

# The Effect of Deantennation on the Dominant-Subordinate Relationship in the American Cockroach (*Periplaneta americana*)<sup>1</sup>

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**ABSTRACT.** The American cockroach has been observed to exhibit complex social behavior. In this study the effect of deantennation on the dominant-subordinate relationship in the American cockroach, *Periplaneta americana*, was investigated. Ablation of the antennae of a dominant individual caused a reversal in status to occur with a previously subordinate male assuming the dominant position.

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## INTRODUCTION

The American cockroach, *Periplaneta americana*, (Orthoptera: Blattellidae), is known to form non-linear dominance hierarchies. These are defined by Bell and Gorton (1978) as "dominance relationships among individuals in which reversals occur and higher ranking individuals do not always defeat lower ranking individuals in more than 50% of encounters." Males of many cockroach species maintain their status in these hierarchies by overt acts of aggression.

Ewing (1966) found that 80% of cockroach deaths were of subordinate individuals. The signs and symptoms Ewing described as occurring in stressed cockroaches (i.e., sluggishness, stiffness, failure of the cockroach to right itself, twitching, vibrating, and paralysis) were also observed before the death of subordinate American cockroaches in the present study. Ewing and Ewing (1973) also found that a subordinate individual could die if it was attacked repeatedly even if it had no visible injuries. Ewing believed that the corpus cardiacum may have an important function in the formation of dominant-subordinate relationships and in stress-related deaths, and demonstrated that there was greatly reduced production of neurosecretions by cockroaches during artificially caused stress.

There are certain advantages to maintaining a dominance hierarchy. Dominant male individuals will have more access to food, water, and shelter. They also have been found to have greater mating success than subordinate males (Breed et al. 1980). The increased frequency of mating is made possible by the ability of the female to determine the status of a male by distinguishing between the odors of individual males.

It has been reported that males can distinguish between dominant and subordinate males by using olfactory cues (Smith and Breed 1982, Moore and Breed 1986). The method by which males determine the status of another male was investigated extensively by Schal and Bell (1983). They found that the following factors had no effect on the dominance hierarchy formed by *Nauphoeta cinerea*: size and mass of the individual, visual cues, factor S (a neuromuscular substance found in the blood), removal of wings, removal of a leg, castration or removal of the corpora allata (an organ which produces pheromones). They determined that removal of the antennae affected male-male interactions. Ablating the antennae of an  $\alpha$ -male

while leaving intact the antennae of the subordinates caused a reversal in status to occur. Removal of antennae from the subordinate male had no effect on the dominant-subordinate relationship. When the antennae of all dominant and subordinate males were removed, no agonism occurred.

The antennae of cockroaches have important functions. In many cockroach species, including *Periplaneta americana*, chemical and tactile stimuli detected by the antennae seem to be the primary releasers of courtship behavior (Fraser and Nelson 1984a). In a study of the deantennation of Madagascan hissing cockroaches (*Gromphadorhina portentosa*) it was found that removal of the antennae from a male individual resulted in fewer copulation attempts, less copulation, and less male antennation, hissing, and posturing (Fraser and Nelson 1984b). Misdirected copulations occurred more frequently and courtship was prolonged. Fraser and Nelson also noticed that males often bit off the antennae of other males. These deantennated males then may have had prolonged courtship with a greater chance of being interrupted by the arrival of another male. Thus, when a male removes the antennae from another male, this might increase his own fitness.

Bell and Sams (1973) found that all the aggressive encounters they observed between male *P. americana* were initiated by mutual antennation (bringing the antennae of one cockroach into contact with the antennae of another cockroach) from the front, or by one male antennating the other from the side or from behind. In other words, fighting always followed antennation.

The present study investigated the hypothesis that deantennation of a dominant male American cockroach (*Periplaneta americana*) would cause a reversal in status to take place, similar to that reported by Schal and Bell (1983) in their study of the cockroach (*Nauphoeta cinerea*).

## MATERIALS AND METHODS

The American cockroaches used in this study were adult males obtained from a large stock colony maintained at the insectary of The Ohio State University, Columbus, OH. The cockroaches were not matched by size and mass because of time constraints and since a previous study by Schal and Bell (1983) determined that these factors were not significant in determining the dominance hierarchy in cockroaches. Each group of three males was kept in a circular plastic container 19 cm deep by 20 cm wide in which the sides had been greased with a mixture of

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petroleum jelly and mineral oil. Environmental conditions were maintained under an approximate 12 hour light: 12 hour dark cycle at 25° C. Non-airtight plastic lids covered the containers at all times. A pellet of dry dog food and a petri dish lid with cotton gauze soaked in water were also placed in each container. A wooden platform with a wooden pole 13 cm high and 8 mm in diameter was mounted in the center of the container.

Twenty-seven adult male cockroaches were anesthetized with CO<sub>2</sub> until they stopped all movement. Each cockroach was marked on the pronotum with red, white, or blue non-toxic tempera paint. Behavioral observations were made three times daily under normal light conditions for five days before deantennation of the  $\alpha$ -males and for four days after the deantennation. The individuals were ranked during each observation by the distance of their pronotum from the top of the pole. The tendency for cockroaches to defend and perch on elevated positions was noted by Seelinger and Schuderer (1985) and Bell and Sams (1973). The  $\alpha$ -male was identified by calculating the relative frequency of each individual at the dominant position near the top of the pole. According to Bell and Gorton (1978), the  $\alpha$ -male can usually be identified by the third day after the beginning of hierarchy formation even though the entire hierarchy may not stabilize until seven to nine days have elapsed.

All the  $\alpha$ -males were again anesthetized with CO<sub>2</sub> and deantennated by removal of their antennae as near as possible to the head. During the experiment any individuals who died were immediately replaced, although individuals who lost legs or antennae were not replaced unless death resulted. The percentage of occurrences in the dominant position by  $\alpha$ -males before and after deantennation of the  $\alpha$ -males, was compared using a paired *t*-test, with significance ascribed to  $P < 0.05$ .

## RESULTS

The percentage of occurrences of the  $\alpha$ -male of each group in the dominant position before and after deantennation were recorded (Table 1). A paired *t*-test revealed a significant difference ( $t = 7.25$ ,  $df = 18$  at  $P < 0.05$ ) between the percentages before and after the removal of antennae. During the course of the experiment four subordinate males died before the removal of antennae from the  $\alpha$ -males. One  $\alpha$ -male died two days after antenna removal. Legs were found missing on several subordinate and dominant individuals during the course of the study, and some individuals had portions of their antennae missing.

## DISCUSSION

This study supports the hypothesis that removal of the antennae from a dominant  $\alpha$ -male American cockroach, (*Periplaneta americana*), causes a reversal in status to take place as was demonstrated in previous studies with *Nauphoeta cinerea* (Schal and Bell 1983) and with *Gromphadorbina portentosa* (Fraser and Nelson 1984b). The unplanned loss of legs and antennae which took place in the present study was probably the result of aggressive male-male encounters. Schal and Bell (1983) observed that fights with dominant individuals sometimes led to the loss of antennae or legs which then resulted in permanent

TABLE 1

Percentage of occurrences in the dominant position by the  $\alpha$ -male American cockroach (*Periplaneta americana*).

Container %	Before deantennation %	After deantennation
1	64	0
2	67	0
3	47	40
4	67	30
5	40	10
6	47	0
7	47	0
8	60	10
9	73	30
mean	57	13
S.D.	12	16
S.E. mean	4	5

subordinate status. Bell and Sams (1973) noted that biting was the main technique used during serious fighting which frequently resulted in removal of legs.

The antennae of an  $\alpha$ -male American cockroach seem to be necessary for it to maintain its dominant position in the hierarchy. It is possible that the  $\alpha$ -male needs to make physical antennal contact with another male to release the aggressive behavior necessary to maintain its position of dominance. This is supported by the observations of *Nauphoeta cinerea* by Bell and Sams (1973) where all aggressive displays were initiated by mutual antennation. Perhaps each cockroach secretes a contact pheromone with a distinct scent which can be detected by antennation. Another possibility is that the antennae are needed by the dominant male to successfully orient and direct his aggressive responses when challenged by subordinate individuals.

Breed and Smith (1982) found that subordinate *N. cinerea* males preferred the scent of a familiar dominant male individual over the scent of an unfamiliar dominant male. They feel that natural selection may favor this trait as a survival mechanism. The results of the present study with *P. americana* support these observations since when a new replacement roach was placed in the container after the death of a subordinate, the new cockroach usually immediately ascended the pole unopposed. Breed and Smith (1982) also reported that subordinates approach dominant male individuals and that it is possible that the male's scent may attract the subordinate males by advertising the fact that females may be present. They also speculated that the maintenance of a minimum distance between the subordinate and dominant individuals was more important than complete avoidance of the dominant individual.

When a dominance hierarchy begins to form, there are a greater number of male-male aggressive interactions according to Bell and Gorton (1978). During this time the individuals may learn which individuals are the most

innately aggressive and grant them dominant status. After this has been determined, a quick mutual antennation may be sufficient to inform the cockroach whether he is confronting a dominant or subordinate individual, and the appropriate response can be made (i.e., a lunge or retreat).

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