Evolution of periodicity in periodical cicadas

（課程博士・様式７）（Doctoral qualification by coursework,Form 7）

学 位 論 文 要 旨

Abstract of Doctoral Thesis

専　　攻：環境・エネルギーシステム　　　氏　名：伊東　啓
Course：Environment and Energy Systems　　Name：Hiromu Ito

論文題目：周期ゼミの周期性進化メカニズムの解明
Title of　Thesis：Evolution of periodicity in periodical cicadas

論文要旨：

Abstract：

Periodical cicadas (*Magicicada* spp.) in the USA are famous for their unique prime-numbered life cycles of 13 and 17 years and their nearly perfectly synchronized mass emergences. Because almost all known species of cicada are non-periodical, periodicity is assumed to be a derived state. Cicadas (Order: *Hemiptera*) are singing insects that are widely distributed from the tropics to temperate zones. Almost all known cicada species have size (weight)-dependent maturation with variable-length life cycles. Their nymphs grow underground at a rate set by resource availability (water from roots that depends on the cumulative temperatures of trees), and when they reach a threshold maturation size, they emerge from the ground and moult into short-lived adults. In contrast, *Magicicada* exhibit time-dependent maturation and emerge after exactly 13 or 17 years. In the current climate (postglacial period), most of them appear to be able to grow to threshold maturation size well within their lifespans of 13 or 17 years. A number of hypotheses address the evolution and maintenance of periodicity and mass emergence in *Magicicada*. One hypothesis is that periodicity with mass emergence is a strategy for predator avoidance, but this hypothesis has a significant flaw: It cannot account for the rarity of periodicity. All cicadas face predation pressure, but only a small number of species are known to be periodical. A leading hypothesis for the evolution of periodicity in *Magicicada* implicates the decline in average temperature during glacial periods. During ice ages, the emergence of any cicadas with size-dependent life cycles may have been delayed many years due to the reduction in yearly cumulative temperatures. It is possible that the long nymphal stage preceding such emergence delays could have significantly increased nymphal mortality, resulting in extremely low adult densities. One way that the ancestors of *Magicicada*

may have survived these challenges was by adopting periodical emergences. During the evolution of periodicity, the determinant of maturation in ancestral cicadas is hypothesized to have switched from size dependence to time (period) dependence. The selection for the prime-numbered cycles should have taken place only after the fixation of periodicity. Here, we build a simple individual-based model of cicadas which incorporates Mendelian inheritance and random mutation under conditions of climatic cooling to explore the fixation of periodicity. We assume a one-locus, two-allele genetic system controlling emergence (i.e., determinant of maturation). In this locus, we assume two types of alleles: (1) temperature (size)-dependent alleles and (2) time-dependent alleles (i.e., temperature-independent or periodicity alleles) that have a specific lifespan length (e.g., 10-20 years). In this paper, we specifically demonstrate how declining average temperature, which directly affects growth rate, could promote the evolution of time-dependent maturation and periodicity from an ancestor with size-dependent maturation. There is a border of extinction such that if the climate is cooler than the threshold, the population usually goes extinct. If the climate is warmer than this threshold, cicadas survive in almost all simulation runs. Periodicity is fixed at and near the boundary of extinction. A wide band of fixed periodicity is found slightly below the boundary of extinction, where the shorter (longer) cycles are fixed at warmer (cooler) cumulative temperatures. Our simulation demonstrates the feasibility of the first step of Yoshimura's (1997) hypothesis for the evolution of periodicity during glacial periods. Our results indicate that various year cycles (10-20 year) could have evolved depending on slight differences in accumulated temperatures. In our model, under cold environments, extremely long juvenile stages lead to extremely low adult densities, limiting mating opportunities and favouring the evolution of synchronized emergence. Our results indicate that these changes, which were triggered by glacial cooling, could have led to the fixation of periodicity in the nonperiodical ancestors.