Group P made significantly more errors than group S on each of the discriminations (*17*) (see Table 1), while group S-P did not differ significantly from either of the other groups, although they consistently made more errors than group S and fewer than group P. All groups improved through the series of reversals, and all solved the fourth reversal with significantly fewer errors than on the first problem. However, there were no differences between the groups on this improvement trend.

Animals in group S did significantly better (Table 2) than either group P ($t = 12.50$, $df = 39$, $P < .001$) or S-P ($t = 8.90$, $df = 34$, $P < .001$). Group S-P did significantly better than group P ($t = 2.90$, $df = 37$, $P < .01$). Only one subject in group P and three in group S-P achieved scores as high as the lowest score in group S.

Since the groups did not differ in the amount of L-phenylalanine administered during the 60 days, the implication is that the age of treatment (or possibly duration of treatment) affected the later behavior. Since Polidora *et al.* (*2*) demonstrated that neither age nor duration of treatment influenced behavior of subjects treated from weaning, the former alternative is the most likely explanation of the difference in performance in the T-maze. In the reasoning test, significant deficit is found whether treatment is started at birth or at 30 days, with the degree of deficit inversely related to age at initiation of treatment. Although age and duration are confounded, the findings of Polidora *et al.* (*2*) are probably relevant for the reasoning test as well, implying that age at initiation of treatment (rather than duration) was the important variable. The reasoning test is a more sensitive instrument for assessing behavioral deficit than the discrimination test with the T-maze.

The improvement trend in the reversal problems, presumably a measure of reversal set, was not different for the various groups, although Rajalakschmi and Jeeves (*18*) suggest a correlation between intellective level and reversal performance. Response stereotypy and rigidity, militating against reversal sets, are not affected by treatment, whereas the ability to form new associations, and especially to combine disparate experiences, is sensitive to L-phenylalanine treatment. However, there may be another interpretation. These data differ from those typically obtained from rats, in that the mean performance on the first reversal was below that on original learning; they are similar to those obtained when successive discrimination problems with new cues (nonreversal shifts) are presented to rats (*19*). If the rats showed nonreversal shifts (*20*), then no reversal set could be formed, and differences in trends would not be expected.

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9. Causes of death and the frequency of each cause are: injection into lungs (12); perforated lungs (4); middle-ear disease (4); unknown (12). The mortality (all causes) for each group was (percent): L-phenylalanine: 39; saline: 32; saline and L-phenylalanine: 35.
10. We thank Sandoz Pharmaceuticals and Ames Company, Inc., for the L-phenylalanine, Phenistix, and Pheniplates.
11. Electrolyte measurements were made to determine the effects of the excess (3 g/kg) ingested L-phenylalanine upon electrolyte balance. Average values (meq/liter) for group P were: Na, 144.8; K, 7.5; Cl, 117; CO_2, 10.4. Average values (meq/liter) for group S were: Na, 143; K, 8.6; Cl 115.9; CO_2, 12.4.
12. Pheniplate PKU assay kit, Ames Company (Division of Miles Laboratories), Elkhart, Indiana.
13. Phenistix reagent strips, Ames Company (Division of Miles Laboratories), Elkhart, Indiana.
14. The 23-day recovery period was chosen somewhat arbitrarily, but with two considerations in mind: the necessity of allowing for recovery from the possible effects of administration (*1*); and the realization that some drug metabolites remain in the body for a prolonged period (*15*).
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20. The expectations in this regard are: (i) performance on the first reversal (reversal 1) should be better than on the original learning (44 of 58 animals performed better between original and reversal 1); (ii) performance on the later presentations of the original problem should show progressive improvements (39 of 58 subjects did progressively better on the original problem, reversal 2, and reversal 4); (iii) successive presentations of the second problem should show progressive improvement (47 of 58 animals did better on reversal 3 than on reversal 1).

13 December 1966

Fighting and Death from Stress in a Cockroach

Abstract. *Fighting behavior, leading to the establishment of stable dominant-subordinate relationships between pairs of males, is described for the cockroach* Nauphoeta cinerea. *Deaths, which do not appear to be due to external damage, occur in subordinate animals as a result of fighting. The situation is likened to death from stress as found in mammals.*

Intraspecific fighting between males has been described for a number of insects including field crickets (*1*), cicada-killer wasps (*2*), ants where fighting occurs between colonies of the same species (*3*), and for a wood roach where the male defends a mating chamber against rivals (*4*). Although no published records have been found, fighting can be observed commonly between adult males of the cockroach *Nauphoeta cinerea*, where it appears to be associated with a loose territorial system. Fighting, which first appears on the 2nd and 3rd days after the imaginal molt, involves a complex sequence of events that eventually establishes a stable dominant-subordinate relationship between members of a fighting pair.

In an encounter between two more-or-less evenly matched males, a fairly consistent sequence of events can be observed. Both animals, with heads lowered, extend upwards the last three or four abdominal segments, simultaneously lifting the body high off the ground (Fig. 1). This posture may be assumed on sight, when one aggressive male crosses the path of another, or after brief but rapid antennal flagellation (fencing) between the two animals. This posture could be described as aggressive. It always preceeds fighting but may cause a less aggressive male to flee. Following this display, two aggressive animals charge towards each other with their heads lowered and butt on contact. If one cockroach successfully engages its pronotum under that of its opponent, it may toss the rival in the air so that it falls on its back. Less frequently, males may grapple with their legs locked together and bite at each other as they roll over and over. A critical stage is usually reached within a few minutes, and one animal emerges superior.

The behavior of the loser is quite characteristic. After prolonged chasing by the dominant, it suddenly lies still

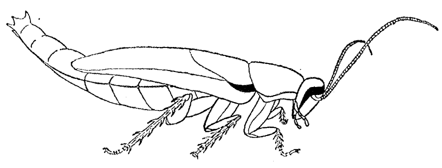

Fig. 1. The aggressive posture.

and tucks its limbs under its body and its head under the shield of the pronotum. The antennae either lie flat on the ground, straight in front of the animal, or, less frequently, pointing backwards, parallel to the body, which is always pressed close to the ground (Fig. 2). Once this posture has been adopted, the subordinate animal no longer attacks the dominant; it runs underneath its superior and adopts the subordinate posture if subjected to attack itself.

It is possible to determine the dominant-subordinate relationship within a pair of males from their response to a test animal, a live adult male attached to a thin balsa-wood stick by means of a wire threaded through the pronotum. Amputation of its tibiae and tarsi restricts the movements of the test animal, thus facilitating manipulation. Antennal contact is allowed between the test animal and the subject, this generally being sufficient to elicit a response. Dominant animals typically adopt the aggressive posture and may attack the test animal, whereas subordinate animals do not respond aggressively and adopt the subordinate posture. Test animals can also be used in the determination of the earliest age at which the fighting response can be elicited in young adult males. Indeed, until fighting has appeared, dominant-subordinate relationships cannot be established.

In the course of experiments to determine the time at which fighting first appears, it was noticed, incidentally, that, over the first few days after the adult molt, the death rate among paired males was rather high. I set up three groups of young adults to see if there was some connection between these deaths and fighting (Table 1).

Table 1. The relationship between fighting and death. Single males, still teneral, were left untouched as controls (group 1); pairs of males, still teneral, were left untouched (group 2); and pairs of males, still teneral, were confronted once daily with the test animal (group 3).

Group	Males (No.)	Deaths (No.)	Deaths in subordinates (No.)
1	30	3	
2	30	7	
3	30	15	12

The numbers of deaths occurring in the first two groups do not differ significantly ($\chi^2 = < .3$). The findings for the third group indicate that there is an increase in the number of deaths following repeated presentation with the test animal and that, where deaths do occur, they occur in subordinate animals in 80 precent of the cases. In all 12 subordinate animals, death occurred on days three and four, that is, after fighting had first appeared in the dominant. The increase in death rate is significantly different from that of the control group ($\chi^2 = .01$) and probably significantly different from group 2 ($\chi^2 = .05$).

It would seem that there is some connection between deaths in subordinate animals and fighting. It is puzzling, however, that more deaths do not occur in group 2. Casual observation suggests that, if these animals fight at all, they fight considerably less than animals of group 3. It may be that cage mates reared together from the time of emergence do not fight each other unless presented with a novel stimulus—in this case, the test animal. This phenomenon is not unknown and has been called passive inhibition. It occurs in young mice that normally fight at 35 days of age but do not fight cage mates with which they have been reared (*5*).

To test whether deaths from fighting occurred in older cockroaches, I set up two more groups. Pairs of males were left together for 24 hours, then presented once with the test animal. As controls, single animals were treated in the same way. Both groups were observed for a period of 10 days, and the deaths were recorded.

No deaths occurred in the control group of 30 animals. Four of the 30 experimental males died, and all of these were subordinate animals. This offers some support for the suggestion that there is some connection between being subordinate and dying after fighting. It also suggests that older adults are less susceptible to death under these conditions.

Some mention must be made of the events leading up to deaths. Once a dominance relationship has been established, the frequency and intensity of fighting is usually reduced. Sometimes,

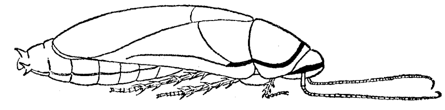

Fig. 2. The subordinate posture.

however, the adoption of a subordinate posture on the part of the inferior animal fails to allay attack, and the dominant animal may continue to fight for long periods of up to 30 minutes. Towards the end of this time the movements of the submissive become sluggish and stiff; the righting reflex disappears; and a state of semi-paralysis, affecting the abdomen and limbs, sets in. Animals in this state apparently do not recover, and death soon follows. They die after an extended bout of fighting but characteristically show no signs of external damage. Some animals do survive prolonged attack over a period of several weeks. Such animals may have entire wings or limbs removed by their superiors.

The situation bears striking resemblance to the social stress found in mammals. Male rats in particular show a well-marked dominant-subordinate behavior. Prolonged aggression produces stress in the subordinate, and ultimately a disease state, characterized by the stress syndrome, leads to death, which cannot be attributed to external damage (*6*). Subordinate cockroaches may die from some internal changes comparable to those accompanying the stress syndrome in mammals.

Several problems arise from these observations; the corpus cardiacum may play some role in the development and maintenance of dominant-subordinate behavior and in death from stress. Indeed, it repeatedly shows severe depletion of neurosecretory material during artificially induced stress, such as forced hyperactivity and electrical shocks (*7*).

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19 December 1966