

extinct (at least in Ireland)? The probable answer to this old dilemma is, I am afraid, rather commonplace. The giant deer flourished in Ireland for only the briefest of times—during the so-called Alleröd interstadial phase at the end of the last glaciation. This period, a minor warm phase between two colder epochs, lasted for about 1,000 years, from 12,000 to 11,000 years before the present. (The Irish Elk had migrated to Ireland during the previous glacial phase when lower sea levels established a connection between Ireland and continental Europe.) Although it was well adapted to the grassy, sparsely wooded, open country of Alleröd times, it apparently could not adapt either to the subarctic tundra that followed in the next cold epoch or to the heavy forestation that developed after the final retreat of the ice sheet.

Extinction is the fate of most species, usually because they fail to adapt rapidly enough to changing conditions of climate or competition. Darwinian evolution decrees that no animal shall actively develop a harmful structure, but it offers no guarantee that useful structures will continue to be adaptive in changed circumstances. The Irish Elk was probably a victim of its own previous success. *Sic transit gloria mundi.*

# 10

## Organic Wisdom, or Why Should a Fly Eat Its Mother from Inside

SINCE MAN CREATED God in his own image, the doctrine of special creation has never failed to explain those adaptations that we understand intuitively. How can we doubt that animals are exquisitely designed for their appointed roles when we watch a lioness hunt, a horse run, or a hippo wallow? The theory of natural selection would never have replaced the doctrine of divine creation if evident, admirable design pervaded all organisms. Charles Darwin understood this, and he focused on features that would be out of place in a world constructed by perfect wisdom. Why, for example, should a sensible designer create only on Australia a suite of marsupials to fill the same roles that placental mammals occupy on all other continents? Darwin even wrote an entire book on orchids to argue that the structures evolved to insure fertilization by insects are jerry-built of available parts used by ancestors for other purposes. Orchids are Rube Goldberg machines; a perfect engineer would certainly have come up with something better.

This principle remains true today. The best illustrations of adaptation by evolution are the ones that strike our intuition as peculiar or bizarre. Science is not “organized common sense”; at its most exciting, it reformulates our view of the world by imposing powerful theories against the ancient, anthropocentric prejudices that we call intuition.

Consider, for example, the *cecidomyian* gall midges. These tiny flies conduct their lives in a way that tends to

evoke feelings of pain or disgust when we empathize with them by applying the inappropriate standards of our own social codes.

Cecidomyian gall midges can grow and develop along one of two pathways. In some situations, they hatch from eggs, go through a normal sequence of larval and pupal molts, and emerge as ordinary, sexually reproducing flies. But in other circumstances, females reproduce by parthenogenesis, bringing forth their young without any fertilization by males. Parthenogenesis is common enough among animals, but the cecidomyians give it an interesting twist. First of all, the parthenogenetic females stop at an early stage of development. They never become normal, adult flies, but reproduce while they are still larvae or pupae. Secondly, these females do not lay eggs. The offspring develop live within their mother's body—not supplied with nutrient and packaged away in a protected uterus but right within the mother's tissues, eventually filling her entire body. In order to grow, the offspring devour their mother from the inside. A few days later, they emerge, leaving a chitinous shell as the only remains of their only parent. And within two days, their own developing children are beginning, literally, to eat them up.

*Micromalthus debilis*, an unrelated beetle, has evolved an almost identical system with a macabre variation. Some parthenogenetic females give birth to a single male offspring. This larva attaches to his mother's cuticle for about four or five days, then inserts his head into her genital aperture and devours her. Greater love hath no woman.

Why has such a peculiar mode of reproduction evolved? For it is unusual even among insects, and not only by the irrelevant standards of our own perceptions. What is the adaptive significance of a mode of life that so strongly violates our intuitions about good design?

To answer these questions, we proceed by the usual mode of argument in evolutionary studies: the comparative method. (Louis Agassiz did not act capriciously when he gave to the building in which I work the name that has puzzled so many generations of visitors to Harvard—the Museum of Comparative Zoology.) We must find an object for compari-

son that is genetically similar, but adapted to a different mode of life. Fortunately, the complex life cycle of cecidomyians provides us with a key. We do not have to compare the asexual, larval mother with a related species of uncertain affinity and genetic resemblance; we may contrast it with the genetically identical, alternate form of the same species—the normal, sexual fly. What then is different about the ecology of parthenogenetic and normal forms?

The cecidomyians feed and dwell on fungi, usually mushrooms. The mobile, normal fly fills the role of discoverer: it finds the new mushroom. Its offspring, now living on a superabundant food resource, reproduce asexually as larvae or pupae and become the flightless, feeding form of the species (a mushroom can support hundreds of these tiny flies). We know that parthenogenetic reproduction will continue as long as food is abundant. One investigator produced 250 consecutive larval generations by supplying enough food and preventing crowding. In nature, however, the mushroom is eventually used up.

H. Ulrich and his coworkers have studied the sequence of changes in response to decreasing food in the species *Mycophila speyeri*. When they have abundant food, parthenogenetic mothers generate all female broods in four to five days. As the supply of food diminishes, all male and mixed male and female broods develop. If female larvae are not fed at all, they grow into normal flies.

These correlations have a fairly unambiguous adaptive basis. The flightless, parthenogenetic female stays on the mushroom and feeds. When it exhausts its resource, it produces winged descendants to find new mushrooms. But this only scratches the surface of our dilemma, for it does not address our central question: Why reproduce so quickly as a larva or pupa, and why self-destruct by a supreme sacrifice to one's children?

I believe that the solution to this dilemma lies in the phrase “so quickly.” Traditional evolutionary theory concentrated on morphology in framing adaptive explanations. What, in this case, is the advantage to mushroom feeders of a persistent juvenile morphology in reproducing females? Tradi-

tional theory never found an answer because it had posed the wrong question. During the last fifteen years, the rise of theoretical population ecology has transformed the study of adaptation. Evolutionists have learned that organisms adapt not only by altering their size and shape but also by adjusting the timing of their lives and the energy invested in different activities (feeding, growth, and reproduction, for example). These adjustments are called "life history strategies."

Organisms evolve different life history strategies to fit different types of environments. Among theories that correlate strategy with environment, the theory of  $r$ - and  $K$ -selection, developed by R. H. MacArthur and E. O. Wilson in the mid-1960s, has surely been the most successful.

Evolution, as usually depicted in textbooks and reported in the popular press, is a process of inexorable improvement in form: animals are delicately "fine tuned" to their environment through constant selection of better-adapted shapes. But several kinds of environments do not call forth such an evolutionary response. Suppose that a species lives in an environment that imposes irregular, catastrophic mortality upon it (ponds that dry up, for example, or shallow seas ripped up by severe storms). Or suppose that food sources are ephemeral and hard to find, but superabundant once located. Organisms cannot fine tune themselves to such environments for there is nothing sufficiently stable to adjust to. Better in such a situation to invest as much energy as possible into reproduction—make as many offspring as you can, as quickly as possible, so that some will survive the catastrophe. Reproduce like hell while you have the ephemeral resource, for it will not last long and some of your progeny must survive to find the next one.

We refer to evolutionary pressures for the maximization of reproductive effort at the expense of delicate morphological adjustment as  $r$ -selection; organisms so adapted are  $r$ -strategists ( $r$  is the traditional measure of "intrinsic rate of increase in population size" in a set of basic, ecological equations). Species that live in stable environments, near the maximum population size that the environment can support, will gain nothing by producing hordes of poorly adjusted progeny.

Better to raise a few, finely tuned offspring. Such species are  $K$ -strategists ( $K$  is the measure of environmental "carrying capacity" in the same set of equations).

The parthenogenetic larval gall midges live in a classical  $r$ -environment. Mushrooms are few and far between, but superabundant when found by such a tiny fly. Cecidomyian gall midges therefore gain a selective advantage if they use newly discovered mushrooms for building up their population as rapidly as possible. What, then, is the most efficient way to build a population quickly? Should the midges simply lay more eggs or should they reproduce as early as possible during their lives? This general issue has inspired a large literature among mathematically inclined ecologists. In most situations, the key to rapid increase is *early* reproduction. A 10 percent decrease in age at first reproduction can often yield the same effect as a 100 percent increase in fecundity.

Finally, we can understand the peculiar reproductive biology of cecidomyian gall midges: they have simply evolved some remarkable adaptations for early reproduction and extremely short generation times. In so doing, they have become consummate  $r$ -strategists in their classical  $r$ -environment of ephemeral, superabundant resources. Thus, they reproduce while still larvae, and almost immediately after hatching, they begin to grow the next generation within themselves. In *Mycophila speyeri*, for example, the parthenogenetic  $r$ -strategist undergoes only one molt, reproduces as a true larva, and manufactures up to 38 offspring in five days. The normal, sexual adults require two weeks to develop. The larval reproducers maintain a phenomenal capacity for increase in population size. Within five weeks after its introduction into a commercial mushroom bed, *Mycophila speyeri* can reach a density of 20,000 reproductive larvae per square foot.

We may again pursue the comparative method to convince ourselves that this explanation makes sense. The cecidomyian pattern has been followed by other insects that inhabit a similar set of environments. Aphids, for example, feed on the sap of leaves. A leaf, to these tiny insects, is much like a mushroom to a gall midge—a large, ephemeral resource to be converted quickly into as many aphids as possible. Most

aphids have alternate parthenogenetic forms—wingless and winged (they also have an overwintering, sexual form, which need not concern us here). As you have probably already guessed, the wingless form is a flightless feeder. Although it is not a larva, it retains many features of juvenile morphology. It also maintains a remarkable capacity for early reproduction. Embryonic development actually begins in a mother's body before her own birth, and two subsequent generations may be telescoped within each "grandmother." (Aphids, however, are not consumed by their offspring.) Their capacity for rapid increase in population size is legendary. If all its offspring lived to reproduce, a single female of *Aphis fabae* could produce 524 billion progeny in a year. Winged aphids develop more slowly when the leaf is used up. They fly off to a new leaf, where their offspring revert to the wingless form and begin their rapid cycling of generations.

What at first seemed so peculiar now seems eminently reasonable. It may even be an optimal strategy for certain environments. This much we cannot claim, for so many aspects of cecidomyian biology are entirely unknown. But we can point to the uncanny convergence upon the same strategy by a completely unrelated organism, the beetle *Micromalthus debilis*. This beetle lives and feeds in wet, rotting wood. When the wood dries out, the beetle develops a sexual form to search for new resources. The wood-dwelling, feeding form has evolved a set of adaptations that repeats the features of cecidomyians down to the most complex and peculiar detail. It also is parthenogenetic. It also reproduces at a morphologically juvenile stage. The young also develop within the mother's body and eventually devour her. Mothers also produce three types of broods: females only when food is abundant and males only or males and females when resources diminish.

We humans with our slow development (see essay 7), extended gestation, and minimal litter size are consummate *K*-strategists and we may look askance at the strategies of other organisms, but in their *r*-selective world the cecidomyians are surely doing something right.