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It's All Life History

Editorial

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Consider grandmaman Cécile: she left behind 14 children of her own, who themselves had 25 children between them. Added to that the 30 great-grandchildren, Cécile had 69 offspring, even though, biologically speaking, she was reproductively active for less than a quarter of her long life of 95 years.

This is a simple story, and yet it encapsulates most fundamental aspects of the branch of biology that concerns itself with the study of 'life history' — the topic of this special issue of *Current Biology*. Life history is so deeply engrained in our everyday experience that even many biologists are unaware that it is an area of study at all — as we discovered when talking to friends and colleagues in preparation for this issue. One aim for this special issue, therefore, was — rather than present more on the well-trodden paths of life-history evolution and theory — to try and provide a wider panorama of the different aspects of biology life history touches upon.

As familiar as human life history is to us, as remarkable it is in biological terms. For one, humans have an unusually long lifespan (the ultimate life-history trait) — almost twice that of a chimpanzee. Thomas Kirkwood and Simon Melov discuss in their review how lifespan and ageing may or may not be viewed as a life-history adaptation. Compared with their primate sister species, humans not only live longer, but also have much shorter intervals between births, and, women at least, an unusually long life after reproduction has ceased; at menopause, Cécile wasn't even halfway through her life. How these human peculiarities, as well as the long and slow life histories of primates in general, can inform life-history theory is discussed in James Holland Jones's review. In fact, although we humans like to attribute our success to our superior brains, our high reproductive potential — a life-history trait — is just as important in explaining how we came to dominate this planet, and even our large brains themselves may be a by-product of an altered life-history pattern.

But of course, even though most life-history research has traditionally focused on animals, life-history strategies are by no means limited to so-called higher organisms. Even the simplest virus can go through phases of a replicative cycle and switch between alternative strategies — consider the lytic and lysogenic modes of phage lambda for instance. Two of the reviews in this issue thus focus on life-history in three less-studied groups: ascomycete fungi, reviewed by Louise Glass and colleagues, and symbiotic rhizobia and mycorrhizal fungi, reviewed by Ford Denison and Toby Kiers.

Life-history research has for a long time been very theory-driven, and in a sense this field is one of the great success stories of putting theory to work in biology. A central concept of life-history theory is the idea of trade-offs. An organism has limited energy to spend and needs to allocate it to the different aspects of its life: finding food and a place to live, finding a partner, raising offspring. One solution to this problem is to assign the different tasks to different stages in the life cycle and to evolve specialised forms to go with them. This strategy is widely used — from the adult mayfly whose sole task it is to find a mate, to the ever-hungry caterpillar — and involves often dramatic bodily transformations between stages. Before the term 'life history' was even coined, such metamorphoses — like the tadpole turning into a frog illustrated on the issue's cover — were what first caught the attention of naturalists and artists. The physiological and developmental mechanisms underlying this and other metamorphoses in vertebrates are discussed in the review by Vincent Laudet.

In the sea, where the main task of larvae is dispersal, the transformations from larva to adult are especially striking: free swimmers become sessile filter feeders, bilateral symmetric animals adopt a secondary radial symmetry and so forth. Yet, such radically different forms are of course made from a single genome. The review by Dustin Marshall and Steve Morgan focuses on how this genetic and morphological linkage between stages may affect the evolution of life history in marine organisms.

If marine organisms are the champions of transformation between stages, parasites are arguably the masters of complexity as far as life-cycles are concerned — a fact paid homage to in the review by Mark Viney and Jo Cable. Aside from the trade-offs that free-living animals face, parasite life histories are also shaped by the need to switch between and adapt to ever-evolving hosts. Parasitism is particularly common in nematodes, where it has evolved several times independently, and one reason why this should be so might lie in their life histories. Many nematodes are able to enter a robust, dormant larval stage, the so-called dauer larva, and this phenotypic plasticity — the hormonal control and evolutionary elaboration of which Ralf Sommer and Akira Ogawa discuss in their review — may have facilitated the evolution of parasitic lifestyles. Phenotypic plasticity is also the topic of Stephen Simpson and colleagues' review, which focuses on the ability of many insect species to adapt alternative guises in response to environmental conditions or signals from conspecifics — a phenomenon known as 'polyphenism'; think: winged and wingless aphids, worker bees and queens, migratory and solitary locusts.

While life history has been predominantly studied from an evolutionary point of view, studies on genetic model organisms have also led to a deep mechanistic understanding of how life-history characteristics are controlled, as exemplified in the molecular control of dauer formation in the nematode *C. elegans* or, as reviewed by Carl Thummel and Jason Tennessen, in the regulation of growth and maturation in *Drosophila*.

All of these reviews from the theoretical to the mechanistic can of course cast no more than spotlights on that vast realm of biology that is life history. From how the tadpole becomes a frog to the disproportionally long lifespans of bats, from plankton and parasites to why we have grandmothers: life history really is everywhere.