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Quantitative Genetic Aspects of the Quality Control of Mass-Reared Insects: The Case of the Melon Fly (Bactrocera cucurbitae) 【Review article】

定量遺傳與大量飼育昆蟲之品質管制：以瓜實蠅(Bactrocera cucurbitae)為例【綜合論述】

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Abstract

Quantitative genetic studies of the life history and behavioral traits are important in the quality control of insect mass-rearing programs. First, the quality control for mass-reared insects is briefly summarized from the view of quantitative genetics. Second, differences in some characteristics between wild and mass-reared melon fly (Bactrocera cucurbitae) strains in Okinawa are reviewed, and the genetic factors which can cause these differences are discussed. Third, some quantitative genetic studies evaluating the quality of mass-reared melon flies are also reviewed. These include heritability estimations and artificial selection experiments. Fourth, recent advances in studies on relationships between clock genes and quality control for sterile insect techniques which depend on the successful mating of released males with wild females are briefly introduced. Finally, genetic relationships between life-history and behavioral traits are discussed using the Okinawa mass-reared melon fly as a model case of quantitative genetic aspects in quality control of mass-reared insects especially for sterile insect techniques.

摘要

在大量飼育昆蟲的品質管制計畫中，生活史及行為特性的定量遺傳研究很重要。本文之內容包括：(一)由定量遺傳之觀點，概要摘述大量飼育昆蟲的品質管制。(二)綜論琉球野生及大量飼育之瓜實蠅在某些特性上之差異，並討論造成這些差異的遺傳因子。(三)綜論數項評估大量飼育瓜實蠅品質管制的定量遺傳研究，如遺傳性估計和人工選育實驗。(四)概述近來有關時鐘基因與不孕性昆蟲品質管制關係之研究進展，其中不孕性昆蟲技術的成效取決於釋放的雄蟲能否成功地與野生雌蟲交尾。(五)以在琉球大量飼育不孕性瓜實蠅品質管制與定量遺傳關聯者為例，討論生活史與行為特性間之遺傳關係。

Key words: heritability, genetic correlation, mass-rearing, selection, sterile insect technique
關鍵詞: 遺傳率、遺傳相關、大量飼養、選汰、不孕性昆蟲技術

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Quantitative Genetic Aspects of the Quality Control of Mass-Reared Insects: The Case of the Melon Fly (*Bactrocera cucurbitae*)

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ABSTRACT

Quantitative genetic studies of the life history and behavioral traits are important in the quality control of insect mass-rearing programs. First, the quality control for mass-reared insects is briefly summarized from the view of quantitative genetics. Second, differences in some characteristics between wild and mass-reared melon fly (*Bactrocera cucurbitae*) strains in Okinawa are reviewed, and the genetic factors which can cause these differences are discussed. Third, some quantitative genetic studies evaluating the quality of mass-reared melon flies are also reviewed. These include heritability estimations and artificial selection experiments. Fourth, recent advances in studies on relationships between clock genes and quality control for sterile insect techniques which depend on the successful mating of released males with wild females are briefly introduced. Finally, genetic relationships between life-history and behavioral traits are discussed using the Okinawa mass-reared melon fly as a model case of quantitative genetic aspects in quality control of mass-reared insects especially for sterile insect techniques.

Key words: heritability, genetic correlation, mass-rearing, selection, sterile insect technique

Introduction

Recently, insect mass-rearing has been widely conducted to produce biological agents and sterile insects to control target pests on an area-wide level. Insect mass-rearing systems require quality control of the mass-reared insects. Quantitative genetic studies of the life history and behavioral traits are important in the quality control of insect mass-rearing programs. In the first place, Finney and Fisher (1964) stated that the goal of a mass-culture program is to produce the maximal number of target insects with minimal man-hours and space, in as short a time and as inexpensively as possible (i.e., production efficiency). However, production efficiency raises a new problem of reduced quality in mass-produced insects. The idea of quality control was introduced in the latter half of the 1960s (Baumhover *et al.*, 1966). In 1971, a symposium on "The Implications of

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Permanent Insect Production" was held in Rome. At the symposium, Boller (1972) stressed aspects of behavior in the quality of mass-reared insects, while Mackauer (1972, 1976) described the genetic basis of changes in physiological and behavioral traits of mass-reared insects. Since then, these topics have been frequently discussed in the framework of sterile insect techniques (e.g., Chambers, 1977; Nakamori, 1988; Calkins, 1989; Calkins *et al*., 1994; Miyatake, 1998a; Suenaga *et al*., 2000; Cayol, 2000). Hence, the importance of the genetic background for variation in traits has been observed in mass-rearing projects involving fruit flies (Leppla, 1989; Miyatake, 1996a, 1998a).

During the eradication project for the melon fly by a sterile insect technique (SIT) in Okinawa Japan (Koyama *et al*. 2004), deterioration in quality of the mass-reared melon flies was observed (Soemori *et al*., 1980; Suzuki and Koyama, 1980, 1981; Nakamori and Soemori, 1981; Iwahashi *et al*., 1983; Kuba *et al*., 1984). The deterioration included the following two aspects: (1) a phenotypic effect (i.e., a decrease in vigor due to poor nutrition and overcrowding in the mass-rearing system), and more importantly, (2) genetic effects (i.e., changes in behavior due to genetic changes that took place during continuous mass-rearing or domestication) (Itô *et al*., 1993). In the mass-production system of Okinawa, great efforts were made to maintain the quality of mass-reared flies to that of wild flies (Itô and Kakinohana, 1995). However, some intentional selections were made in the earlier stages of the mass-rearing program to increase production efficiency. For example, flies were selected to oviposit at an earlier age in adult life (Soemori and Nakamori, 1981), and to shorten larval developmental times (Miyatake and Yamagishi, 1999).

Differences between Wild and Mass-reared Melon Fly Strains

Differences in some characteristics between wild and mass-reared melon fly strains have been extensively studied in Okinawa (see Miyatake 1998a for details). Sixteen experiments comparing wild and mass-reared melon flies were conducted for 27 traits. They could be grouped into three categories: (1) life-history traits, (2) behavioral traits, and (3) physiological traits. Life-history traits included three characters: reproduction, duration and timing in life-history, and variation among individuals. In reproduction, mass-reared flies had greater fecundity, a higher percentage of females that laid eggs, higher egg hatchability, higher frequency of oviposition, and a larger number of matings, than did wild flies. Mass-reared flies had shorter stage periods of their life-history than did wild flies. The mass-reared flies had smaller individual variations in the pre-oviposition period, in fecundity, in the frequency of oviposition, and in the number of matings than did wild ones, whereas individual variations in longevity and the pre-mating period were similar. Behavioral traits included dispersal ability and mating behavior. The flight abilities measured by a flight mill system in the laboratory and the dispersal ability measured by the mark-recapture method of mass-reared flies in the field were lower than those of wild flies. Recapture rates in traps of mass-reared flies in the field were lower than those of wild flies. The mating time of day (i.e., the time when copulation began) of mass-reared flies was earlier than that of wild flies. Wing vibration behavior, which is performed before mating to emit male sex pheromones (Kuba and Sokei, 1988), began earlier in mass-reared flies than in wild flies. However, when mass-reared flies were reared in field cages, mating took place mainly on tree leaves as it did with wild flies. There was no difference in the diurnal rhythm of CO_2 output, a physiological trait of the fly.

Introduction, Establishment, and Successive Rearing

Factors during the introduction and establishment of wild flies in the laboratory and successive rearing may have caused these characteristic differences between wild and mass-reared flies. When introducing a wild population from the field, the genetic variability of the base population is important (due to the founder effect). Initially, during rearing, individuals are selected to better adapt to the artificial rearing conditions: for example, adaptation to an artificial diet, rearing temperature and humidity, and limited space in the rearing cages. If the population size decreases drastically due to ill-adaptation to the artificial rearing conditions during this stage, the population might face a bottleneck effect that decreases the genetic variability of the population. Thereafter, we could obtain a strain (a laboratory stock) that was well adapted to laboratory conditions (establishment). In the laboratory stock, inbreeding depression and random genetic drift are important when the effective number of breeding individuals or the effective population size, N_e, is small (Hill, 1982). However, artificial selection pressures have important effects when N_e is large enough for selection to overcome genetic drift (Crow and Kimura, 1970).

In the melon fly eradication project of Okinawa Prefecture (Koyama *et al.* 2004), 19,281 larvae were collected from fields for use in establishing a mass-rearing strain (Kakinohana, 1996). The founder effect could be ignored, because the introduced population was huge. Therefore, bottleneck effects were never reported in the mass-reared melon flies of Okinawa. Some life-history traits were artificially selected for during the establishment of the mass-reared strain. For example, flies that developed faster, oviposited earlier, and laid more eggs than other flies were intentionally selected for the next generation (Soemori and Nakamori, 1981). Such traits are preferred for eradication projects, which require the release of a huge number of flies. Evidently, the established strain for mass rearing was more fecund and began oviposition far earlier than did wild flies (Sugimoto, 1978; Soemori and Nakamori, 1981), and had a shorter development period than wild flies (Miyatake, 1993). Unintentional selection also occurred during the mass-rearing project. For example, flies that had a higher mating ability in an adult cage, in which fly density was abnormally high compared to natural conditions (Soemori *et al.*, 1980; see also Miyatake and Haraguchi, 1996), and flies that began mating behavior earlier in the day than wild flies (Suzuki and Koyama, 1980; Kuba and Koyama, 1982) would have a selective advantage. In short, artificial selection pressures may have more drastic effects than inbreeding depression and random genetic drift in the mass-reared strain of the Okinawan melon fly. This is because a huge number of flies were collected from fields as the base population for the mass-rearing, and 5×10^6 adult flies were maintained throughout the mass-rearing process (Kakinohana, 1996).

Heritability Estimates

Genetic variance of target traits is necessary to respond to selection, and thus, enable improvement of these traits. Heritability, h^2, is a commonly used index of genetic variance. Assuming no epistasis and the statistical independence of loci, total phenotypic variance, V_P, is divided into the following variance components:

$$V_P = V_A + V_D + V_E;$$

where V_A is the additive genetic variance, V_D is the dominance variance, and V_E is the environmental variance.

Genetic variance, V_G, is represented by $V_A + V_D$. In general, heritability in the narrow sense is defined as

$h^2 = V_A/V_P$ (= additive genetic variance / total phenotypic variance).

Heritability varies between zero and one; at zero there is no resemblance between parent and offspring due to the additive effects of genes, while at one, the mean offspring value equals the midparent value.

Three methods are commonly used to estimate heritability: (1) offspring-parent regression, (2) sib analysis, and (3) realized heritability from selection experiments. For detailed methods to estimate heritability, see Falconer (1989), Becker (1992) and Lynch and Walsh (1998).

Heritabilities were measured in five traits of the mass-reared melon fly of Okinawa. Heritabilities measured for morphological traits included adult body size: 0.327 (Nakamori, unpubl. data), pupal weight: 0.382 (Nakamori and Murakami, unpubl. data), and wing length: 0.542 (Miyatake, unpubl. data). Heritabilities of life-history traits measured by realized heritability included developmental period (from egg to adult emergence) for males 0.217-0.246, and for females 0.226-0.250, each for the two replicate lines, respectively (Miyatake, 1995). Heritability in the pre-mating period was measured as 0.254 by sib-analysis (Miyatake, 1998b). The heritability estimates for the three morphological traits were higher than those of the two life-history traits. In general, characters with the lowest heritabilities are those most closely connected with reproductive fitness, such as life-history traits, while characters with the highest heritabilities, such as morphological traits, are those that might be judged to be the least important as determinants of natural fitness (Falconer, 1989).

Artificial Selection Experiments

Two life-history traits, the age at reproduction and developmental period, were intentionally selected to improve the production efficiency of mass-reared melon flies of Okinawa (Soemori and Nakamori, 1981; Miyatake and Yamagishi, 1999). Therefore, artificial selection for the traits of age at reproduction (Miyatake, 1997a) and developmental period (Miyatake, 1995) was conducted to examine the direct and correlated responses to these selections. The lines originating from the eggs collected at different ages were named young lines (Y-lines: eggs collected at 10-15 days after emergence), and old lines (O-lines: eggs collected at 55-60 days). Three selection replicates for young and old lines were initiated at the same time. Another selection for shorter (S-lines) and longer (L-lines) developmental period lines were also selected (Miyatake, 1995). Two selection replicates for S- and L-lines were initiated at the same time.

Females from the O-lines survived longer than did Y-line females as an indirect and/or direct response to selection (Miyatake, 1997a). Females from the Y-lines had higher fecundites at an early age, shorter pre-oviposition periods, and an earlier age of peak fecundity period than females from the O-lines. However, total fecundity per lifespan did not differ between the two lines. These results suggest a genetic trade-off between early fecundity and longevity in the population examined, which may be controlled by pleiotropy or linkage. The larval period of the O-lines was longer than that of the Y-lines, but there were no significant effects on the hatchability of eggs, or on the pre-adult survival rate. By monitoring their locomotor activities, the circadian period in constant darkness (i.e., free-running period) was compared between selected lines. And the time of mating in a day was also measured for both lines. Results showed that flies from the Y-lines had shorter circadian periods and

earlier mating times than did flies from the O-lines (Miyatake, 2002a).

Although selection for a longer developmental period was successful, selection for a short developmental period showed only a slight response (Miyatake, 1995). The selection responses for a long developmental period were mainly due to a prolonged larval period. Comparisons of the adult body size and pre-adult survival rate revealed that the longer developmental period was associated with larger adults, but they also had lower survival rates during the larval and pupal stages. There were no consistent differences in the eight life-history traits between long and short lines (Miyatake, 1996b). A later time of mating was associated with longer developmental periods than those of short developmental periods (Miyatake, 1997b). When comparing the circadian period between lines, longer developmental periods were associated with longer circadian periods, and shorter developmental periods were associated with shorter circadian periods (Shimizu *et al*., 1997). The results of crossing the flies in the selected lines pointed to a major gene (with the contribution of a few minor genes) controlling the circadian period. This suggests the existence of a gene pleiotropically controlling developmental and circadian periods in the melon fly (Shimizu *et al*., 1997).

Clock Genes, Reproductive Isolation, and Quality Control

Studies on reproductive isolation were conducted using the melon fly (Miyatake and Shimizu, 1999; Miyatake *et al*., 2002). Melon fly lines artificially selected for short and long developmental periods differ in their circadian periods and thus in their preferred times of mating during the evening as described above (Miyatake, 1997b). This allochronic difference translated into significant pre-mating reproductive isolation, as measured by mate choice tests (Miyatake and Shimizu, 1999). In some cases, such a mechanism could explain the evolution of reproductive isolation; genetic correlations between life history and behavioral traits may cause reproductive isolation via a difference in mating times between populations. A pleiotropic gene that controls developmental and circadian periods in the melon fly was detected (Shimizu *et al*., 1997). The function of *period* gene expression is closely correlated to the locomotory rhythm and the time of mating in the melon fly, suggesting that clock genes can cause reproductive isolation via the pleiotropic effect as a change in the time of mating (Miyatake, 2002b; Miyatake *et al*., 2002). These results also suggest that clock genes are the key to genetic quality control of the mass-reared melon fly, because clock genes can cause the mating times of mass-reared melon fly populations to differ from those of wild populations and thus may cause decreased efficiency of the sterile insect technique, which depends on successful mating of released males with wild females. Molecular analyses for clock genes including *period*, *doubletime*, and *cryptochrome*, are ongoing in the melon fly.

Genetic Relationships among Traits

Trait selection may affect other traits through genetic correlations due to pleiotropic effects or linkage (Falconer, 1989). Figure 1 illustrates the genetic relationships between life-history and behavioral traits in the mass-reared melon fly. During the mass-rearing project, the flies that laid eggs at a younger age and developed faster were selected intentionally to improve the production efficiency (dotted lines with a hollow arrow on one end in Fig. 1: Soemori and Nakamori, 1981; Miyatake and Yamagishi, 1999). Mass-reared flies selected for a younger age of reproduction had a shortened longevity. This was due to either a negative

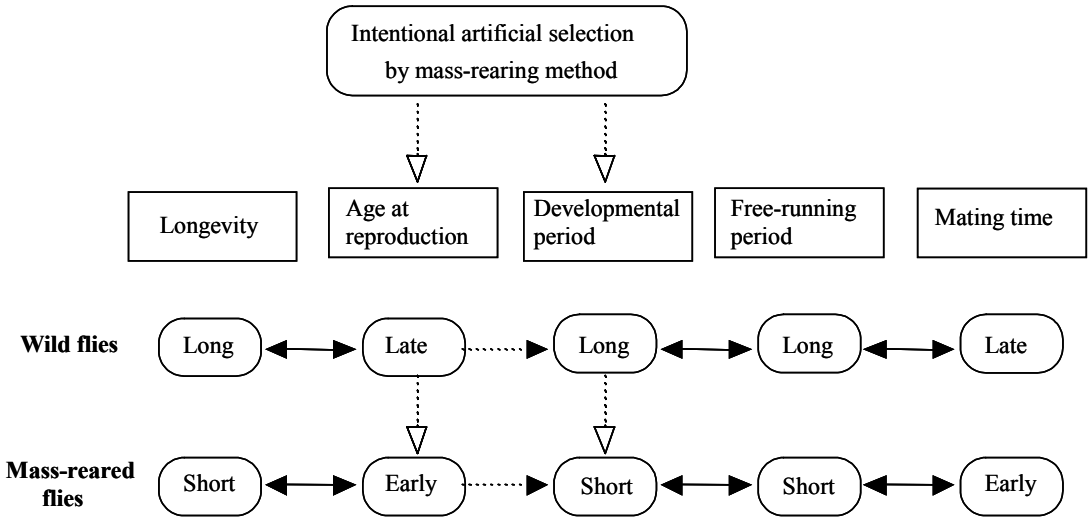

Fig. 1. Genetic relationships between life history and behavioral traits in the mass-reared melon fly (after Miyatake, 1998a). Dotted lines with a hollow arrow on one end depict the direction of artificial selection due to the mass-rearing method. Solid lines with arrows on both ends indicate a genetic correlation between the two traits. Dotted lines with a solid arrow on one end indicate the direction of inadvertent selection.

genetic correlation between early fecundity and longevity (solid lines with arrows on both ends which present genetic correlations between the two traits in the figure: Miyatake, 1997a), or by the accumulation of mutants with deleterious effects late in life (Zwaan *et al.*, 1995). The selection for a younger age of reproduction also shortened the developmental period (indicated by a dotted line with a solid arrow on one end of the figure; Miyatake, 1997a). However, selection for developmental period was associated with neither reproductive age nor longevity (Miyatake, 1996b). This suggests the absence of a genetic correlation between reproductive age and developmental period in the mass-reared melon fly.

The selection experiment for the developmental period indicated that longer developmental periods were associated with longer circadian periods of adult flies, and a later mating time (the time when copulation is initiated). Shorter developmental periods were associated with shorter circadian periods and an earlier mating time (Miyatake, 1997b; Shimizu *et al.*, 1997). It has been demonstrated that this relationship depends on a gene pleiotropically controlling developmental and circadian periods in the melon fly (Shimizu *et al.*, 1997). The change in the time of mating is important for the quality of released flies, because a precondition of the sterile insect technique is mating success of sterile males with wild females. The difference in time of mating between the two populations causes a significant pre-mating isolation which supports this (Miyatake and Shimizu, 1999).

Figure 1 presents two combinations of life-history traits of the melon fly. The first combination is of flies with increased longevity, an older age at reproduction, a longer developmental period, a longer circadian period of adult flies, and a later time of mating. These characters are similar to those of wild flies measured in the laboratory as described above. The

second combination is of flies with a decreased longevity, a younger age at reproduction, a shorter developmental period, a shorter circadian period of adult flies, and an earlier time of mating. These characters are similar to those of mass-reared flies. The results indicate two facts. First, two traits, a younger age at reproduction and a shorter developmental period of the mass-reared melon fly, have directly responded to selection during the mass-rearing method. Second, the other three traits, shorter longevity, a shorter circadian period, and an earlier time of mating, of mass-reared flies have been changed by correlated responses to selection (but longevity may also be directly selected for by artificial selection for age at reproduction, see Zwaan *et al*., 1995).

The relationships between these traits can be used to improve the quality of mass-reared melon flies. During the mass-rearing process, longevity decreases through the generations of flies (Kakinohana and Yamagishi, 1991). The decrease in longevity could be reversed by selecting for older age at reproduction (Miyatake, 1997a). The mass-reared flies had earlier mating times than wild flies (Suzuki and Koyama, 1980; Kuba and Koyama, 1982), and this study reveals that the time of mating can be controlled by selection for the developmental period (Miyatake, 1997b). Although direct selection for longevity or time of mating may be time-consuming and labor intensive, and may not be appropriate as a regular part of a mass-rearing program, longevity or time of mating can easily be selected for by using selection of reproductive age or developmental period.

The problem of incorporating a selection regime in a mass-rearing system is maintaining a balance between the production efficiency and the quality of mass-reared insects for sterile insect techniques. The results described above indicate that a negative genetic correlation between traits causes conflict between these aspects of mass-rearing. For example, increased longevity is associated with a later age of reproduction (Miyatake, 1997a). A later time of mating is associated with a longer developmental period (Miyatake, 1997b), and with a low pre-adult survival rate (Miyatake, 1995). Therefore these genetic trade-offs between traits should be taken into account in insect mass-rearing programs. In particular, it is important to ascertain whether there is a real genetic correlation between traits. Quantitative genetic methods, including the classical half-sib design or selection experiments for both traits under the trade-off, are required to clarify the real genetic trade-off relationship.

Future Prospects

The family Tephritidae of fruit flies contains several species for which the molecular genetics is rapidly expanding. However, molecular techniques have not been examined for the Okinawan melon fly. In the future, molecular genetic analyses would be an important research area for quality control of the melon fly. We must search for useful genes for quality improvement of released melon fly males. One candidate is a gene controlling the biological clock of flies. The biological clock controls the time of mating in the melon fly (Shimizu *et al*., 1997; Miyatake *et al*., 2002). If the difference in time of mating between two melon fly populations changes by over 1 hour, a significant pre-mating isolation occurs in cages (Miyatake and Shimizu, 1999). A difference in mating time causes deterioration of SIT efficiency, because released males must mate with wild females at a certain time in the wild. A research project to explore the biological clock gene of melon fly has just begun as described above.

As with other genetic aspects of quality control of mass-reared flies, research on the genetic diversity of reared fly-

strains at DNA levels would be important. In the mass-rearing facility of Okinawa, some mutant flies have been retained (Toda and Kasuya, 1993; Yamagishi, 1993). These mutants will also be useful for molecular analyses.

What is the important trait of mass-reared flies for successful SIT? It is the ability of mass-reared males to mate with wild female flies in the field. To accomplish this, we must select males with increased mating ability and attraction to wild female flies, or search for useful genes and appropriate techniques to translate the genes into a fly for making transgenic agent flies. If wild females will mate more frequently with our mass-reared flies selected artificially, or genetically altered, then artificial manipulations of the melon fly will become active. To use these techniques for the practical mass-rearing for SIT, we must accumulate information on many genetic parameters. We must also consider the cost effectiveness of these techniques for the SIT project.

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定量遺傳與大量飼育昆蟲之品質管制：以瓜實蠅(*Bactrocera cucurbitae*)爲例

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摘　要

在大量飼育昆蟲的品質管制計畫中，生活史及行爲特性的定量遺傳研究很重要。本文之內容包括：(一)由定量遺傳之觀點，概要摘述大量飼育昆蟲的品質管制。(二)綜論琉球野生及大量飼育之瓜實蠅在某些特性上之差異，並討論造成這些差異的遺傳因子。(三)綜論數項評估大量飼育瓜實蠅品質管制的定量遺傳研究，如遺傳性估計和人工選育實驗。(四)概述近來有關時鐘基因與不孕性昆蟲品質管制關係之研究進展，其中不孕性昆蟲技術的成效取決於釋放的雄蟲能否成功地與野生雌蟲交尾。(五)以在琉球大量飼育不孕性瓜實蠅品質管制與定量遺傳關聯者爲例，討論生活史與行爲特性間之遺傳關係。

關鍵詞：遺傳率、遺傳相關、大量飼養、選汰、不孕性昆蟲技術。

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