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Ecological study of the micropredator, *Taimenobdella amurensis*, a piscivorous leech: filling the gap between predation and parasitism

（魚類捕食性エゾビルの生態学的研究：捕食と寄生の間を埋めるマイクロプレデーション）

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Predator-prey and parasite-host relationships are ubiquitous in nature and have been extensively studied in the fields of ecology and evolution. The main difference between predators and parasites are the number of victims: individual predators kill many prey throughout their life, while parasites usually spend their entire or each stage of their life within a single host, which does not necessarily result with host death. However, there is another trophic strategy in between, which has been neglected. These are "micropredators", animals such as mosquitoes and vampire bats, that consume only a part of the prey's body without killing it, but requires multiple prey throughout their life. Despite covering a broad range of species within the kingdom Animalia and possessing a number of traits that distinguish them from parasites, micropredators are nevertheless often grouped with parasites, and not predators which they possess many similarities with. Compared to micropredators, parasitoids (animals that require the death of their host as part of their lifecycle, such as parasitoid wasps) are a well established and documented group of organisms, despite being largely restricted phylogenetically to only a few phyla (i.e. Arthropoda and Nematomorpha). Yet, even with their numerous similarities to parasites, parasitoids are always carefully separated from other kinds of parasitic lifestyles, and never included with classical parasites such as the helminths. As this is the case it is reasonable to ask why not also properly classify micropredators? Some studies have clearly separated micropredation from other trophic strategies and pointed out the importance of treating them separately, but the concept of micropredation has been underappreciated or even misused. Studies on micropredator-prey relationships from different aspects are certainly needed.

In this PhD thesis, I firstly reviewed the history of the terminology to see how the term has been used in scientific literature since its first appearance in the 1970's. The original term used for this trophic category is as mentioned above, but later it has also been used for small (i.e. micro) predators, like bacteria eating other bacteria. The terminology has been greatly underused even after a seminal review paper in 2002 that clearly categorized different trophic strategies. To determine how the term was used in the scientific literature, I collected search results for all cases of the term "micropredator" from its earliest use until the end of 2019 on Google Scholar and SCOPUS. Surprisingly, while the image of a micropredator is often a mosquito or tick, in the literature marine crustaceans were far more likely to be referred to as micropredators. I listed a variety of taxa that fall into the category of micropredator based on the defined criteria, and found that micropredators exist within diverse animal groups, such as Ixodida, Siphonaptera, Diptera, Lepidoptera, Piscicolidae, lampreys, vertebrate fishes, birds, and mammals, suggesting the parallel evolution or convergence of the strategy. In the literature they were rarely referred to as micropredators: rather, some of them (e.g. lampreys and leeches) were often called “parasites”, while the most representative groups (i.e. mosquitoes and ticks) were called “vectors”. In fact, many micropredators are haematophagous (blood-sucking) and have significant impacts on ecosystems through the transmission of diseases. Micropredation is not limited to haematophagy, and covers a range of opportunistic feeders and scavengers that consume chunks of prey tissue, symbiotic cleaners, and scale- or fin- clipping fishes. By definition herbivores also fall into the category of "micropredator" and have a number of key similarities, but also several important differences, especially in regard to relative size between a herbivore and its prey, and greater levels of co-evolution between plants and herbivores. The evolution of micropredation, is driven by their feeding habits or predator-prey size divergence in the shift from predation to micropredation. Due to these traits and specific evolutionary restrictions in parasites, micropredators are always descendants of predatory ancestors. Compared with parasitism, which requires significant co-evolutionary history between parasite and host, micropredators possess only limited specialization towards prey species, only modifying existing free-living traits to better exploit prey. Expanding on this, their co-evolutionary history is therefore weak compared to parasite-host relationships, but appears to be stronger than predator-prey relationships. I noted that the reason for the relative ignorance of micropredators is partly due to the lack of clear examples, especially model systems.

I then provide a case study of the micropredatory fish leech, *Taimenobdella amurensis*, and their main prey fish, *Salvelinus curilus*, in the Sorachi River, Hokkaido, Japan. Since the metapopulation dynamics and genetics of the prey fish have been studied for more than 20 years, it is ideal for investigating micropredator-prey relationships. Additionally, as a stream dwelling species, these micropredators live in a highly restricted environment, preventing active dispersal of the micropredator between stream populations within the same river due to the unidirectional flow of the current and narrow width of the stream environment. Here, I specifically focused on the genetic structure of the leech, testing if they mirror parasite-host co-structures or show independent structure from their prey, despite depending on dispersal via prey fish. Because of the close parasite-host co-evolutionary relationship, parasite populations often closely mirror the populations of their most vagile hosts, and due to their lack of such relationships, predator-prey populations rarely display such a pattern. Under such conditions, I expected these leeches to form highly structured metapopulations as a result of the low rates of geneflow between stream populations, independent of trends in prey fish movement. Thirteen custom microsatellite primers were designed and tested specifically for this leech, with primer amplification varying considerably across sampling sites. Population genetic analysis showed extremely high genetic divergence even among neighboring streams, without any pattern of isolation-by-distance, and were temporally stable. This strongly suggests that there is no functional gene flow among the tributary populations and the effects of genetic drift have accumulated. This contrasted with the genetic structure of the prey fish and suggested that the functional dispersal by attaching to their prey is minimal. This also indicates that these leeches can form independent local populations even with very small population sizes. Among many micropredatory taxa, leeches have relatively long interaction times with their prey, up to a few hours while feeding. Yet, even with the seemingly long periods of attachment and prey specificity, this micropredatory leech does not form a parasite-host like relationship with prey fish: rather, a predator-prey like free-living model is more suitable. Further monitoring is required to clarify these micropredator-prey metapopulation dynamics.

Finally, I examined the generality of micropredator-prey genetic structure by systematic review. Passive dispersal by prey or hosts movement should depend on the contact time and the contact time is longest in parasites, shortest in predators, and intermediate in micropredators. Thus, I predicted that gene flow among local populations is higher in parasites, followed by micropredators, and then predators or free-living organisms, all else being equal. To test my predictions, I chose to collect microsatellite data, due to bi-parental inheritance and higher marker resolution, from a wide range of free-living, micropredators, and parasites. However, no clear effect of trophic strategy (i.e. micropredators, parasites, and free-living animals) on genetic divergence was detected. This was partly due to large variations within trophic strategies: for example, some terrestrial micropredatory leeches showed very strong genetic divergence, which is consistent with my study, but another species that attaches to the eyes of seabirds was genetically homogenous, because of long-distance dispersal via avian migration. The taxonomic differences between species used to represent different trophic strategies was likely also a confounding variable. More critically, there were too few case studies to confirm the general patterns. The large variations of genetic divergence among and within micropredators probably result from the variations in the degree of passive dispersal. Passive dispersal of micropredators via prey movement should depend on contact time with their prey and is highly variable; from seconds in the case of many biting flies, to hours in the case of leeches. Some micropredators spend even days or weeks in contact with their prey, such as wintering ticks or migrating lamprey. Other factors such as body size and generation time can have both a positive and negative effect on dispersal, since it limits the distance and time possible for dispersal when compared with larger free-living species, but also increase the effective population size and efficiency of passive dispersal. The greatest dispersers, I would argue, are species that can utilize the advantages of both active and passive dispersal, possessing both high vagility themselves and long host interaction, while still maintaining low prey specialization. Despite this setback, based on the data I have collected so far a general pattern supporting my predictions was still possible, as parasites appear to have less structuring than micropredators or free-living animals.

Overall, I concluded that micropredators are relatively common, though not as common as predators and parasites, in many ecosystems. Micropredation appears to lack the extensive evolutionary adaptations required for a parasitic lifestyle, and seems to have evolved from various free-living feeding behaviours, such as blood, fruit, or nectar feeding, independently on multiple occasions. They have unique ecological characteristics, sometimes shared with either parasites or predators. We should incorporate and distinguish them as a legitimate ecological strategy, including separate models and methods of studying them, so as not to have them mistakenly grouped together with parasites. Micropredators constitute some of the most influential species ecologically, medically, and economically as a result of their role as vectors for diseases in humans and other animals. I hope this case study of the leech-fish system inspires studies on other micropredator-prey systems.