

Sex-Gender-Conflicts in Aquatic Hermaphrodites: are Genes Immortal?

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Abstract

When the first edition of Richard Dawkins' book *The Selfish Gene* was published (1976), the view that "altruistic behaviour" in animal populations is a common phenomenon was widely accepted. Dawkins questioned this interpretation and proposed his concept of the selfish (i.e., immortal) gene, which explains a number of phenomena, such as the evolution of anisogamy, or the roles of males vs. females during sexual reproduction in gonochorists (birds, mammals). In this 40th-2016-anniversary-analysis of Dawkins book I argue, based on observations on populations of "egoistic", (hermaphroditic) freshwater leeches of the genus *Erpobdella* characterized by intraspecific cocoon cannibalism, that his theoretical deductions were basically correct. In addition, sex-gender-conflicts in leeches are discussed with reference to the avoidance of the female role in populations of these hermaphrodites. The idea of the "immortal (i.e., selfish) gene" is attributed to the 19th-century-work of the German zoologist August Weismann, and the "Post-Dawkinsian" concept of intragenomic conflicts is addressed.

Keywords Dawkins; Cannibalism; Leeches; Selfish gene; Sex-gender-conflict

Introduction

In a recent article published in this journal it has been documented that the terms "sex" (i.e., fertilization) and "gender" (i.e., the development of juveniles into adult, fertile males/females), as well as the distinction between gonochorists (such as birds or mammals) and hermaphrodites, originated in the 19th century [1]. In this contribution, I will focus on hermaphroditic invertebrates (Annelida). The majority of leeches (annelids, class Hirudinea/Clitellata) inhabit freshwater and/or marine ecosystems (Figure 1).

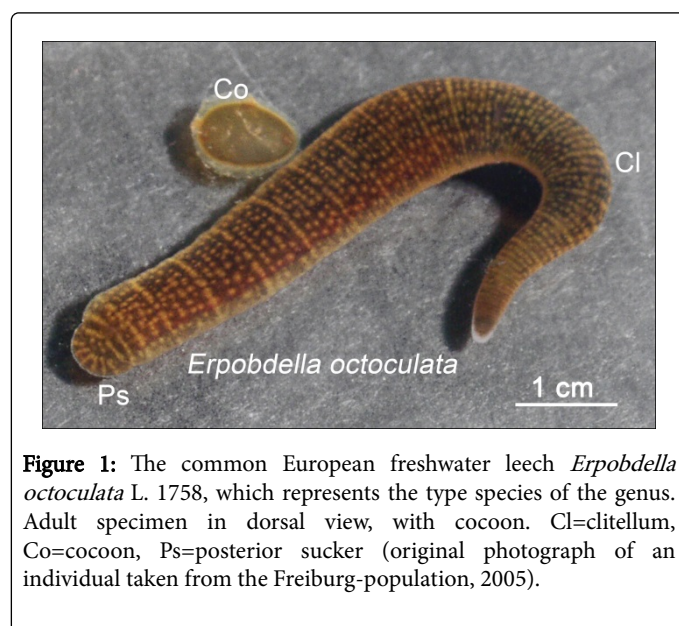


Figure 1: The common European freshwater leech *Erpobdella octoculata* L. 1758, which represents the type species of the genus. Adult specimen in dorsal view, with cocoon. Cl=clitellum, Co=cocoon, Ps=posterior sucker (original photograph of an individual taken from the Freiburg-population, 2005).

They are, like earthworms, protandric hermaphrodites, and hence first act as males (distributors of sperm), and thereafter as females (providers of egg cells) [2]. Accordingly, "sex and gender-conflicts" have long been suggested to exist in these highly evolved "worms of character" [3-5].

Over the past 40 years, the reproductive behaviour of several members of the Hirudinea was studied by the author, notably that of the morphologically simple "worm-leeches" of the genus *Erpobdella*. These predators suck off prey organisms with the aid of their muscular pharynx [6]. The following account is based in part on unpublished observations on populations of the type-species *E. octoculata* L. 1758 (body length ca. 5 cm) that were maintained in freshwater aquaria.

The results are discussed with reference to Richard Dawkins' book *The Selfish* (or *Immortal*) *Gene* (1. ed. 1976; 40 th-anniversary ed. 2016) [7]. In addition, the neglected ideas of the German zoologist August Weismann (1834-1914) are addressed [8,9].

Selfish Behavior in Freshwater Leeches

During the warm season (May to September), adult leeches, when kept isolated for a few days, readily copulate as shown in Figure 2A. The annelids first act as males (production and distribution of sperm), and thereafter as females (provision of eggs).

In these protandric hermaphrodites, the transfer of sperm occurs via so-called "pseudospermatophores" (Psp.), i.e., canula-like transient copulatory organs that are produced within the male gonopore (Figure 2B and 2C). These solid structures are actively pushed into the body wall of the partner and thereby cause a large wound that is visible after the Psp. has lost its function and degrades (traumatic insemination).

Hence, in *Erpobdella* and related taxa, the "sex-act" (fertilization) [1] is a violent sequence of events, but usually leeches 1 and 2 mutually transfer a Psp. in a "give-and-take-like"-mode of copulation [4,5,10,11]. As Figure 2C shows, sperm is pumped into the body of the partner.

As a result, the male gametes reach the ovaries, where they fertilize the eggs. Since both mature adult leeches first function as distributors of sperm (male) and thereafter as providers of egg cells (female), their gender roles are in most cases identical [1] (self-fertilization does not occur in *Erpobdella*).

However, I have occasionally observed that individual hermaphrodites rapidly transfer their Psp. and then disappear without being “stabbed” by the corresponding Psp. of the attacked, sexually mature partner. Hence, in accordance with observations on other hirudineans [11,12], “worm-leeches” of the genus *Erpobdella* may have a tendency to act as males and avoid the gender role of being female (i.e., to release the fertilized eggs into a capsule, the cocoon).

A few days after copulation, the “female” (gravid) leeches produce cocoons via the secretion of a transparent fluid from the clitellar region of their body. This process (Figure 3A) has been described in detail for different members of the Erpobdellidae and appears to be rather uniform. In 1979, I discovered that, whenever a hungry *E. octoculata* that is not about to produce a cocoon, creeps by chance into the vicinity of a reproducing conspecific in the female role, a rapid, fierce attack occurs. Using its pharynx, the leech sucks off the proteinaceous fluid from the emerging cocoon of the reproducing conspecific, inclusive of the enclosed eggs. Hence, intra-specific destruction and feeding on the cocoons of competing individuals is a well-documented phenomenon [11-15].

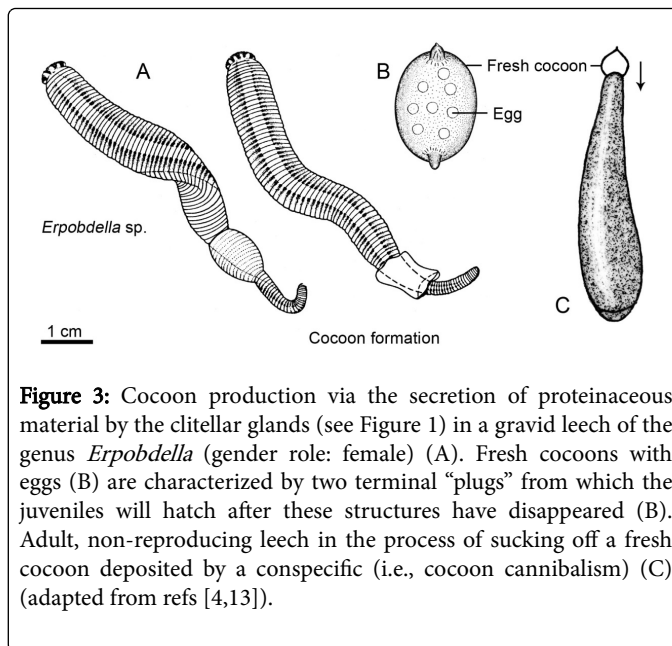


Figure 3: Cocoon production via the secretion of proteinaceous material by the clitellar glands (see Figure 1) in a gravid leech of the genus *Erpobdella* (gender role: female) (A). Fresh cocoons with eggs (B) are characterized by two terminal “plugs” from which the juveniles will hatch after these structures have disappeared (B). Adult, non-reproducing leech in the process of sucking off a fresh cocoon deposited by a conspecific (i.e., cocoon cannibalism) (C) (adapted from refs [4,13]).

The predatory leeches can not store blood etc. and therefore are always in search of food (insect larvae, small annelids etc. are rapidly sucked off with the aid of the muscular pharynx) [13-15]. Hence, whenever they detect a fresh cocoon of a reproducing individual, they “interpret” this proteinaceous, soft material as prey, so that the term “intraspecific cocoon cannibalism” is appropriate [6].

However, I have never observed that a gravid leech attacks its own cocoon (with fertilized eggs, i.e., offspring). Therefore, it is obvious that only the offspring of competitors is removed from the population, and hence the Darwinian fitness (i.e., number of surviving juveniles) of the attacking, predatory leech is maximized via this “egocentric” behaviour.

In 1979, a cannibalistic population of *E. octoculata* that existed in a pond in Freiburg i. Br. (Germany) was analyzed [13]. Twenty-five-years later, i.e., in a distant population comprised of members of the ca. 25th generation of these aggressive “1979-leeches” (Figure 1), I observed/documentated the same “egocentric” behavior (unpublished results). This finding indicates that this drastic form of intraspecific competition has a genetic basis. It should be noted that in other populations of *E. octoculata* (and related species) the intensity of intraspecific cocoon cannibalism was not so severe as that described for the “Freiburg-leeches” [11-15].

Evolution of Sex Roles in Hermaphrodites

Dawkins [7] interpreted the “evolution of the sexes (male/female)”, specifically anisogamy, in the light of “selfish reproductive elements”, i.e., small, motile sperm cells that exploit the resources stored in large egg cells, see refs [1,16,17]. This gametic asymmetry in male/female resource investment explained, why the occurrence of maternal care is common, whereas paternal breeding activities in males is rare (for gonochorists). It should be noted that these behavioural patterns are also apparent in hermaphrodites. These animals produce male gametes (sperm) and egg cells within the same body, so that they can perform both sex roles during reproduction [1].

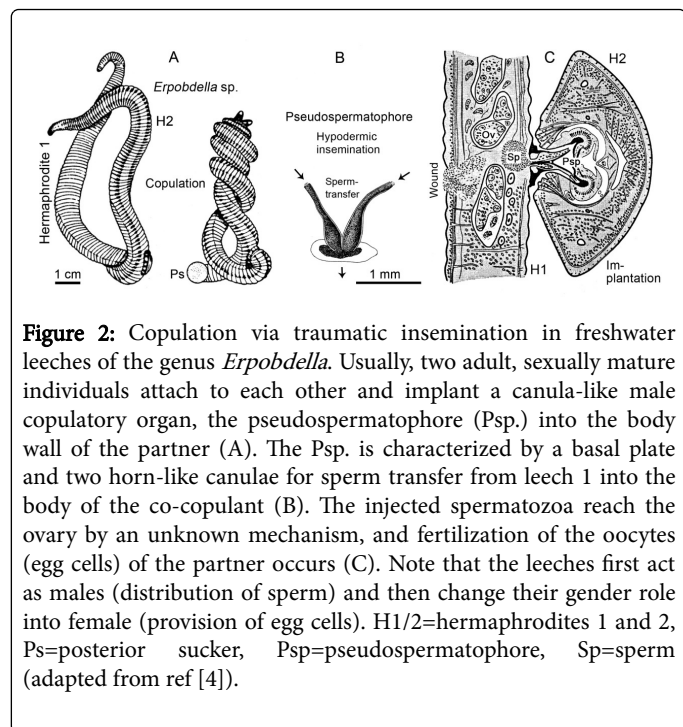


Figure 2: Copulation via traumatic insemination in freshwater leeches of the genus *Erpobdella*. Usually, two adult, sexually mature individuals attach to each other and implant a canula-like male copulatory organ, the pseudospermatophore (Psp.) into the body wall of the partner (A). The Psp. is characterized by a basal plate and two horn-like canulae for sperm transfer from leech 1 into the body of the co-copulant (B). The injected spermatozoa reach the ovary by an unknown mechanism, and fertilization of the oocytes (egg cells) of the partner occurs (C). Note that the leeches first act as males (distribution of sperm) and then change their gender role into female (provision of egg cells). H1/2=hermaphrodites 1 and 2, Ps=posterior sucker, Psp=pseudospermatophore, Sp=sperm (adapted from ref [4]).

Density Regulation vs. Selfish Individuals

During the 1980s, I had interpreted this behaviour as a means for altruistic (unselfish) “density regulation” in growing populations of *Erpobdella* spp. However, a few years later, and after many more observations, I re-interpreted this behaviour in the light of Dawkin’s principle of “egocistic” individuals (or genes) [7] (Figure 3).

As discussed above, and illustrated in Figures 2 and 3, sexually mature leeches of the genus *Erpobdella* (as well as those of the genera *Helobdella* and *Glossiphonia*; unpublished results) prefer to act as males rather than function as females. However, more work is required to further analyze this evolved “gender-bias” in different groups of the Hirudinea.

Selfish Elements and the Idea of the Immortal Gene

As briefly mentioned in passing by Dawkins [7], the “Immortality-of-life-hypothesis” originated with the work of August Weismann. The German zoologist is the founder of the “germ plasm” concept of heredity and the Neo-Darwinian theory of biological evolution. In addition, he was a pioneer in hydrobiology and aging research [8,9]. According to Weismann, the “germ plasm”, which he regarded as a special part of the germ cells (eggs and sperm), serves to carry over, from generation to generation, the factors of inheritance, which are, in modern terms, the chromosomes composed of DNA and protein [18,19].

Weismann [19,20] was convinced that the germ plasm is continuous, from living organisms back to the earliest forms of life. Moreover, he distinguished between the potentially immortal germline vs. the somatic cells constituting the body of the animal, which dies soon after sexual reproduction. Weismann wrote that “Life is continuous ... ever since its first appearance on earth, in the lowest organisms, it has continued without break; every individual alive today ... is to be derived in an unbroken line from the first and lowest forms” [20].

In this sentence, the essence of Dawkins “immortal (or selfish gene)-concept is encapsulated [20], which may explain reproductive patterns in both gonochorists and hermaphrodites (Figures 2 and 3). With respect to humans, it says that our body (i.e., Weismann’s soma) is only a vehicle for the transfer of ancient factors of heredity (replicators), which later evolved into genes, via the continuous germline. However, according to Dawkins, humans have the power to “rebel against the tyranny of the selfish replicators” (i.e., genes), despite the fact that “we are build as gene machines, and cultured as meme machines” [7].

Finally, it should be noted that Weismann [20] extended the “Darwin-Wallace-principle of natural selection” from individual organisms down to cells and heritable units. Hence, in 1913, the German biologist pre-figured the “Dawkinsian” view of gene-centered evolution [7].

Conclusion

In his book the *Selfish Gene*, Dawkins [7] discussed/criticized several interrelated issues: conflicts with respect to sexual reproduction [A], the significance of group selection in populations of “egocentric” animals [B], and the notion of immortal (selfish) genes [C]. Based on ca. 40 years of studies on populations of freshwater leeches (Figures 1-3), it is illustrated here that the “Dawkinsian” interpretations [A] and [B] can be verified. This unequivocal conclusion rests on numerous observations and experiments [6,11-15]. However, the idea [C], proposing selfish DNA-sequences, is more controversial. In a metaphorical sense, “genes” are potentially immortal, and natural selection of competing (“egoistic”) individuals, as well as sex-gender-conflicts, are a reality in evolving populations of animals, plants and some microbes.

Finally, “Post-Dawkinsian” theorists have proposed that the genome of every organism should be interpreted as a “battlefield of conflicting interests” [21,22]. This concept of “intragenomic conflicts” via “selfish genetic elements” should be explored in more detail in order to extend the insights summarized four decades ago by the British biologist Richard Dawkins in his seminal book [7].

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