

Conflict avoidance among rhesus monkeys: coping with short-term crowding

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Abstract. Two contrasting models were examined, each of which predicts a relationship between space and aggression in primates. A 'spatial density' model predicts that as spatial densities increase aggressive responses also increase. A more recent 'coping model' suggests that, over long periods of time, animals will adapt to crowded conditions by increasing appeasement behaviour and allogrooming to reduce social tension and the incidence of aggression. This study evaluated these models within the context of a traditional short-term crowding experiment by examining changes in behaviour when a well-established group of 61 rhesus macaques, *Macaca mulatta*, was periodically crowded into a familiar area one-fifth the size of its normal enclosure. Data from a sample of 20 adult subjects of both sexes showed that no significant increases in intense aggression occurred. Only mild forms of aggressive behaviour increased under the crowded conditions (threat and rough behaviour) and increases in rough behaviour were highest towards infants. Submissive behaviour such as avoidance and the bared-teeth display increased during crowding, and increases in the bared-teeth display were highest between same-sexed adult partners. Analysis of the rank distance between the performer and recipient of bared-teeth displays indicated that increases were most pronounced from the lowest- to the highest-ranking animals. Crowding produced a general increase in huddling with a corresponding decrease in grooming, and these changes across conditions were mostly attributable to interactions among kin. Results provide only partial evidence for both models and indicate that neither one by itself is adequate to explain behaviour in short-term crowding situations. Under short-term crowding, this group appeared to adopt a conflict-avoidance strategy rather than a more active tension-reduction strategy.

Modification of social behaviour in response to immediate changes in the environment represents intraspecific variation in social systems (Lott 1984). In contrast to genetically determined behavioural changes resulting from long-term evolutionary adaptations, intraspecific variations in social systems are short-term behavioural changes that represent a capacity within the present genome to make adaptive behavioural adjustments in response to the current environment (e.g. predation; food availability; population density; and habitat availability). One example from over 100 vertebrate cases catalogued in Lott's review is the behaviour of deer mice, *Peromyscus maniculatus*, which are territorial at high densities but exhibit undefended home ranges when population densities drop (Mihok 1979). Although such shifts in social behaviour are typically investigated through

socioecological studies conducted in the field, behavioural flexibility in response to changes in environment can also be assessed in the laboratory (e.g. Anderson & Hill 1965). Captive studies represent the extreme of a continuum of environmental pressures, but may reveal adaptive capacities not readily identified in the field. Studies of non-human primates are of particular interest because their complex cognitive abilities in the social domain (e.g. de Waal 1989b; Cheney & Seyfarth 1990) may underlie adaptive capabilities not evident in other species.

A 'spatial density' model proposes that as population densities increase, aggressive behaviour also increases. The popularization of this relationship can be attributed to Calhoun's (1962) classic study of the effects of overcrowding on the behaviour of rats. When confined colonies were allowed to breed until overpopulated, aggressive behaviour increased. Similar effects of crowding have been found in other species (e.g. rabbits, *Oryctolagus*

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