論 文 の 内 容 の 要 旨

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論文題目　Effects of the seed parasitoid wasp *Macrodasyceras hirsutum* Kamijo on the bird-dispersed tree *Ilex integra* Thunb. in the plant-insect-bird triad system
（植物－昆虫－鳥類間相互作用系において種子捕食寄生蜂モチノキタネオナガコバチがモチノキに及ぼす影響）

Many phytophagous insects are known to feed on fruits and seeds. On the other hand, vertebrate-dispersed trees often have conspicuously coloured fruits. Frugivorous birds are attracted by fleshy fruits and disperse the seeds but avoid unripe, green fruits.

The focus of many classical and contemporary studies in ecology, however, has been on pairwise interactions between species: plant-insect and plant-bird interactions have been treated separately. Recently, an appreciation has been developed of how multi-species interactions synergistically or antagonistically alter the ecological outcomes of interactions from outcomes predicted by pairwise interactions. Little consideration, however, has been made for the effects of frugivorous insects on plant-bird interactions.

The seed parasitoid wasp *Macrodasyceras hirsutum* Kamijo (Hymenoptera: Torymidae) attacks seeds of the bird-dispersed tree *Ilex integra* Thunb. (Aquifoliaceae). In this plant-insect-frugivorous bird triad system, there may be three interactions among them; (1) seed consumption by the wasp, (2) seed dispersal by the birds, and (3) indirect effects of the wasp on the birds via modified berry traits. The aim of this study was to

reveal the effects of the wasp on plant-insect-frugivorous bird triad system.

Selective oviposition in fertilised seeds by *M. hirsutum*

Oviposition of some seed parasitoid wasps induces unfertilised seeds to accumulate storage material in conifers. Therefore, it is speculated that ability of wasps to manipulate the accumulation of storage material varies depending on the temporal relationship between wasp oviposition and tree ovule fertilisation. To test the hypothesis, berries of *I. integra* were dissected immediately after the end of flight season of the seed parasitoid wasp in the field and the berries bearing unfertilised seeds were also dissected after being exposed to wasp females in the laboratory. Almost all the eggs were found in fertilised seeds in the field. Unfertilised seeds did not show the accumulation of storage material in them after being exposed wasps. Both results indicated that the wasp did not oviposit in unfertilised seeds, supporting the hypothesis and indicating that the substantial proportion of seedless berries did not function as an egg sink.

Egg distribution pattern among seeds and berries

Selection of oviposition sites by phytophagous insects is crucial for the fate of offspring. As *M. hirsutum* selectively lays the eggs into the fertilised seeds and only one larva develops in a seed, a uniform distribution pattern of wasp eggs may be expected among fertilised seeds and berries. To test the hypothesis, the wasp eggs in seeds and berries were counted for the first generations over five years. Dissection of 531 berries showed that the wasps deposited one to five eggs into a fertilised seed. Iwao's patchiness regression analysis revealed that the eggs showed a uniform distribution pattern among fertilised seeds and a random distribution pattern among berries. Destroying the connection of seeds within berries revealed that female wasps randomly selected berries for oviposition in most trees. Generalised linear mixed models (GLMM) showed that the number of fertilised seeds in a berry could not explain the number of eggs in a seed but could explain the number of eggs in a berry. Therefore, this study suggests that the wasp females did not discriminate between berries with different numbers of fertilised seeds but discriminated the egg loads in a seed.

Life cycle of *M. hirsutum* with relation to amount of available seeds

Facultative diapause is a strategy that decides whether insects initiate an

additional generation or stop the development depending on the environmental conditions. Although food supply is assumed to dominate the most summer diapauses of phytophagous insects, very few studies have reported the influence of food supply on the induction of summer diapause. Dissection of berries at various occasions in the field showed that some individuals of the first generation of *M. hirsutum* emerged as an adult in early summer and formed the second generation whereas the others entered the diapause and overwintered as a larva. The GLMM showed that the proportion of summer diapause larvae was not affected by the proportions of seeds available to oviposition per berry and branch but by the proportion of available seeds per tree.

Yearly fluctuation in berry productions and seed parasitism by *M. hirsutum*

Production of fruits and seeds fluctuate from year to year in many tree species. As flower buds of *I. integra* are formed in the previous year and the berries grow in the current year, the production of fruits and seeds are closely related to environmental conditions such as sunlight, water, and nutrients in the previous and current years. To determine the relationship of the production of *I. integra* seeds and berries to seed parasitism by *M. hirsutum*, berry density per one-year-old twig and seed parasitism by *M. hirsutum* were investigated over five years. Some trees changed the sex. Any female trees showed marked, yearly fluctuation in berry density per twig, which was not in synchronisation among trees in a plantation. There was a difference in the mean number of wasp-parasitised seeds per berry among trees in each spring, but there was no relationship between berry density per twig and percent seed parasitism. The GLMM showed that the percent seed parasitism in autumn was not related significantly to the berry production in the following year. These suggest that yearly fluctuations in the berry production of *I. integra* trees are not determined by *M. hirsutum* populations.

Trait-mediated indirect effects by *M. hirsutum* on frugivorous birds

Frugivorous and seed-feeding insects may alter the traits of fruits, such as shape and size, which may influence fruit attractiveness to frugivorous birds. Consequently, trait-mediated interactions may occur in systems where plants, seed-dispersing frugivorous vertebrates and frugivorous or seed-feeding insects interact. I investigated colour manipulation in *I. integra* berries caused by the seed parasitoid wasp and how the manipulation relates to fruit attractiveness for frugivorous birds. Observation in winter showed that the colour of *I. integra* berries varied from green to red, but most berries

were greenish, indicating that the berries were immature. Berry dissection indicated that the number of live parasitoid larvae present within each berry was closely related to berry colour—greater the number of live larvae, more intense is the green colour of the berry. However, the wasp larvae did not modify the shape or size of the berries. More than 98% of berries that were protected from the insects by gauze bags ripened and turned red. In this study, berries with unfertilised seeds alone turned red. Field feeding preference tests showed that the frugivorous birds preferred red berries to green berries. I demonstrated that the seed parasitoid wasp manipulates the berry colour, but not its shape or size, in a density-dependent manner. Because green berries suffered less from bird foraging, I believe that this colour manipulation helps the wasps to avoid being killed by the birds. The present study indicates that manipulation by wasps may reduce the level of mutualism between the tree and seed-dispersing birds.

Conclusion

Insect seed parasitoids and predators have received relatively little attention in the context of the organisation and functioning of natural and agricultural ecosystems compared to other functionally important insect groups such as pollinators. Although insect seed predators frequently kill >90% of developing seeds, it has been considered that a high rate of seed parasitism does not necessarily have a substantial effects on the plant populations due to critical action of post-dispersal mortality factors on the recruitments, leading to a underestimate of insect seed predators. In addition, both plant-insect and plant-bird interactions have been studied separately and little attention has been attracted to the effects of frugivorous and seed-feeding insects on plant-bird interactions. The doctoral thesis, however, is the first report to indicate that the seed parasitoid inhibits the seed dispersal through a trait-mediated indirect effect of the seed parasitoid wasp on frugivorous birds in addition to seed predation. It also shows that insect seed predators may cause far heavier losses in plant reproduction than expected by direct seed mortality. Full understanding of the ecology of insect seed predator-plant interactions will be valuable to conservation and management in a range of natural and agricultural systems.