Phase polyphenism in the desert locust, Schistocerca Gregaria (Orthoptera: Acrididae): Physiological adaptations to crowding and maternal effects on progeny characteristics

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【 学位論文題目 】

Phase polymorphism in the desert locust ,Schistocerca Gregaria (Orthoptera: Acrididae): Physiological adaptations tocrowding and maternal effects on progeny characters(サバクトビバッタの相変異：混み合いに対する生理的適応と子に及ぼす母親の影響)

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1. The desert locust, *Schistocerca gregaria,* shows density-dependent phase polyphenism in behavioral, morphological and physiological traits. Female locusts modify progeny quality and quantity depending on the population density experienced as adults. This thesis consists of 6 chapters: the first three chapters focus on the physiological adaptations of *S. gregaria* to crowding and the last three concern with the mechanism of maternal effects on the progeny characters.

2. Sexual behavior of *S. gregaria* was investigated for a gynandromorphy. The information obtained was used to establish an experimental system to produce hatchlings with different phase-dependent characteristics (Chapter 1). The gynandromorph observed had a mixture of male and female morphological characteristics. By presenting sexually mature adults to this gynandromorph, it was found that this individual was attracted to normal females but it was recognized as a female by normal males. This observation suggests that the gynandromorph might have had a female-specific pheromone.

3. I investigated how phase-dependent differences in hatchling body coloration would influence the body-color polyphenism at a late nymphal stage at different population densities in *S. gregaria* (Chapter 2). Under isolated conditions, the background body color was either greenish or brownish. Most individuals were greenish

and the highest percentage of brownish insects was obtained from hatchlings with the darkest body color. Under crowded conditions, the background color was yellow or orange and the percentage of yellowish nymphs tended to decrease when they were darker at hatching. These results indicated that the background color of last-stadium nymphs was influenced not only by the rearing density during nymphal development but also by the body color at hatching and the latter exerted its influence more strongly under crowded conditions than under isolated conditions. The intensity of black patterns differed depending on the body colors at hatching and subsequent rearing density. Most isolated-reared nymphs exhibit few or no black patterns, but nymphs with some black patterns also appeared, particularly among those that had been dark at hatching. Under crowded conditions, the black patterns became more intensive when they were darker at hatching. These results indicated that the body coloration of hatchlings and rearing density influenced the intensity of black patterns at the last-nymphal stadium, and that the former had a significant impact especially under crowded conditions. Therefore, last-stadium nymphs with typical solitarious or gregarious body coloration appeared when they had the phase-specific body coloration at hatching as well. The present results demonstrated that both body color at hatching and rearing density during nymphal development influenced the body coloration at the last- nymphal stadium.

4. The effects of hatchling body size on several developmental and reproductive traits were examined under different rearing densities to elucidate the physiological responses to crowding (Chapter 3). The results indicated that small hatchlings typical of

solitarious forms grew faster under crowded conditions than under isolated conditions at the expense of the final body size. On the other hand, larger hatchlings typical of gregarious forms also grew faster under crowded conditions than under isolated conditions, but without becoming smaller as adults. Thus, under isolated conditions, large hatchlings grew faster but emerged as larger adults than did small hatchlings except for some individuals of the latter group that underwent extra molting. Under crowded conditions, large and small hatchlings grew at a similar rate, but the former became larger adults than the latter. Small hatchlings showed a trade-off between development time and body size at maturation, but this constraint was avoided by large hatchlings. Phase-specific as well as body size–dependent differences were also detected in reproductive performance. As adult body size increased, females of a solitarious line produced more but slightly smaller eggs, whereas those of a gregarious line produced more and larger eggs. Total egg mass per pod was larger in gregarious forms than in solitarious forms on average. A trade-off between egg size and number was shown by a solitarious line but not by a gregarious line that produced relatively large eggs with similar numbers of eggs per pod. These results suggested that phase transformation involves not just a shift of resource allocation but also an enhanced capability expressed in response to crowding.

5. The genetic control of phase-specific body color polymorphism was studied using two genetic mutants and a normal strain of *S. gregaria* (Chapter 4). A reddish-brown (RB) mutant found in a laboratory colony developed reddish brown

patterns rather than black patterns in the nymphal stage. Reciprocal crosses between the RB mutant and normal strains indicated that the RB phenotype was recessive to the normal phenotype and controlled by a simple Mendelian unit. Reciprocal crosses between the RB mutant and another mutant (albino) produced only normal phenotypes in the F1 generation. In the F2 generation, the normal, RB and albino phenotypes appeared in a ratio of 9:3:4, indicating that two Mendelian units, which control the appearance of dark body color and the intensity of melanization under crowded conditions, may be involved in the regulation of body coloration. To test a hypothesis that the appearance of reddish-brown patterns in the RB strain is due to a reduced concentration of the dark-color inducing hormone, [His^7]-corazonin, the hormone was injected into nymphs of the mutant. This treatment, which is known to be ineffective in inducing dark color in albino nymphs, produced a dose-dependent darkening in RB nymphs, some of which became indistinguishable from normal individuals by appearance. These results may suggest that the RB mutant gene regulates the degree of melanization, possibly through controlling the production and/or release of [His^7]-corazonin under crowded conditions.

6. The mechanism controlling the body color of hatchlings was studied for *S. gregaria* (Chapter 5.1). A pheromonal factor secreted by gregarious female adults into the foam plugs of egg pods has been suggested for a decade to cause darkening in their progeny. I re-examined the role of this maternal factor by washing or separating eggs at deposition. Eggs produced by crowd-reared female adults were washed with saline or

separated individually without being washed immediately after deposition and the body color of the hatchlings from them was compared with that from the eggs unwashed and kept in the egg pod until hatching. Most hatchlings were dark and no significant difference was found in the proportions of dark- and light-colored hatchlings between the treatments and controls. Likewise, eggs separated before the foam plug deposition produced dark-colored hatchlings as in the un-separated controls. These results demonstrated that neither washing nor separation of eggs at deposition affected the hatchling body coloration. The variation in hatchling body color was correlated closely to the body weight at hatching, indicating that hatchling body color had been determined maternally. Green hatchlings reared under crowded conditions remained green until the second stadium at which black patterns were induced. It was concluded that body color at hatching has been determined maternally and crowding during the first nymphal stadium influences nymphal body color but its effect is not manifested until the second stadium. This study casts doubts on the presence of the pheromonal factor recently suggested.

Simpson and his colleague (2007) wrote a review article in which two possibilities were pointed out to explain the differences between their results and ours. One of these possibilities was that our eggs used in the experiments had a high rate of mortality which excluded all green hatchlings, thus leaving only black hatchlings. The other possibility was that our eggs had been exposed to the active compound in the oviduct because they were withheld in the mother's body too long. The latter happened because the mother was deprived of ovipositing substrate during the nighttime, according to

Simpson and Miller (2007). Therefore, I tested these possibilities and evaluated their revised version of the foam hypothesis based on the results obtained in this study (Chapter 5.2). Early separation was performed on eggs with a low mortality rate. The results showed that egg separation did not increase the incidence of green hatchlings. Once eggs were chorionated in the ovary, egg size remained unchanged until the second day after oviposition in either isolated or crowded locusts. This and other results suggested that the phase-dependent differences in body size and color of hatchlings are established in the ovary and that modifications by the accessory gland factor either in the oviduct or after deposition are unlikely.

The results obtained from Chapter 5 cast doubt on the validity of the revised version of the foam hypothesis proposed by Simpson and his colleague. This leads to the question of exactly where the phase-dependent body size and color of hatchlings are determined. The results in Chapter 5.2 suggested that the determination of hatchling characteristics occurs in the ovary rather than in the oviduct or after oviposition Simpson and Miller (2007) claimed.

7. Corresponding to these studies, to investigate how a mixture of green and black hatchlings appears even from egg pods produced by solitarious or gregarious females, I investigated the effects of rearing density and mother's age on the progeny size, number and coloration in *S. gregaria* (Chapter 6). Isolated-reared females deposited smaller but more eggs than crowd-reared females. The former produced gradually smaller and more eggs with their age, whereas the latter showed a tendency to produce larger and fewer

eggs as the mother grew older. A similar tendency was also obtained from virgin females, indicating that mating or males are not important in this phenomenon. It was found that the first egg pod produced by each crowd-reared female contained significantly smaller and more eggs than did the subsequent egg pods. The former often produced many green hatchlings (0–100%) characteristics of solitarious forms, whereas the egg pods deposited after the first one predominantly produced black hatchlings typical of gregarious forms. This discovery not only revealed a new aspect of phase polyphenism in locusts but also provided an explanation for the discrepancy in results between the Oxford research group and ours (Chapter 5). Adults were highly sensitive to a shift in rearing density and quickly modified the quality and quantity of their progeny depending on the density encountered. The number of eggs per pod was influenced not only by the mother's rearing density but also by the grandmother's. The present results demonstrated that the progeny characters are influenced not only by the crowding condition experienced by the mother and the grandmother but also by the mother's reproductive cycle and age.

8. In conclusion, the evidence presented in this study revealed that developmental and reproductive performance is greatly influenced by the hatchling characters and crowding conditions. As a whole, gregarious (crowd-reared) hatchlings do better than solitarious (isolated-reared) ones particularly under crowded conditions. The highly efficient developmental and reproductive performance of gregarious forms seems to

contribute to rapid population growth during outbreaks. The progeny characteristics are determined or pre-determined in the ovary of the mother according to the population density experienced during her reproductive period, but not by the foam factor suggested for another strain of the same species. The discovery of the age- and reproductive cycle-dependent variation in progeny characters suggests that inter-egg-pod variation needs to be considered when one studies underlying the mechanism controlling the progeny characters.

（別紙１）　　論文審査の結果の要旨

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要　　旨

本研究は、相変異、移動して緑の植生を食いつくし、農作物にも甚大な被害を与えるトビバッタ類の中でもその影響がもっとも大きくこれまでの研究の蓄積もある *Schistocerca gregaria* を材料にして、形態と、行動、色彩、発生パターンと親から子への影響について、生理的な適応と遺伝的な影響を詳細に調べたものである。

第１章は性特異的な行動について雌雄同体のバッタを用いてその特徴を記載した。

第２章は孵化幼虫の色とその後の飼育密度による終齢幼虫の色彩への影響について調べた。このバッタは胸部や複眼に特徴的な色彩パターンがあらわれる。終齢幼虫の色彩には、孵化幼虫とその後の混み合いが影響することがわかった。

第３章では、卵サイズと卵数の関係に二つの相間にトレードオフの関係があることを見つけ、Ｋ－型とｒ－型の繁殖戦略が込み合いの程度によって分かれて発現することを示した。孤独相は小さい卵をたくさん産み、群棲相は逆に大きい卵を少数生む傾向が示された。孤独相として育つものは５齢で羽化するものと６齢で羽化するものがあり、後者のほうが大きな成虫となるが、大きな雌でも産卵数は増加するが卵サイズは大きくならない。トビバッタの色彩には、褐色-緑色系のシステムと褐色-黒色系のシステムが存在すると考えられてきた。

第４章は色彩突然変異系統の遺伝的な制御様式と、ホルモンによる制御様式を解析し、Pigmentation gene, Pp と Melanization gene, Mm の複対立遺伝子システムによる説明を試みた。２つのシステムのコンビネーションによって突然変異株と野生株の交雑後の表現形の分離が説明された。混み合いの影響が次世代に伝達されるという報告があり、この情報がどのように伝えられるかが、生物学的には興味のもてる問題として残る。第５章はこの問題について次世代の色彩パターンが母親による分泌物によって制御されているというオックスフォードグループのデータを再検討し、この可能性を排除している。

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第６章は混み合いと母親の日齢の影響を調べている。２つの相では顕著な違いが示された。すなわち、一般には、孤独相は小さい卵をたくさん産むが、群棲相では、大きな卵を少数産む。母親の日齢が進んだ時には孤独相の卵サイズは小さくなるが、群棲相では後に産む卵のほうが大きくなる傾向があり、繁殖戦略の違いがいっそう強調されて表現される。このような違いが、オックスフォードグループによる誤ったデータの由来ではないかと解釈された。

研究結果は着実な努力によって、学会誌に投稿され、掲載されている。また、国際無脊椎動物繁殖および発生学会のポスターセッションでは優秀賞を取っているので、発表のほうでも優れていると考えられる。本研究は貴重な集積であり、よって、学位申請者前野浩太郎は博士〈農学〉の学位を得る資格があると認める。