Threat and attack in the alpha male rat

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Threat and attack behavior in the socially dominant (alpha) male rat are defined, and a proposed interpretation of their related functional significance is presented. It is suggested that temporal proximity of threat to attack facilitates social avoidance learning by the attacked conspecific. Threat behaviors constitute a varied, multisensory display, biologically more economical than repeated attacks, in achieving the posthaste withdrawal of unfamiliar male intruders. Biting attack and associated pain determine the significance of threat for the subordinate male. Threat and attack constitute parallel social behaviors for effecting the denial of continued presence to unfamiliar males and thereby limiting their copulatory access to receptive females.

An early study of wild-trapped rats made specific reference to their aggressive nature, noting in detail the behavior of colony residents in response to conspecific intruders: "A most pronounced characteristic of gray rats, and one that time and captivity have not changed to any extent as yet, is their decided aversion to the presence of strange rats. If the inhabitants of the cage are adults, they will at once attack and soon kill the intruder, no matter how large it may be. Even if the new arrival had formerly been housed in the cage, and had been absent but a day or two, it promptly meets with the same fate as that of a total stranger. When a rearrangement of adult rats of mixed sexes is necessary, the only way to insure each of the individuals more than a fair chance of life is to etherize all of the rats, give them a bath in a fairly strong solution of some disinfectant, such as creolin or larkspur, and then place them in a recently sterilized cage containing a quantity of sterilized bedding. The bath destroys the nest odor of the rats and sterilization removes all other animal odors from the cage and bedding. The rats huddle together under the bedding for some time, dazed by the ether and thoroughly cowed by the treatment they have received. When they have become dry and have ventured from hiding to inspect their new quarters, they are usually friendly and do not fight subsequently. Even this drastic treatment is not always effective, however, and after this procedure it is not uncommon to find on the following day that one or more of the individuals have been killed" (King & Donaldson, 1929, pp. 66-67). Supplementary descriptions of intruder-elicited aggression have been widely circulated with comparable emphases upon the significance of olfaction (Adams, 1976; Alberts & Galef, 1973; Barnett, 1955, 1958a; Calhoun, 1962; Flannelly & Thor, 1976; Steiniger, 1950).

THREAT VS. ATTACK

An apparent and useful classification of intermale conspecific aggression is that of threat and attack. Attack normally refers to the rapid bite and kick

sequence that occurs infrequently but is capable of inflicting lethal wounding. Repeated attacks and sustained threat contribute to internal stress-related trauma (stomach ulcers and thin-walled intestines), as described by Lore and Luciano (1977); enlargement of adrenals and kidney ulceration have also been described (Barnett, 1958b; Barnett, Hocking, Munro, & Walker, 1975). Deaths have been observed in the absence of external wounds (Barnett & Evans, 1965).

Threat behaviors include postures, movements, sounds, and odors that appear to signal a clear warning to the intruder. The intruder reacts to such display by decreasing ambulation or withdrawing. Some threat behaviors appear quite obvious and generally occur immediately prior to attack (i.e., piloerection, tooth-chattering, and lateral display); other forms are not immediately apparent to the human observer, such as the generation of certain odors (Barnett, 1964) and ultrasonic vocalizations (Sales, 1972). Detailed discussions of specific forms of threat are available elsewhere (Barnett, 1958a; Blanchard & Blanchard, 1977; Grant, 1963; Grant & Mackintosh, 1963).

The topography of intermale aggression differs from predatory behavior. In the former, threat is more prevalent than biting attack; in the latter, speed and efficiency of lethal attack are more distinctive (O'Boyle, 1974). Blanchard and Blanchard (1977) noted that bites on a conspecific male intruder are typically found on the dorsal skin surfaces (70% on back and shoulders) and the tail or limb areas (11%), that is, areas not particularly vulnerable. A mouse kill, in comparison, frequently occurs with a deep bite through the cervical spine; unattended neonatal rat pups are simply picked up by the front paws and eaten without evidence of arousal (Paul & Kupferschmidt, 1975).

Lethal attacks upon conspecifics and number of deaths recorded have been emphasized in a number of reports. But this extreme aspect of aggressive behavior may have overshadowed the prevalence and significance of threat. Availability of escape routes would very likely decrease the number of conspecifics killed or seriously

wounded since eviction appears to be the primary goal.

When two alphas meet on neutral territory, both may initially exhibit threat and attack, but within a matter of minutes one animal is "defeated" and thereafter assumes only defensive behavior (Thor & Carr, in press). The dominant alpha continues to threaten and occasionally attack; however, threat then constitutes a far greater proportion of aggressive activity than does attack. Attacks occur infrequently and are of very brief duration (at most, 1 or 2 sec), but threats occur frequently, in a variety of forms, and may be sustained for intervals as long as several minutes. Threats and attacks have been reported to occur sporadically over the course of days or weeks; hence, the persistence of alpha in maintaining vigilance and harassment is particularly noteworthy (Barnett, 1955, 1958a).

Attack must have great significance in determining the outcome of an encounter between paired alphas. While observing approximately 40 such pairings, it became evident that biting attacks always preceded the point at which one alpha assumed the submissive role (Thor & Carr, in press). Victor and vanquished were readily identified thereafter, since the victor always threatened or attacked and the vanquished always avoided or assumed defensive postures. Avoidance included attempts to escape from the test enclosure, hiding in a remote area, or freezing. In the few instances where no biting attacks occurred, there were no comparably precise delineations of dominance.

Blanchard and Blanchard (1977) compared the relative behaviors of attacker and defender. In their taxonomy, piloerection, tooth-chattering, posturing, and approach-sniff were all designated as attack behaviors. In the present analysis, the distinction between attack (bite) and threat (posture, chase, box, piloerection, vocalization, odor) is of specific interest. *Attack* is defined as hostile behaviors that induce external, physical wounding; *threat* is defined as aggressive behaviors that appear to intimidate but result in no observable external wounding.

INTERPRETATION

It is hypothesized that biting attack conveys the definitive signal of superiority or dominance and constitutes the ultimate warning that continued presence will not be tolerated. Threat often occurs during approach of the attacker and appears to function as a discriminative avoidance signal to the defender (see Lott, 1972). As the attacker approaches, it perceives noxious social stimuli in higher concentration. But release of full biting-kicking attack presumably requires some unknown threshold, contingent upon number of prior attacks, present energy level, maturity, presence of females, and former social experience, in addition to current behavior of the defender.

Repeated departure and return of the attacker to the more stationary defender may serve to repeatedly present the defender with the option of retreat. Movement of the defender while the attacker is nearby, however, leads to further approach, threat, and attack. If the defender flees, the attacker often pursues.

The present interpretation is that the aggressive behavior of alpha is primarily designed to effect the withdrawal of the conspecific male intruder and to achieve this result as readily as possible with the least effort. Lethal attacks occur, but such attacks are more likely when no escape is available. In a highly populated area, death may eventually be the result of attacks by many alphas as the intruder traverses a number of established territories, repeatedly escaping only to confront another dominant male (see Calhoun, 1948). Socially naive males (isolates) sustain more wounds than do socially experienced males (Luciano & Lore, 1975), and previously attacked males are less vigorously attacked than are males lacking former attack exposure (Lore, Flannelly, & Farina, 1976). The behavior of a subordinate male, therefore, seems to confer some degree of protection and may consist of a variety of sensory cues (olfactory, visual, auditory) that decrease the intensity of attack by the resident alpha. A prepubertally castrated mature male is not attacked by an alpha male (Flannelly & Thor, 1978).

FUNCTION

Lactating females, in defense of their nest, will threaten and/or attack either male or female intruders. Estrous females occasionally bite a sluggish male that is slow in initiating copulation; after extended bouts of copulation, females commonly bite and/or threaten males that persist in mounting. In both instances of attack by females, there is no male reprisal.

Threat and attack by males or by females occur in specific social situations and serve specific social functions. The distinctive and frequently reported threat and attack behavior of the alpha male is directed primarily against sexually mature, foreign male intruders and serves to exclude such adult males from the territory or home range occupied by the alpha and its colony. Exclusion of unfamiliar males preserves reproductive access for alpha and for other colony males that are likely to share kinship with alpha. In this way, threat and attack behavior of the alpha maintain inclusive fitness (see Hamilton, 1964; Maynard-Smith, 1964).

A variety of explanations have been proposed for the observed aggressive behavior of dominant males. These include defense of territory (Calhoun, 1962; Telle, 1966), dispersal of population (Barnett, 1958a; Barnett & Evans, 1965), aggressive drive (Lorenz, 1966), and fear conditioning (Seward, 1945). None of the preceding accounts considered the proposed requirement for the

exclusion or containment of male intruders to block their potential for inseminating estrous females (Thor & Flannelly, 1979).

CONCLUSION

Efficacy of threat is contingent upon its temporal and spatial proximity to attack as well as the multisensory diversity of threat signals. Threat and attack constitute the critical behaviors for maintaining genetic integrity by exclusion of foreign males. This inferential analysis is speculative but amenable to experimental inquiry. Theoretical implications include a more intimate association of sex and aggression in this species and a laboratory basis for investigating reproductive strategies.

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