博　士　論　文　の　内　容　の　要　旨
Abstract of Doctoral Dissertation

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論文題目 Dissertation Title	The effects of flower visitors on intraspecific trait variation in some entomophilous plants (虫媒植物の種内形質変異に対して訪花者がもたらす影響)

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One of the largest goals in evolutionary biology is to elucidate mechanisms of diversification of various traits. Focusing on intraspecific variation, where speciation is still incomplete, can contribute to elucidation of mechanisms of trait diversification and early stages of speciation. It has been pointed out that occurrence of intraspecific trait differences can lead to reproductive isolation and speciation. This is because when trait differences occur between different populations within the same species, even in the case of secondary contact, both of which have undergone local adaptation, reproductive isolation may be established due to reduced fitness of hybrids and/or morphological mismatch.

Pollination is one of the major biotic interactions between insects and plants. It has contributed greatly to the diversification of plant traits. For example, flower-visitor trait-matching has been well studied, as the classic example of the relationship between orchid and hawkmoth by Darwin. Since 25% of the diversification events in angiosperms has been caused by flower visitor shifts, focusing on plant traits related to pollination will be useful for understanding the mechanisms of trait diversification and speciation. Therefore, I focused on morphological differences at the level of intraspecific variation and between ecotypes and examined how pollination faunas relate to and influence these differences, using some plant species, as described below.

In Chapter 1, I used *Cimicifuga simplex* (Ranunculaceae) as a material to detect the differentiation of reproductive systems among the three pollination morphs within the species. Morph I was distributed at high altitude (1350–2370 m) and was pollinated mainly by bumblebees, and morph II was found at middle altitudes (920–1500 m) and was pollinated mainly by butterflies. Morph III occurred at low altitude (650–1350 m) and was pollinated mainly by dipteran insects although the visitation rates were low. In addition, each morph had a different reproductive system. Morph I, which had a high outcrossing rate, produced mainly gynodioecious ramets (i.e., they produced hermaphroditic and unisexual female ramets), along with a few andromonoecious ramets (i.e., ramets with a hermaphroditic primary raceme and lateral racemes with unisexual male flowers). Morph II, which had a high outcrossing rate, produced hermaphroditic and andromonoecious ramets. Morph III, which had a low outcrossing rate, produced mainly hermaphroditic ramets, along with a few andromonoecious ramets.

Based on these results, in Chapter 2, I clarified the seasonal changes in the quantity and quality of the flower visitors for three morphs. There were marked differences in the flower visitor environment among the three morphs, and these differences are related to the

reproductive systems of each morph. As few examples of different reproductive systems at the ecotype level within a species have been reported thus far, *C. simplex* is shown to be a good material for examining the relationship between the flower visitor faunas and reproductive systems.

In Chapters 3 and 4, I investigated the flower-visitors trait-matching across multiple mountain regions using *Lamium album* var. *barbatum* and *Aquilegia buergeriana* var. *buergeriana* as materials. I conducted population genetic analysis to clarify the evolutionary history of the geographic variation in floral size. First, for both species, geographic variations of floral size and flower visitor size consistently matched. In other words, in all mountain regions, plant populations visited by large visitors had larger floral sizes, while those visited by small visitors had smaller floral sizes. Second, there was no relationship between the similarity of floral size between populations and their genetic similarity. Thus, populations within the same mountain region were genetically close to each other, but populations in different mountain regions were genetically differentiated. These results suggest that the floral size evolved independently among different mountain regions adapting to the flower visitor size of each plant population.

In Chapter 5, I investigated the floral size bimodality in a population of *L. album* var. *barbatum*. In this population, the flower visitors (small and large bees) tended to visit and pollinate flowers of similar size. As a result of this flower visitor preference, the fitness of ramets with floral size of intermediate length was lower than that of ramets with long or short floral size. Microsatellite DNA analysis revealed a slight genetic differentiation between ramets with long or short floral size. Additional genetic analysis showed no evidence of secondary contact with allopatric populations with long or short floral size. These results strongly suggest that, in the population, the bimodal distribution of floral size has sympatric origin and is maintained by disruptive selection resulting from the flower visitor preferences to floral size.

These results elucidate some aspects of plant trait evolution in response to the local flower visitor fauna. The results of Chapters 1 and 2 suggest that even among closely related plant ecotypes, the flower visitor faunas can differ greatly, and that the reproductive system of each ecotype evolved to its own flower visitor fauna through adaptation. In Chapters 3 and 4, I found that the evolution of floral size among populations occurs independently among mountain regions. This indicates that floral size can evolve rapidly in response to differences in visitor size among local populations, and that such evolution has repeatedly occurred in different mountain regions. The results in Chapter 5 suggest that intraspecific floral size bimodality within a population may be maintained by differences in the behavior of the two types of flower visitors. This series of studies has provided new insights into the effects of flower visitors on intraspecific trait variation in entomophilous plants from three perspectives that have not been previously focused on: differences in reproductive systems between ecotypes, the relationship between local adaptation of floral traits and population genetic structure, and the maintenance mechanism of trait bimodality within a single population.