 min encounters (e.g., the latency to contact, the nature of that contact, and the anatomical location of contact), but there was no patent evidence of population differences in these behaviors. Statistical analyses of these data usually showed only subtle behavioral differences between populations with little indication of cross-population incompatibility. However, dramatic evidence of a signaling incompatibility was observed when male Alberta deermice encountered female Texas deermice. Three Alberta males began to eat their anesthetized female Texas cage mates immediately after making physical contact. This observation was reinforced in the 24 h tests, the results of which are shown in Fig. 1, where three more Alberta males killed and partially devoured Texas females (P < 0.01 by Fisher Exact Probability Test). Of the remaining five test pairs of this particular combination, two other females were severely bitten and near death. In sharp contrast, all other deermouse pairings resulted in shared nesting and no female had been bitten after 24 h. The 24 h observations of house mice, also shown in Fig. 1 reveal a relatively high occurrence of separate nesting and two cases where females were killed, but no suggestion that cross-stock pairings were more incompatible than same stock pairs in this regard.

Primer Compatibility

As background in our test of primer compatibility, it is well established now in both house mice and laboratory stocks of P. m. bairdii that the female’s ovulatory cycle is markedly dependent upon priming cues emanating from males. The effects of such primer