Heterokairy as an anti-predator strategy for parasitic species

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Heterokairy refers to plasticity in the timing of onset of developmental events at the level of an individual. When two developmental stages do not share the same ecological niche, referred to as ‘ontogenetic niches’, the control of the niche shift through a change in developmental timing can be advantageous for the individual (e.g., when mortality risk is different in the two niches). Heterokairy can arise either from plasticity in developmental rate (ontogenetic shift) or by a purely behavioral decision (behavioral shift). Parasitic species living inside of their hosts often inherit the predators of their hosts. To cope with the predation risk on their hosts, parasites and parasitoids show either host-manipulation abilities or either host-leaving strategies. Nevertheless, leaving the host should be associated with developmental costs, since the parasitic individuals are usually unable to parasitize another host. This process is thus related to the classical trade-off between size and developmental time. Recent studies provided examples of behavioral heterokairy in invertebrates. The goal of this publication is to review and discuss recent results on developmental plasticity in parasitic species in an evolutionary perspective.

Heterokairy: Definition

Phenotypic plasticity in development time allows individuals to deal with unpredictable environments.1 Heterokairy refers to plasticity in the timing of developmental events at the level of an individual.2 “Heterokairy” is the individual equivalent of evolutionary “heterochrony,”3 and can arise either from plasticity in developmental rate (ontogenetic shift)4,5 or by a purely behavioral decision.6,7 Exposure to predators have been shown to deal with unpredictable environments.1 Heterokairy refers to plasticity in the timing of onset of developmental events at the level of an individual.2 “Heterokairy” is the individual equivalent of evolutionary “heterochrony,”3 and can arise either from plas-

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Parasitic species living inside of their hosts often inherit the predators of their hosts.7 Parasitoids are organisms that develop inside or on another organism (host); they feed on the host tissues and kill the host as a direct or indirect result of its development. For a long time, parasitic species were considered to live in a predictable environment (hosts) that does not require adaptive phenotypic plasticity. Thomas et al.7 challenged this view by discussing the state-dependent strategies adopted by parasitic species to maximize their reproductive success according to external conditions.7 The environment of parasites is made up of at least two dimensions, which are ecologically different: the host (i.e., the immediate environment) and the habitat of the host (i.e., the ecosystem).7 For instance, it is frequently observed that parasite virulence is higher when the host is in poor condition or experiencing stressful conditions.8 It may be possible for parasites to perceive the external environment of their hosts, such as the predation risk of their hosts, and adjust their strategy accordingly. Free-living crustaceans can evaluate the abundance of fish predators, without the need to see them directly, by detecting components of the fish mucus in the water.9

The role of predation in the evolutionary ecology of animal communities has long been a focus of ecological research but, to date, sparse attention has been given to the responses of parasites...
when their hosts are victims of predation.6 One option for parasitic species to reduce the risk of mortality by predation of its host is to reduce the encounter rate with potential predators of host by altering the behavior of the host,20,21 a process known as “host manipulation.”23 A step further is the induction of unusual patterns in the host’s behavior in order to reduce encounters with parasitoid specific natural enemies, such as hyperparasitoids, a process known as “usurpation.”24-26 The option would be to leave the endangered host.

### Heterokairy as an Antipredator Strategy for Parasitic Species

Host-leaving event leads to “heterokairy” since the individual will end its endoparasitic development to enter another step of development. Timing of the onset of developmental events is plastic according to the mortality risks within and outside of the host.

One example of such anti-predatory strategy has been found for the hairworm *Paragordius tricuspidatus* (Nematomorpha: Gordiida). These worms parasitize mainly crickets, which they manipulate to commit “induced suicide” by jumping into the water. In the water, the worm comes out to freely live its adult life.23 First, it has been shown that if a parasitized cricket that enters the water is eaten by a fish or a frog, the hairworm is able to escape not only from its insect host but also from the digestive tract of the predator.27 The worm emerges alive from the mouth, gills or nose of the predators and continues its life cycle without any apparent fitness costs.28 Moreover, worm emergence from the host has been shown to be induced by predatory notonectid.6

Recently, it has been shown that the predation on host induced early emergence in the endoparasitic fly *Endaphis fugitiva* (Diptera: Cecidomyiidae).7 As a larva, this aphid parasitoid develops inside the host body and emerges as a mature larva to pupate in the soil.28 Plasticity in the timing of emergence allows the parasitoid to respond to mortality risk occurring while inside its host. Artificial injuries on host, as well as predator attack on host, induced parasitoid larvae to leave the host. When a parasitized aphid is bitten by a predatory Hemerobiid larva, the parasitoid larva quickly flees from its host. Moreover, it has been observed that the predator goes on feeding on the remains of the host’s body, while the parasitoid is emerging. This allows the parasitoid larvae to perform jumps and escape from further direct predator attack.29

### Costs of Heterokairy and Evolutionary Processes

Whether to grow larger at the cost of longer development time, or to develop more rapidly at the cost of reduced size is a classical trade-off in life history evolution. However, it might be that the developmental constraints on some parasitic species will influence the evolution of heterokairy. Indeed, in a few hymenopterous endoparasitoid clades (e.g., Microgastrinae, Braconidae), parasitoid larvae consume only a small fraction of available host tissues (primarily fat body and hemolymph) and emerge from the still living host by perforating the host cuticle with their mandibles and pupating externally.30 It is hypothesized that developmental constraints might come from differences in the way species feed on host tissues: leading some species to emerge when fixed critical size is reached, while other species have to

### Table 1. Species for which heterokairy have been shown

| Sp            | Order       | Effect of mortality risk | Mortality risk         | Cue                             | References                      |
|---------------|-------------|--------------------------|------------------------|---------------------------------|---------------------------------|
| Coregonus sp. | Fish        | Early hatching of eggs   | bacterial infection    | water borne chemical cues from infected eggs | Wedekind, 2002 |
| *Bufo americanus* | Amphibia    | Early hatching of eggs   | infection by Saprolegniaeae water mold | unknown                          | Gomez-Mestre, et al. 2006 |
| *Rana sylvatica* | Amphibia    | Early hatching of eggs   | infection by Saprolegniaeae water mold | unknown                          | Gomez-Mestre, et al. 2006 |
| *Hyla regilla* | Amphibia    | Early hatching of eggs   | predation by leeches   | chemical cue(s) from predator and injured eggs | Chivers, et al. 2001 |
| *Rana cascadae* | Amphibia    | Early hatching of eggs   | predation by leeches   | chemical cue(s) from predator | Chivers, et al. 2001 |
| *Agalychnis callidrya* | Amphibia   | Early hatching of eggs   | predation by wasps, predation by snakes | hypothetically mechanical stimulus | Warkentin 1995, 2000 |
| *Ambystoma texanum & A. barbouri* | Amphibia | Delayed hatching of eggs | predation of larva by flatworms | water-borne chemical cues from predator | Sih & Moore, 1993 |
| *Scytodes pallida* | Arachnida | Early hatching of eggs   | predation by jumping spiders | Chemical cue(s) on draglines of the predatory spider | Li, 2002 |
| *Endaphis fugitiva* | Insecta    | Precocious emergence of mature larva | predation by brown lacewing | unknown                          | Muratori, et al. 2010 |
| *Paragordius tricuspidatus* | Nematomorpha | Speed up emergence time | predation by notonectid larva | unknown                          | Sanchez, et al. 2008; Ponton, et al. 2006 |
consume the entire host before emergence.\textsuperscript{15} It might be that the evolution of heterokairy has been driven by the selective advantages of individuals that freed themselves from the constraint of total consumption of the host body before shifting to the next developmental step.

Organisms should switch life history stages when their mortality/growth ratio is lower in the following stage than the current stage.\textsuperscript{8} Obviously, mortality risk due to host predation should be frequent enough to induce a selective pressure on the parasitic individual. Therefore, predators should not be able to discriminate between parasitized and unparasitized hosts. In the Endaphis system, we tested this assumption by studying the behavior of a single aphid predator foraging in a patch containing 3 healthy and 3 parasitized hosts (n = 13). We showed that the probability of being attacked was not related to the presence of a parasitoid larva in the host (Fig. 1). The binomial response (attack or leave) of the predator to aphid encounter was not statistically different between the healthy and parasitized hosts (Wald = 0.872, df = 1, p = 0.35; Generalized Estimating Equations, binomial distribution, logit link function, “geepack” for R\textsuperscript{32}). This suggests that selective pressure on the parasitoid is not reduced by discrimination abilities from the predator.

If mortality risk is high enough, the benefit of saving its life against the costs associated with early emergence as well as the development and maintenance of sensory machinery is clearly biased towards the selection of responsive parasitoids. Working on the spitting spider system, Li showed that hatchings from predator exposed eggs were smaller than unexposed ones.\textsuperscript{15} Muratori et al. did not find costs associated to early emergence in hairworms (Paragordius tricuspidatus), which produce similar offspring as controls.\textsuperscript{16} While costs associated with heterokairy have been shown in many vertebrate systems,\textsuperscript{8,11} studies on induced niche-shift in invertebrate parasitic species are unfortunately too scarce to draw any conclusions.

Emphasis has been placed on studying adaptive developmental plasticity in the context of anti-predator defenses, but it is also likely to be effective in response to environmental heterogeneity in other factors (abiotic, pathogens, competition).\textsuperscript{9} Several sources of selection for plasticity in itself might have had a positive effect on the conservation of this trait. On the evolutionary point of view, it might be that adaptive niche shift is a process common for concealed species that emerge as larvae to pulate outside their shelter/host. For example, Endaphis fugax belongs to the Cecidomyiidae family in which both predatory, parasitoid and phytophagous species are found.\textsuperscript{29} Many of the phytophagous Cecidomyiids are galling insects. It would be interesting to test if adaptive niche-shift is present in these species.

![Figure 1](image-url). Number of attacks on healthy and Endaphis parasitized hosts by the aphid predator, Micromus timidus. The aphid predator does not discriminate parasitized host, which keeps a strong selection pressure on the parasitoid for induced emergence response.

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