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【Research report】

年齡與經驗對雄性蟑螂(Nauphoeta cinerea)間強弱關係之影響【研究報告】

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Abstract

摘要

在灰色蟑螂(Nauphoeta cinerea)雄性之間的對峙中，直到28日齡左右，年齡較大的雄蟲有成為強者的趨勢。雄蟲一旦有弱者的經驗，在以後與其他雄蟲相遇時，會明顯減少其成為強者的機會。在一連串的相遇中，每次建立關係所需時間不呈顯著性遞減。去除精巢並不影響其以後成為強者的機會。雌蟲在T型氣味選擇試驗中，並不會趨向強者或有強者傾向的雄蟲。本文對如何分辨雄蟲社會階級的機制有進一步的探討。

Key words:
關鍵詞: Nauphoeta cinerea、經驗、強弱關係、社會行為、蟑螂。

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Impact of Age and Experience on Dominance Relationships of Male Cockroach, *Nauphoeta cinerea*

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ABSTRACT

In male-male agonistic encounters of the cockroach *Nauphoeta cinerea*, older males are more likely to dominate younger ones, up to an adult age of about 28 days. Prior subordinate experience significantly reduces males' chances to dominate subsequent encounters. The required time for establishing a relationship showed no significant decrease with successive encounters. Ablation of the testes showed no effect on subsequent dominance status. Females did not actively approach dominant or potential dominant males in a T-shaped olfactometer test. Mechanisms for the discrimination of males of different social status are discussed.

Key words: *Nauphoeta cinerea*, experience, dominance, social behavior, cockroach.

年齡與經驗對雄性蟑螂(*Nauphoeta cinerea*)間强弱關係之影響

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摘　要

在灰色蟑螂(*Nauphoeta cinerea*)雄性之間的對峙中，直到28日齡左右，年齡較大的雄蟲有成爲强者的趨勢。雄蟲一旦有弱者的經驗，在以後與其他雄蟲相遇時，會明顯減少其成爲强者的機會。在一連串的相遇中，每次建立關係所需時間不呈顯著性遞減。去除精巢並不影響其以後成爲强者的機會。雌蟲在T型氣味選擇試驗中，並不會趨向强者或有强者傾向的雄蟲。本文對如何分辨雄蟲社會階級的機制有進一步的探討。

關鍵詞： *Nauphoeta cinerea* 、經驗、强弱關係、社會行爲、蟑螂。

Introduction

The gregarious cockroach *Nauphoeta cinerea* has a social dominance hierarchy among males (Moore, *et al.*, 1988), which acts to reduce the likelihood of fighting. Although no one factor has been shown to be the key predictor of dominant-subordinate relationships, some are known to correlate significantly with status, including age (Schal and Bell, 1983), previous social experience (Ewing and Ewing, 1973; Schal and Bell, 1983; Moore, *et al.*, 1988), and presence of females (Breed, *et al.*, 1980; Schal and Bell, 1983). Subordinate males not only can recognize individual males but can also distinguish between the odors of familiar and unfamiliar dominant males (Smith and Breed, 1982).

The number of offspring of females is independent of their mates' status, as males do not provide nutrients in the spermatophore or tergal gland secretion (Moore, 1988). However, females can discriminate between dominant and non-dominant males on the basis of odor (Breed, *et al.*, 1980) and tend to approach dominant males more quickly (Moore, 1988). Female choice thus confers a fitness advantage to high dominance status (Moore, 1990).

We investigate here some factors that influence the establishment of social status among males of *N. cinerea*. Males of different age were used in a series of contests to determine the influence of age and prior experience. Testectomized males were used to test for a relationship between reproductive capability and social stutus. We also investigated whether females could discriminate males of different status or social experience by odor only.

Materials and Methods

The culture of the cockroach

The cinereous cockroach, *Nauphoeta cinerea*, was obtained from a culture kept in our department for at least 2 years. Cockroaches were placed in a transparent plastic jar (18cm dia. X 23cm) with President® dog chow and water. Several pieces of Styrofoam were provided as hiding places. The plastic jars were under constant 28°C, 16L:8D conditions. All cockroaches were isolated immediately after emergence to ensure their virginity. Each individual adult was kept in a transparent plastic cup (8 cm dia. X 5.5 cm) with a screen lid, with dog chow and water provided. Adults were kept in the same environmental chamber as immatures.

Age and experience effects

Each adult male was marked with an inked number over a white paint spot. A newly

emerged male and a 7-day-old male were placed in an 8 X 55 cm arena to compete for dominant status. After relationship was established they were isolated for another 7 days and then exposed to another round of competition, then again isolated for 7 days. This process lasted for 2 months. The dominance relationship was recognized by the first avoidance behavior. The dominant male was recognized as he was chasing or pushing away the other, and he usually held the floor of the arena. The Subordinate male avoided encounter and usually kept to the wall of the arena. If the two males stood together or showed no avoidance within 15 min of the start of testing, the interaction was scored as non-agonistic. Both the status of each male and the time taken to determine the relationship were recorded. Twenty pairs of males were used in this experiment.

To further test whether previous experience as a subordinate affects competitive ability, randomly selected virgin males of different ages were paired to establish dominance. All subordinates were then paired with other virgin males and the outcome recorded.

Testectomy effects

Newly emerged males were fasted in a humid environment for 24 hours, then testes were surgically ablated. They were immobilized during the operation with crushed ice, as an alternative to chemical anesthesia. The operated males were allowed to recover in a humid vial (8 cm dia. X 5.5cm) without food for another 24 hours and then given free access to dog chow and water. After 7 days of recovery, the testectomized males competed with sham operated males for dominance. Verification of the testectomy was determined by dissection at the end of the experiment. The frequency of being dominant was analysized by the G-test for goodness of fit (Sokal and Rohlf, 1981) for departure from a 50% probability.

Female choice

A T-maze (Fig.1) was used to test whether females preferentially approach dominant males on the basis of odor. Seven-day-old virgin females were selected, since females of this age had the highest mating rate in the laboratory (personal observation). Each was given a choice between two 7-day-old males confined in the two upper chambers. The perforated end panels of the chambers allowed an airflow toward the lower chamber. Two equal airflows were created by suction from a vacuum pump connected to the base of the lower chamber. A female was released from the lower chamber and allowed 30 minutes to make a choice. A choice was recorded as a turn toward one or the other upper chamber. Ten pairs of males used in the test had already established their relationships. Another 10 pairs of males had not established relationships before the choice test and were allowed to do so immediately afterward. After each test, the T-maze was wiped clean with 75% alcohol and aerated by vacuum for 30 minutes to eliminate odor. The frequency of choice was analyzed by the G-test for goodness of fit (Sokal and Rohlf, 1981) against random choice.

Results

Age and experience effects

Age had definite effects on dominance status when males of 7 days age difference were paired (Fig.2). Older males in the pairs increased their frequency of becoming dominant from 20% at 7 days to 75% at 28 days old. Due to the increasing frequency of non- agonistic pairs after the 4th competition (28-day-old vs. 21-day-old pairs), the dominant frequency of older males decreased. Throughout the 8 consecutive tests, the frequency of younger males being dominant remained low ($\leq 10\%$). The results indicate that the increasing dominant males from the 1st to 4th competition were largely converted from non-agonistic males. The dominant males, however, did sometimes become subordinate or non-agonistic in subsequent contests.

Previous subordinate experience likewise showed a significant influence on subsequent competitions (Fig.3). The result indicates that subordinate males rarely changed their status to become dominant (6.45%). Subordinate males tended to avoid other males, so that their status

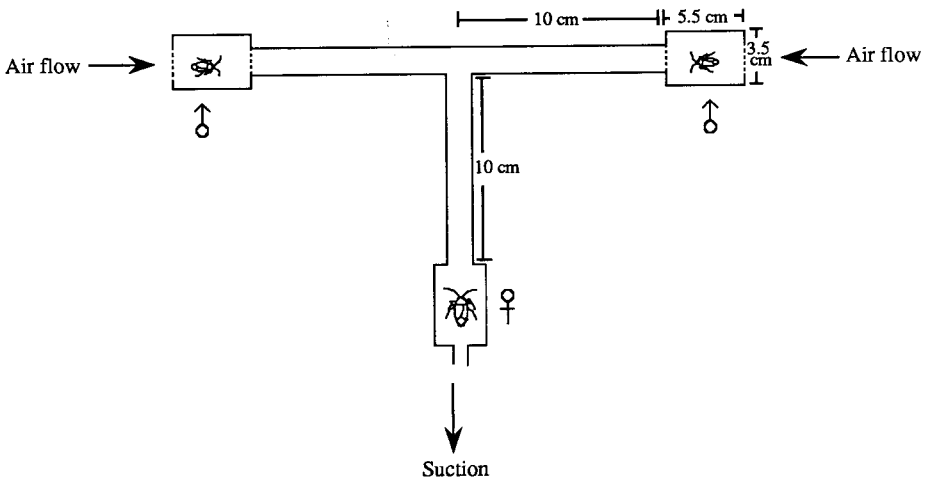

Figure 1. The T-maze used in testing for female choice. Converging airflows were created by suction from a vacuum pump connected to the base of the lower chamber. The maze was made of acrylic.

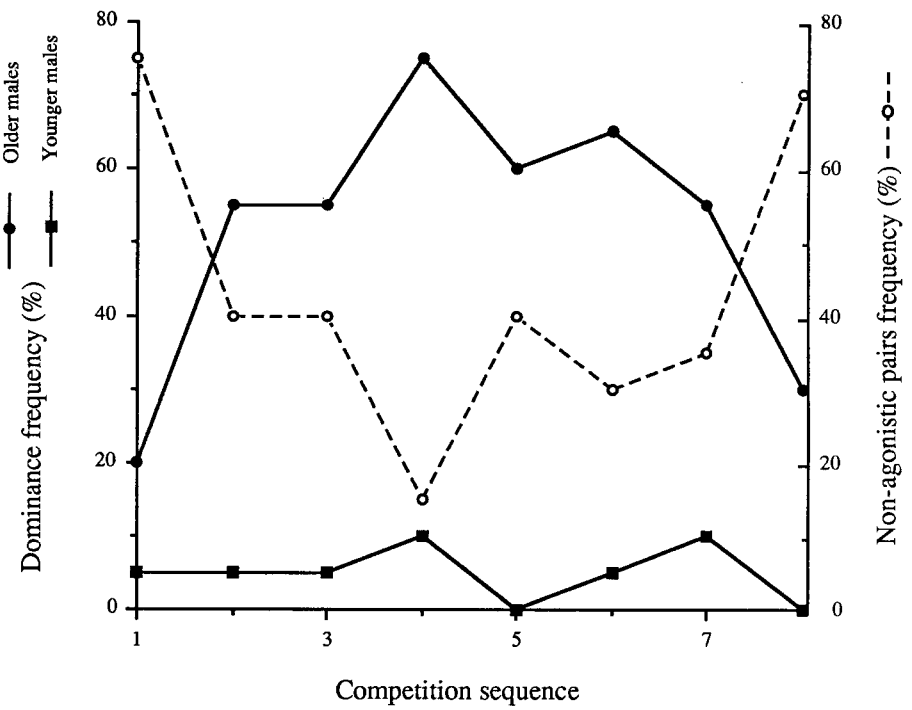

Figure 2. Effects of age on dominance relationship among male cockroaches, *Nauphoeta cinerea*. For each competition, 20 pairs of virgin males were used.

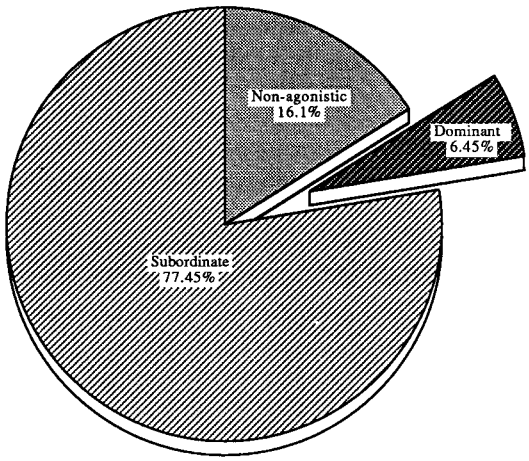

Figure 3. Effects of prior subordinate experience on subsequent male-male dominance competition in cockroaches, *Nauphoeta cinerea*. Thirty-one subordinate male were used.

remained the same (77.45%) in the subsequent competitions.

Previous experience did not significantly shorten the time required for determination of dominance relationship when competing with the same male (Fig.4). The large standard deviation indicates individual variation. Although no statistical relationship was found between experience and time required for determination of status, two pairs did show time reduction in the subsequent contests (Fig.4B).

Testectomy effects

Testectomy had some effect on the chances of becoming dominant males, although the effects were not very convincing ($P<0.75$)(Fig.5). Only 30% of testectomized males became dominant (Fig. 5B). Since 60% of sham operated males were dominant when paired with males of control group, side effects of operation procedure can be discounted.

Female choice

Sexually mature virgin females did not significantly prefer to approach dominant males ($P<0.75$ for relationships established before

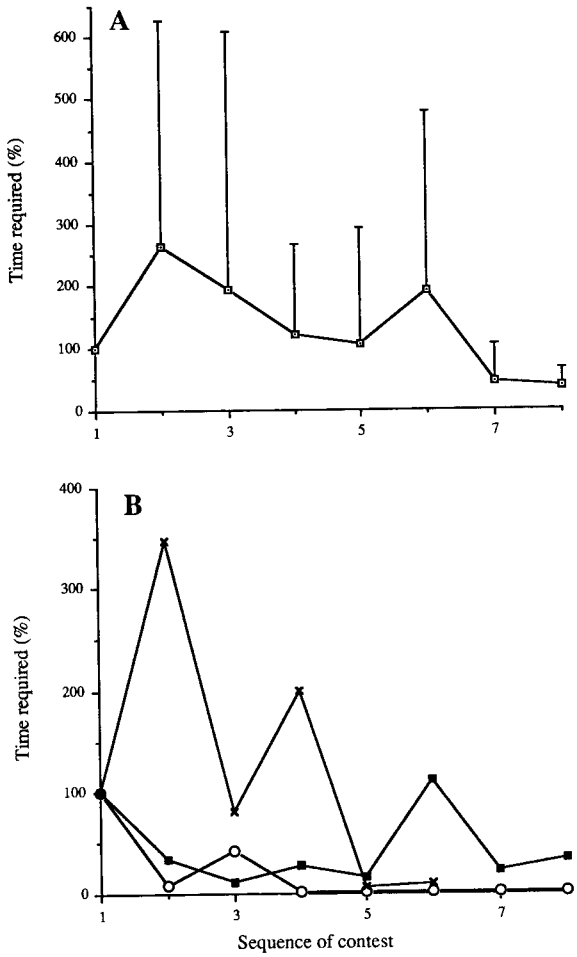

Figure 4. Effects of previous experience on the time required for determination of dominance relationship among male cockroaches, *Nauphoeta cinerea*. (A) Average time required (n = 20). The vertical bar indicates one standard deviation. (B) Three examples of individual variation. Time required is expressed as % of time required in the first contest.

female choice and $P<0.95$ for relationships established after choice) in a two-choice test (Fig.6). The results showed virgin females approached males randomly when they could only choose by odor.

Discussion

The establishment of social status among male *Nauphoeta cinerea* has been inferred as a

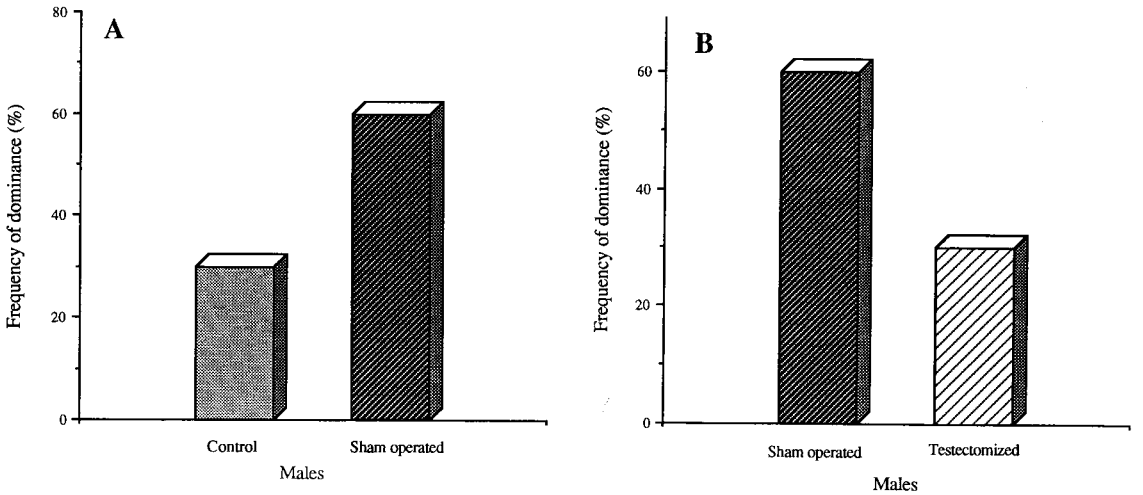

Figure 5. Effects of testectomy on dominance relationship among male cockroaches, *Nauphoeta cinerea* (n = 10). (A) Comparison between sham-operated and control cockroaches. (B) Comparison between sham-operated and testectomized males. No significant differences were found between treatments ($P < 0.75$, G-test).

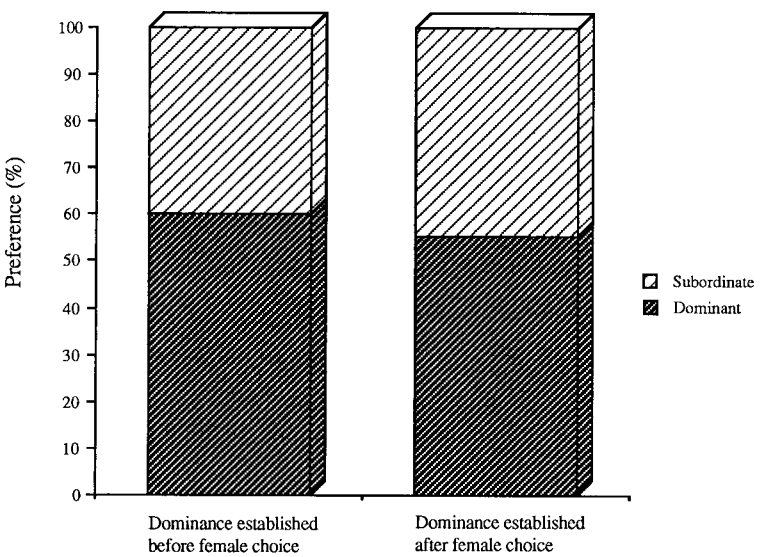

Figure 6. Attractiveness of male odor to female cockroaches, *Nauphoeta cinerea* (n = 20). The left histogram represents female choices among males whose relative status was determined before the test. The right histogram represents choice among males whose status was determined immediately after the test. No was found in either conditions ($P < 0.75$ for the former and $P < 0.95$ for the latter, significant preference G-test).

mechanism for reducing aggression in gregarious living (Moore and Breed, 1986; Moore, *et al.*, 1988). Whenever a dominant male approaches a subordinate, the latter moves aside or runs away and thus reduces confrontation. Because subordinates still have opportunities to mate, it is advantageous to avoid escalation to fights which they would likely lose (Thornhill, 1984). Our finding of substantial stability in dominance relations is consistent with this view (Fig.3).

Age has been shown to be a significant predictor of male social status in *N. cinerea* (Schal and Bell, 1983). Our results confirmed this and indicate that dominance status tends to peak at about 4 weeks of adult age (Fig. 1). This reflects the development of reproductive potential from sexually immature (newly emerged) adults to the sexually active stage (4 weeks). Since dominant males have a higher mating rate (Breed, *et al.*, 1980), it is beneficial for sexual active males to be dominant.

Although dominance status affects male reproductive success, the presence of testes is not essential for the establishment of high status (Fig.5). This finding not only eliminates the sperm factor as a key criterion in establishing dominance, but also suggests that recognition of dominance status does not require the presence of testes. Based on the finding of a male pheromone (Fukui and Takahashi, 1983), we suggest the quantity or quality of this pheromone as the main factor in dominance recognition. Comparable pheromone production which is not controlled by gonads is also found in the brown-banded cockroach, *Supella longipalpa*, whose sex pheromone production and calling were not eliminated in ovariectomized females (Smith and Schal, 1990).

Since social experience will influence the establishment of a male dominance hierarchy (Moore, *et al.*, 1988), males should have some capability of individual recognition. Although we doubt the existence of a linear dominance hierarchy, the males at least should know their own status relative to familiar individuals. From our findings, the average time required to determine status did not decrease with subsequent trials (Fig.4). Since the pairs had only 15 minutes of contact in every 7 days, this may have inhibited individual recognition. However, an inter-male recognition pheromone has been identified and synthesized (Fukui and Takahashi, 1983; Takahashi and Fukui, 1983). We suggest that by means of this pheromone they should be able to recognize an opponent's status even without individual recognition. It may be that dominant males produce more pheromone than subordinates. Furthermore, the chemical composition of the pheromone may differ with status. Males and females could therefore assess an individual male's status even without prior experience with him.

Females preferentially mate with dominant males, whom they can recognize by odor (Breed, *et al.*, 1980). However, our choice test did not show any significant female approach-tendency toward dominant males, regardless of whether status was determined before or after the choice test (Fig.6). Since we suggest that males producing more pheromone are recognized as dominants after contests, dominant-subordinate relationships should require a lengthy time for changes in pheromone production. Subordinate males may, however, produce less pheromone due to inhibition from dominant males. This very interesting question awaits experimental testing.

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