

aroused the animal, the greater the immunosuppression. Subjects receiving inescapable stress may experience greater arousal, as indicated by emotional responses and physiological changes, than subjects receiving escapable stress (6-11).

Recent evidence suggests that two immunological mechanisms are involved in tumor defense. After the primary tumor is established, the nonsensitized macrophages and lymphocytes destroy the developing tumor mass and inhibit regrowth (13). The second mechanism involves defense against metastasis, whereby sensitized T cells destroy cells that dislodge from the primary mass (14).

In summary, inescapable shock decreased tumor rejection. The low rate of tumor rejection was not a function of shock per se, but resulted from the animals' lack of control over shock. The psychological experience somehow interfered with the ability of the organism to resist tumor development. These results are consistent with those of Sklar and Anisman (12), and demonstrate that a psychological variable can decrease an animal's ability to reject a tumor.

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16. Each shock box was 30.5 cm long, 20.4 cm wide, and 19.7 cm high. The sides were clear plexi-

glass and the end walls were stainless steel. The floor was a stainless steel grid with bars 0.65 cm in diameter and 1.90 cm apart. On the left-hand wall was a lever 6.80 cm wide protruding 1.5 cm into the box and 6.0 cm above the grid floor.

17. Ten 0.2-cm² portions of the preparation were randomly sampled and tested for cell viability by trypan blue exclusion. Portions yielding 6×10^3 viable cells were used for implantation.
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23. We thank J. Radcliffe for his advice and for supplying the tumor. Supported by National Institutes of Health medical scientist training grant GM 07170 to J.R.V. and by National Institute of Mental Health grant 19604 and University of Pennsylvania biomedical research grant 524 341 to M.E.P.S.

30 December 1981

Behavioral Sequences During Dominance Hierarchy Formation in Chickens

Abstract. Dominance hierarchies near linearity (containing mostly transitive and few intransitive triads) are common in many species. Analysis of the possible sequences for forming dominance relationships shows that two ensure transitivity, and two others produce either transitive or intransitive triads. Experiments with chickens show that in groups of three and four they most often use the two sequences that ensure transitivity and thus linear hierarchies. Examination of such sequences may help explain the formation of near linear hierarchies in other species.

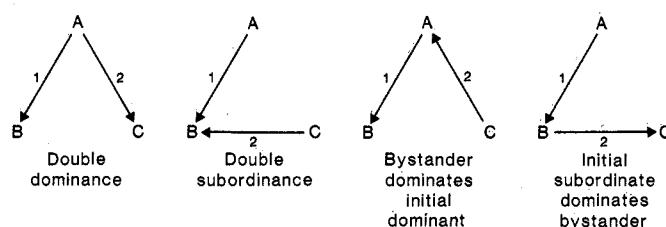
Although research in social ethology has provided information about the impact of social relationships and roles on behavior and fitness in animals (1), much less is known about the processes or mechanisms through which social relationships are formed and roles occupied (2). This study describes behavioral processes used by chickens in forming one of the classic social structures in ethology: linear and near linear dominance hierarchies. Such hierarchies are found across a broad range of species including, for example, wasps, bumble bees, chickens, cows, buffaloes, rhesus monkeys, and young humans (3, 3a).

Earlier research has attempted to explain the structural form of dominance hierarchies by differences in individual attributes like aggressiveness, size, hormone levels, and past social performance or differences in pairwise competitive ability (1). However, analytical work by Landau and Chase (4), and experimental results of Bernstein and Gordon and King (5) indicate that although individual difference and pairwise ability models provide useful information about dominance relationships, they do not explain hierarchy structures themselves.

In order to discover the behavioral processes used in hierarchy formation I observed the establishment of dominance relationships in groups of chickens. Chickens are a good choice because they readily form linear hierarchies in small groups, and their dominance behavior is well defined. In the first experiment I used 24 groups, each with three white Leghorn hens (triads), and in the second experiment I used 14 groups of four (tetrads). The hens in each group were either unacquainted, or if acquainted, had been separated for several months—enough time to forget previous relationships (6). Hens were housed individually before triad and tetrad grouping and were observed in a neutral cage in a separate room.

When put together, all occurrences of three aggressive contact behaviors were recorded: peck (including feather pull), scratch (with the claws), and jump on. An SSR keyboard (7) was used to record data for the triads and an Apple microcomputer for the tetrads. The triads were observed for 4 hours each and the tetrads for 12 hours (8) each; a combined total of 2801 aggressive acts were recorded for the triads and 7402 acts for the tetrads (9).

Fig. 1. The four possible sequences in the formation of the first two dominance relationships in triads. Relationships are numbered in order of formation.



One hen was considered to dominate another if she delivered any three aggressive actions in a row to the other and there was a 30-minute period following the third action during which the receiver did not attack the initiator. Once formed, a dominance relationship could be reversed if the subordinate fulfilled the criteria against the dominant (10).

I used these dominance criteria to determine the sequential patterns used in forming the first two dominance relationships in triads. There are only four possible patterns for the first two dominance relationships (Fig. 1): the initially dominant individual (A) can go on to dominate the bystander (C), the bystander can dominate the initially subordinate individual (B), the bystander can dominate the initial dominant, or the initial subordinate can go on to dominate the bystander. These patterns are labeled, respectively, double dominance (DD), double subordination (DS), bystander dominates initial dominant (BDID), and initial subordinate dominates bystander (ISDB). If it is assumed that the direction of the dominance relationship is determined randomly for each pair, then each of the four patterns would have an equal probability of occurring. However, the four patterns do not have equivalent implications for the formation of linear hierarchies. In a linear hierarchy, the dominance relationships in all possible component triads are, by definition, transitive. In a triad with a transitive dominance relationship, if A dominates B, and B dominates C, then A also dominates C. If a hierarchy is not linear, then it contains at least one component intransitive triad, and the more intransitive the triad, the further it is from a linearity hierarchy. In an intransitive triad if A dominates B, and B dominates C, then C dominates, rather than is dominated by, A (Fig. 2). The DD and DS patterns guarantee transitive triads regardless of the direction of the third relationship, but the BDID and ISDB patterns can lead to either transitive or intransitive triads (11). Consequently, if all the component triads in a larger group have either DD or DS patterns, a linear hierarchy will necessarily result. On the other hand, if some component triads have either BDID or ISDB patterns, a nonlinear hierarchy can occur.

In the first experiment with isolated triads, 21 out of 23 (12) triads (91 percent) had the patterns guaranteeing transitivity: 17 (74 percent) had DD, four (17

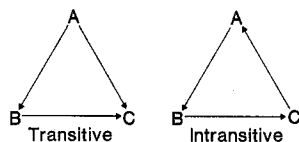


Fig. 2. The configuration of relationships in transitive and intransitive triads.

percent) DS, one each (4 percent) BDID and ISDB [$\chi^2(3) = 30.4$, $P < .001$]. In other words, the results indicate that initial winners frequently go on to win again, bystanders are usually successful only against initial losers, and initial losers usually withdraw from further dominance contests (13).

Although tetrads have only one more member than triads, the number of component triads goes from one to four, and in this experiment I tallied the pattern frequencies using the first two dominance relationships in each component triad (9, 14). The results corroborated those of the first experiment and indicated that the majority (48 out of 55 component triads or 87 percent) again exhibited the two patterns ensuring transitive dominance relationships: 33 (60 percent) exhibited DD, 15 (27 percent) DS, three (6 percent) BDID, and four (7 percent) ISDB (9, 12) [$\chi^2(3) = 42.4$, $P < .001$]. Thirteen out of 14 tetrads had linear hierarchies by the end of the observation period, and one tetrad had a hierarchy guaranteed to be linear regardless of the direction of a missing dominance relationship [$\chi^2(1) = 23.3$, $P < .001$].

These results support what might be termed a "jigsaw puzzle" model of hierarchy formation where the "pieces" can be represented by triadic interaction patterns. This model, then, proposes that the linear and near linear hierarchies commonly observed in small flocks of chickens result from a predominance of double dominance and double subordination patterns in component triads of larger groups. The model does not suggest, however, that chickens purposively strive to create transitive dominance relationships, but rather that triadic patterns are the outcome of interactions during hierarchy formation.

The mechanisms suggested here for hierarchy formation may be independent of animal type and the jigsaw puzzle approach may have wide applicability for the many species that commonly form linear and near linear hierarchies. For example, Barchas and Mendoza (15) found the exclusive use of double domi-

nance and double subordination patterns in both male and female rhesus monkey triads.

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8. Tetrads were observed for 6 hours on each of two successive days; partitions separated the chickens in the observation cage when data were not being collected.
9. See I. D. Chase (*Behaviour*, in press) for further information on methods.
10. Although somewhat arbitrary, these criteria appear to be valid indicators of stable dominance relationships; out of 52 dominance relationships initially formed in the triads, only two were later reversed.
11. For example, when the third relationship is formed, the one between B and C, the DD pattern results in either (i) A dominates B, B dominates C, and A dominates C, or (ii) A dominates C, C dominates B, and A dominates B, both transitive triads. In the BDID pattern, if B later dominates C, there is an intransitive triad, but if C later dominates B, there is a transitive triad.
12. One triad did not form at least two dominance relationships and was dropped from this analysis.
13. G. McBride [*Anim. Behav.* 6, 87 (1958)] reports a similar "lag effect": hens that win initial pairwise contests tend to win successive ones, but hens that lose tend to keep losing.
14. For example, if dominance relationships in tetrad ABCD were formed in the following sequence: A > B, A > C, A > D, B > C, B > D, D > C, then component triad ABC would have a DD pattern, triad ABD a DD, triad ACD a DD, and triad BCD a DD.
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22 September 1981; revised 12 January 1982