The reproductive strategies of hydra

Two in One

Dr. Anita Kaliszewicz studies evolutionary biology at the Center for Ecological Research. She is intrigued by reproductive strategies, especially the evolutionary and ecological implications of asexual reproduction and the mechanisms behind the evolution of hermaphroditism

ANITA KALISZEWICZ
Center for Ecological Research, Dziekanów Leśny
Polish Academy of Sciences
a.kaliszewicz@cbe-pan.pl

Why is the sexual mode of reproduction so common in nature? What are the advantages of hermaphroditism? Studying water hydra, capable of both sexual and asexual reproduction, may help us better understand the evolution of different reproductive strategies

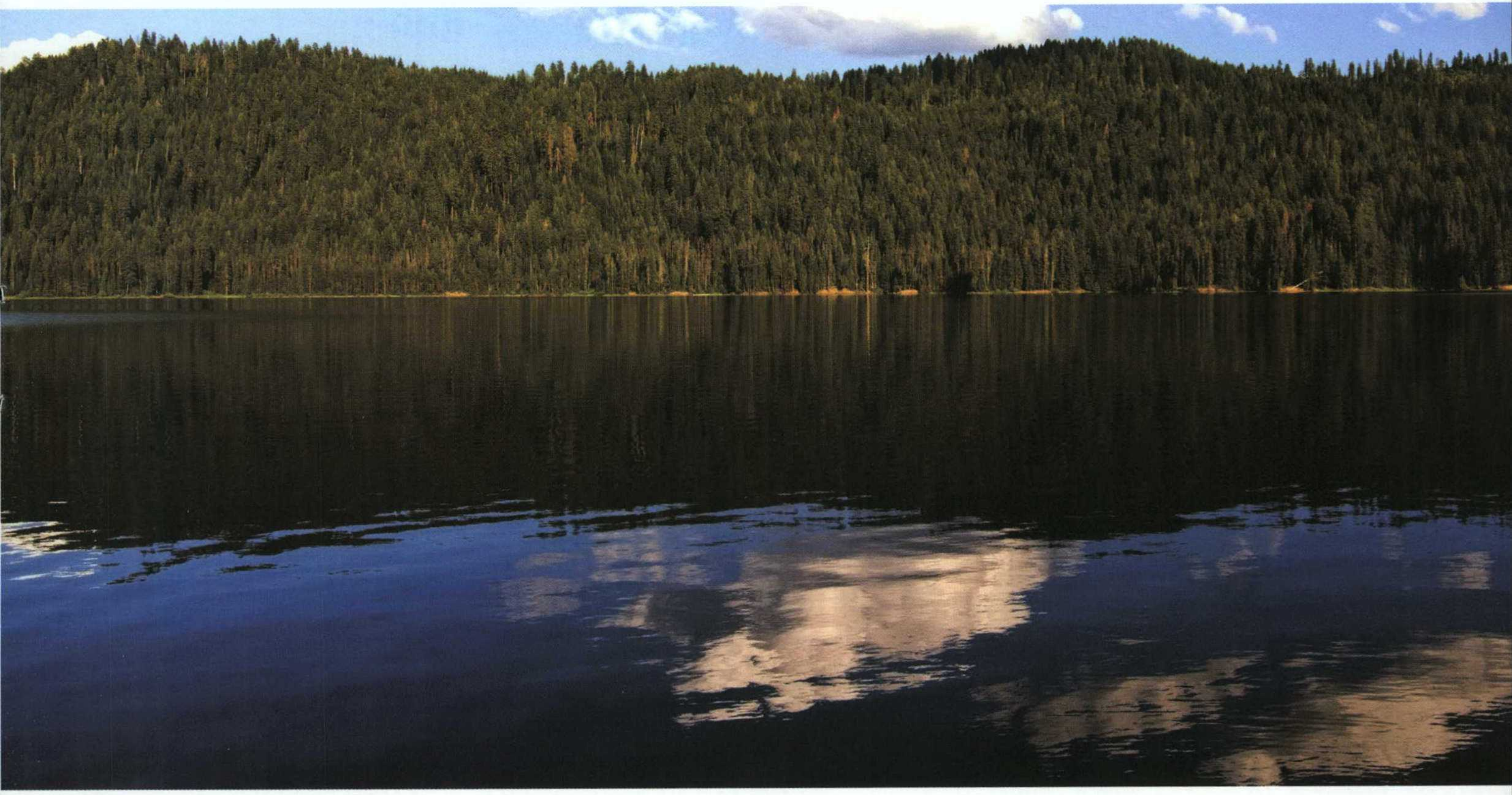
Reproduction, a pivotal issue for evolutionary biology, has spawned a great many theories. From the standpoint of an individual specimen, asexual reproduction without gametes seems to be the most favorable strategy. Under the "selfish gene" concept proposed by Richard Dawkins, such reproduction affords the parent a clear advantage over individuals that reproduce sexually. Asexual reproduction gives rise to many identical copies within a short time. Such a parent represents the beginning of a clone, whose numbers rise exponentially, giving the parent impressive reproductive success. Every one of the progeny inherits genetic information identical to that of the parent, whereas the offspring of sexually reproducing organisms only inherit half of the genetic information of each of their parents.

Sex or no sex?

Why, then, is sexual reproduction so commonly found in nature? This is a question that has long intrigued biologists. Sexual reproduction always gives rise to new genotypes, through recombination. Why is sexual reproduction chosen, therefore, if producing identical copies of an existing advantageous genotype seems more favorable? And why is *dioecism* (having distinct male and female genders in different individuals) so widespread? Wouldn't *hermaphroditism* (having individuals with both male and female organs) be more advantageous? Theories about the energy allocation involved in sexual reproduction suggest that the reproductive success of a hermaph-

Anita Kaliszewicz

In populations of the brown hydra, *Hydra oligactis*, males may account for as much as 80% of all sexually mature individuals



Benjamin Earwicker, www.sxc.hu

roditic specimen is the sum of the successes achieved by its male and female functions. The cost of sexuality is 25% lower for hermaphrodites than for dioecious individuals.

Moreover, sexual reproduction demands that additional energy be invested in seeking a partner. Hermaphroditism, on the other hand, has the option of self-fertilization as a kind of safety mechanism in the event no partner is found. Seen in this light, dioecism is the least advantageous reproductive strategy. But since sexual reproduction and the existence of separate genders is so widespread, the strategy must nevertheless yield other advantages that are not explained in terms of simple energy balance or number of offspring.

The Red Queen Theory

Many theories have been posited to explain the evolution of sexuality. The most well-known is the "Red Queen Hypothesis" put forward by Leigh Van Valen - it maintains that biotic conditions change so rapidly that they must continually demand new combinations of genes, which can only be supplied by sexual processes. This is particularly important in the co-evolution of a parasite-host pair. Because asexually reproduced offspring inherit identical sets of the parent genes, parasites that fare well within the parent organism will be able to attack all its offspring just as successfully, whereas sexual reproduction gives rise to new combinations of genotypes that are possibly more parasite resistant. The Red Queen Hypothesis cannot, however, explain the existence of species that do not reproduce sexually at all, such as rotifers from the order Bdelloidea, for which males are unknown.

Interestingly, there are quite a few animal species that gain benefits from sexual reproduction while simultaneously reducing its costs by retaining a capacity for asexual reproduction without gametes. They therefore exhibit two different forms of reproduction, both sexual and asexual. This group includes representatives of Cnidaria, Platyhelminthes, Nemertini, Annelida (Polychaeta, Oligochaeta and Aphanoneura), and Echinodermata (Asteroidea, Ophiuroidea and Holothuroidea). The example of hydras (Hydriatae, Cnidaria) shows that the main means of reproduction for such animals is asexual (in this case budding). Sexual reproduction, on the other hand, produces zygotes capable of surviving through harsh conditions, such as low temperatures.

All the hydra are fresh-water species inhabiting lakes, ponds, and slow-moving currents. But despite being closely related and inhabiting similar habitats, different species exhibit very different reproductive strategies

The reproductive strategies of hydra

A green hydra, *Chlorohydra viridis*, here reproducing asexually by budding

Anita Kaliszewicz

Because of this capacity for both kinds of reproduction, hydras offer an excellent chance to identify evolutionary factors that underpin different reproductive strategies.

Why do strategies differ?

All the species in the *Hydra* genus manifest similar strategies of asexual reproduction, yet differ in terms of their sexual reproduction method. The brown hydra, *Hydra oligactis*, is dioecious. The common hydra, *Hydra vulgaris*, is described as a hermaphroditic species although populations consisting of dioecious and hermaphroditic individuals can be encountered. For the green hydra, *Chlorohydra viridissima*, specimens within the same clone (genetically identical offspring produced through budding) may be differentiated in terms of their method of sexual reproduction. Overall, although hydra have been a subject of biological study for some time (their regenerative abilities were known as far back as in the 18th century), the mechanisms responsible for the evolution of their differing sexual reproduction strategies remain ill understood. Individual hydra species also differ in terms of the times at which they produce gonads and engage in sexual reproduction. In moderate climates, the brown hydra and common hydra reproduce sexually from October to December. In these species, sexual reproduction is induced by a temperature drop. But the green hydra, on the other hand, reproduces sexually from May to June, when temperatures increase.

What underlies the different reproductive strategies of such closely-related species inhabiting similar habitats? All the hydra are fresh-water species inhabiting lakes, ponds, and slow-moving currents. Why are some species or populations dioecious, others hermaphroditic? We still have no clear-cut answer to those questions. Possibly, species whose specimens have low costs of self-maintenance or have symbiotes as an additional source of energy (such as the green hydra, living in symbiosis with algae from the *Chlorella* order) will be able to produce both types of gonads, male and female. But even if hermaphroditism is the optimal breeding strategy, species for which resources are at a premium will be forced to compromise by producing gametes of only one type - this raises the number of gametes, contributes to individual reproductive success, and favors dioecism.

Competing for a partner

An alternative hypothesis to this limited-resources theory is the notion that competing for a partner has an impact - based on existing theories on the evolution of hermaphroditism (the low density model, gene dispersal model). Low mobility plus the consequent limited partner availability favors hermaphroditism. This can be observed, for instance, among sedentary organisms. But this hypothesis fails to explain why both hermaphroditic and dioecious species can be found among various sedentary and semi-sedentary species of Cnidaria (including water hydra). It is possible that sexual reproduction strategies could be influenced by a combination of both mechanisms: energy resources on the one hand, dispersal and partner availability on the other.

Individual hydra species, despite being closely related and having similar ways of life, do differ in terms of several traits such as body size, the presence of symbiotes, and habitat conditions (optimal temperature or water-body size for their development). This enables us to test the impact of many factors on reproductive strategies. Interestingly, the dioecious brown hydra also shows an atypical gender ratio: rather than the 1:1 ratio commonly observed in nature, as many as 80% of sexually mature brown hydra are male, although the ratio changes over the sexual breeding season. In 1930, Fisher explained the widely dominant 1:1 gender ratio in terms of selection based on changes in the frequency of occurrence of individuals of both genders. The gender that is less numerous always gains an advantage among offspring. Selection promotes individuals that produce offspring of the rarer gender, until the proportions balance out within the whole population. Since that theory was published, however, many cases of exceptions to the even gender ratio have been published.

Gender inequality

For certain dioecious animals, the predominance of one gender within a population may reach as high as 90% (e.g. certain Nematoda, Ostracoda, Hymenoptera). Wide deviations from a balanced 1:1 gender ratio are also observed in animals capable of both asexual and sexual reproduction, including Ophiuroidea. They may derive from varying costs of producing offspring of a specific gender, or may involve gender-specific differences in egg survival or mortality rates. In the case of hydra, the gender ratio may be affected by different paces of asexual reproduction between immature males and females. Clones produced through asexual reproduction of course have the same gender as their parent. If males exhibit a faster pace of asexual reproduction than females, they will then dominate the population. It is also possible that the prevalence of males is caused by their earlier switchover to sexual reproduction, which means easier induction of sexual reproduction and faster development of gonads than females. Because the prevalence of males is highest at the outset of the sexual breeding season but then gradually lowers, this latter hypothesis seems the most likely.

Groups of organisms like hydra, which combine different reproductive strategies in different ways, therefore offer an excellent testing ground for studying the evolution of gender, mechanisms responsible for different reproductive strategies, and what factors determine whether a species is hermaphroditic or dioecious. ■

Further reading:

Charlesworth B. (1980). The cost of sex in relation to mating system. *Journal of Theoretical Biology, 84,* 655-671.

Charnov E.L. (1982). *The theory of sex allocation.* New Jersey: Princeton University Press.

Maynard-Smith J. (1978). *The evolution of sex.* United Kingdom: Cambridge University Press.

Stagni A. (1966). Some aspects of sexual polymorphism in *Chlorohydra viridissima. Journal of Experimental Zoology, 163,* 87-92.

Anita Kaliszewicz

A hermaphroditic specimen of the common hydra, *Hydra vulgaris*. The male gonads are situated higher (under the ring of tentacles) than the female ones