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REVIEW

Terrestrial gastropods - how do they reproduce?

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Abstract

Molluscs are the most diverse group in respect of sexual systems and strategies. They can be dioecious with separate sexes or hermaphroditic. Within hermaphroditism, it is possible to distinguish a number of modifications of this type of reproduction, such as protandry, protogyny, sex reversal, or protandry with some overlap. It is thought that dioecy was ancestral because it occurs in most classes of molluscs. Hermaphroditism evolved independently several times, and sequential and simultaneous hermaphroditism are more closely related to each other than to dioecy. This publication presents a general review of sexual systems and strategies in terrestrial gastropods with special emphasis on mating, fertilization, presence of love darts, reproductive strategies (semelparity vs. iteroparity) and modes (oviparity, ovoviviparity, viviparity), production of eggs and egg cannibalism.

Key Words: copulation; mating; oviposition; reproductive systems; sequential hermaphrodite; simultaneous hermaphrodite; terrestrial gastropods

Introduction

Most animal species belong to invertebrates. Molluscs constitute the second most numerous type and the majority of them are gastropods (O'Connor and Crowe, 2005). It is estimated that the number of molluscs species detected so far varies from 80,000 to 135,000 worldwide (Abbott, 1989). Molluscs are a diverse group of animals due to their morphological forms, occurrence in different environments - water (marine and freshwater) and land, ways of feeding, but also because of various types of reproduction (Policansky, 1982). The main functions of their reproductive systems are: 1) production of male and female gametes: sperm and ova, 2) nutrition and storage of mature gametes, 3) transport of sperm produced by one specimen (autosperm) to reproductive ducts of another specimen, 4) reception of sperm produced by the same individual (allosperm), 5) providing appropriate environmental conditions for the ovum fertilized by sperm, 6) covering of zygote by protective and nutrient layers, 7) laying eggs (oviposition) and 8) resorption of remains and excess of products of the reproductive process (Gómez, 2001).

The aforementioned animals can be dioecious (gonochorism or dioecism) and can have separate sexes (female and male gonads occur in different, separate individuals) or hermaphroditic (an individual contains both male and female reproductive organs). Hermaphrodites can be simultaneous, which means that an organism has both male and female organs at the same time, or sequential - during their life their sexes change (Wilson and Harder, 2003). Among these, there is protandry (male-to-female change) and protogyny (female-to-male change), but the first one is more frequent in molluscs (Larsen *et al.*, 2013). Sequential and simultaneous hermaphroditism are more closely related to each other than to dioecy (Collin, 2013). Phylogenetic evidence indicates that dioecy is ancestral in the Mollusca phylum (Kocot *et al.*, 2011; Smith *et al.*, 2011; Collin, 2013). Monoplacophora, Caudofoveata, Polyplacophora, Scaphopoda and Cephalopoda are exclusively dioecious, while Solenogastres are simultaneous hermaphrodites. Among molluscs, gastropods and bivalves are the most diverse in terms of their reproductive systems - they are dioecious, simultaneous, or sequential hermaphrodites. There are some exceptions, for example the cases of a sequential hermaphrodite in cephalopods, one simultaneous hermaphrodite in Monoplacophora - *Micropilina arntzi*, and one genus (*Lepidochitona*) with a simultaneous hermaphrodite within Polyplacophora (Eernisse, 1988; Haszprunar and Schaefer, 1996; Lamprell and Scheltema, 2001). A very interesting case of reproductive strategy is sex reversal, which means that an animal can change its sex during its life more than once *(*Park *et al.*,

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2012). A specific case of reproduction has been observed in a few patellogastropods, which are protandric with some overlap. It differs from common protandry due to the fact that there is a short period of time during the development when both male and female gonads occur in an animal. After that, it is possible to distinguish only one type of gonad (Collin, 2013). Most studies devoted to reproductive systems and strategies concern marine and freshwater molluscs (Guo *et al*., 1998; Siddiqui and Ahmad, 2002; Chen *et al*., 2004; Calvo and Templado, 2005; Collin *et al*., 2005; Brante *et al*., 2011) and only some of them focus on terrestrial snails.

A relatively small number of terrestrial gastropods are dioecious and most of them are sequential or simultaneous hermaphrodites (Heller, 1993). Dioecy occurs in some families of land Neritomorpha (Helicinidae, Hydrocenidae) and in all land Caenogastropoda. Usually the sex ratio is 1:1, but there are some exceptions to this principle. The main advantages of the presence of this type of reproduction are: 1) increased fitness of the offspring and 2) decreased inbred depression in conjunction with preventing self-fertilization (Leonard, 2010). The problems connected with reproduction can result from the impossibility to find a partner to mate. Dioecious animals incur the same costs associated with reproduction (energy or mortality), both parents take care of the offspring (biparental care) if this behavior is present in species, and there are no differences in mortality and growth between the sexes (Warner, 1988).

Simultaneous hermaphrodites can produce male and female gametes in the same gonad (ovotestis) or separately in the ovary and the testis (Hodgson, 2009). This type of reproduction is common in organisms living in groups. Detecting simultaneous hermaphrodites is relatively simple because the anatomical section is usually sufficient (Policansky, 1982; Collin, 2013). Discovering sequential hermaphrodites is more complicated because sex change depends on many environmental factors and it is difficult to capture the moment of this phenomenon. Depending on whether we deal with protandry or protogyny, there are dissimilarities in mortality and growth. In protandry, females have a higher mortality rate, males grow faster and female functions are more costly than male functions, while in the case of protogyny, the situation is reverse (Warner, 1988). The main advantages of hermaphroditism are: 1) possibility of reproduction by self-fertilization because some species have difficulties in finding a partner to copulate, 2) higher probability of meeting a potential partner as every encountered individual can be a potential partner, 3) increased productivity due to the discharge of their functions and division of resources, 4) egg production takes place in stages, not at one time (Crowley *et al*., 1998) and 5) increased variability in fitness (Wilson and Harder, 2003). The main disadvantage is that individuals have to put a lot of energy into growth and subsistence of both types of reproductive organs (Hodgson, 2009; Leonard, 2010).

In literature one can find several hypotheses which explain the presence of hermaphroditism among animals. The most cited ones in papers are "*low density model*" and "*size advantage model*" which are connected with sequential or simultaneous hermaphroditism (Munday *et al*., 2006). The low density model proposed by Tomlinson (1966) assumes that individuals from populations with low densities are more likely to meet the suitable partner than in the case of dioecious organisms (Borgia and Blick, 1981). This model focuses on simultaneous hermaphrodites. The "size advantage model" is connected with sequential hermaphrodites and it was proposed by Ghiselin in 1969 (Ghiselin, 1969). This model is linked with the sex allocation theory and it was designed to explain the occurrence of protandry and its evolution. It states that if a small male and large female have a much higher reproductive efficiency, the male to female change will be favored along with an increase in the size of the animal. In protandry, small individuals (males) have higher reproductive fitness than larger males. It is the same in the case of females - large females have higher reproductive fitness than smaller ones. This means that reproductive functions are better realized when the animal is of the appropriate size. Moreover, males can increase their reproductive success by copulating with many females (Warner, 1988; Wright, 1988; Erisman *et al*., 2009). Sex change is present in plants and animals, not only in molluscs, but also in echinoderms, annelids, crustaceans, and fishes (Policansky, 1982).

There are many good reviews of sexual systems and strategies in molluscs (for example Baur, 1994b; Leonard, 1999, 2006, 2013; Heller, 2001; Davison and Mordan, 2007; Jordaens *et al*., 2007; Yusa, 2007; Collin, 2013; Nakadera and Koene, 2013), but in this paper we put emphasis on these issues in terrestrial gastropods and summarize the important data on this group of animals in the context of mating, fertilization, presence of love darts, reproductive strategies (semelparity vs. iteroparity) and modes (oviparity, ovoviviparity, viviparity), production of eggs and egg cannibalism in terrestrial gastropods.

Description of genitalia

Terrestrial gastropods can be dioecious and have separate sexes (*e.g*., Cyclophoridae) or hermaphroditic as stylommatophorans. The reproductive system of dioecious gastropods consists of gonad and duct called coelomic gonoduct, both structures have a mesodermal origin. Gonoduct is divided into two parts, bigger is called renal oviduct or renal gonoduct, and smaller, distal portion - pallial gonoduct (Fretter and Graham, 1962). Renal gonoduct is narrow, tubular structure in both sexes, whereas pallial gonoduct is different in males and females. In case of males, pallial gonoduct is wide with thin walls forming prostatic gland, which secrete semen. In females, walls of pallial gonoduct are divided into several parts which are able to secrete nutritious and protective substances, these are called albumen and capsule glands located side by side. On the pallial gonoduct there are situated two types of sperm pounches: bursa copulatrix and receptaculum seminis. Bursa copulatrix obtains allospermatozoa and prostatic liquid from the proccess of mating, while receptaculum seminis is used for storing these substances for future oocyte fertilization (Gómez, 2001). Another structure of reproductive system is muscular penis, usually located on the right side of the head, it was created from the anterior body wall (Gómez, 2001).

Reproductive system of stylommatophoran hermaphroditic gastropods contains gonad with gonoduct, the carrefour, albumen gland, spermoviduct, free oviduct, vagina, vas deferens, epiphallus, spermatophore, penis, diverticulum, bursa copulatrix, penial flagellum, genital atrium and other auxiliary copulatory organs (Gómez, 2001).

In stylommatophorans occur single gonad called ovotestis, which produces oocytes and spermatozoa. Ovotestis is located among patches of the digestive glands, it is composed of few or many rounded or pear-shaped sac acini and contain both male and female germ cells. Ovotestis opens to gonoduct, also called hermaphodite duct, along which germ cells are transported.

Another structure of reproductive system is the carrefour, which consists of spermatheca or female sperm-storage organ for allosperm storage, protein coating of zygotes or oocyte fertilization (Gómez, 2001). There is a huge variability in structures and morphology of the carrefour. For example, it may be divided into spermatheca and fertilization chamber, as in the case of *Trigonephrus gypsinus* (Dorcasiidae), or single spermathecal tubule beside the fertilization chamber, what is observed in *Oxychilus draparnaudi* (Zonitidae) or *Bradybaena fruticum* (Bradybaenidae) (Flasar, 1967; Brinders and Sirgel, 1992; Bojat *et al*., 2001). In some species there is variation in number of spermathecal tubules: 2 - 9 in *A*. *arbustorum* or 4 - 19 in *C*. *aspersum* (Haase and Baur, 1995; Baminger and Haase, 1999; Koemtzopoulos and Staikou, 2007; Chase and Darbyson, 2008).

In the early phase of the sexual activity of the gastropod albumen glad has small size. It develops fully when the gonad is starting to leave the eggs. Gastropods differ in the shape of the gland, for example rounded and shield-shape in Agriolimacidae, while Limacidae has this structure worn and tongue-shape. The size of the gland changes is negatively correlated with size of the gonad, e. g. when the gonad is large, the albumen gland is small and vice versa (Wiktor, 1989). Albumen gland produces albumen or perivitelline substances, whereas secretory cells secrete galactogen which is a polymere of galactose (Duncan, 1975).

The vas deferens is narrow, partly folded duct whose main function is transport of autosperm whereas highly muscular epiphallus participates in spermatophore formation. Spermatophore is built of epiphallus and flagellum during copulation and has species-specific shape and taxonomic significance (Mann, 1984; Baur, 1998). It is composed of substances containing mucoproteins and glycosaminoglycans (Mann, 1984). Spermatophore is not present in all stylommatophorans, it is produced singly during mating and exchanged between partners inversely (Mann, 1984).

Penis is a copulatory organ with huge diversity within stylommatophorans, but at the same time, it is not present in all species (Reise, 2007). Its shape is typical for a particular species. Penis is used also for identifying a partner during mating and it affects success of copulation (Gómez, 2001). External sperm exchange occurs in some stylommatophoran species from Succineidae, Polygyridae, Helicodiscidae, Limacidae and Agriolimacidae families (Emberton, 1994; Reise, 2007).

Diverticulum is a bursa tract from which the spermatophore is taken during mating (Barker, 2001). The length of this structure may be variable, van Osselaer and Tursch (2000) studied a population of 79 individuals of *H*. *pomatia*. They discovered, that 34 % of them were deprived of diverticulum, whereas at the rest of them, its length varied from 1 mm to 9 mm (van Osselaer and Tursch, 2000). In these species, where diverticulum is absent, the spermatophore is deposited in bursa copulatrix (Barker, 2001), which is also called gametolytic gland (Tompa, 1984). The main function of this organ is extracellular digestion and further resorption of excess gametes, secretions and residues of the spermatophore (Beese *et al*., 2006).

Penial flagellum is responsible for production of spermatophore tail (Gómez, 2001). Genital atrium is the final section of the reproductive system, where male and female organs are reunited (Wiktor, 1989).

Mating and fertilization

It is estimated that the number of gastropod species inhabiting the Earth ranges from 60,000 to 105,000 (Bouchet *et al*., 2005), whereas there are about 35,000 species of terrestrial gastropods (van Bruggen, 1995). Terrestrial snails and slugs have worldwide distribution and can be found in diverse land environments, such as different types of forests, gardens, rock surfaces, steppes and dry habitats, desserts, humid biotopes, they are present in Hydrocenoidea, Helicinoidea, Cyclophoroidea, Rissoidea, Littorinoidea superfamilies, and in many families within Heterobranchia clade (Bouchet *et al*., 2005). Most terrestrial gastropods belong to Stylommatophora superorder in Heterobranchia, and the number of species is about 20,000 (Solem, 1978) grouped in 71 to 92 families (Emberton *et al*., 1990). Stylommatophorans are air-breathing terrestrial gastropods characterized by two pairs of invaginable head tentacles (Dayrat and Tillier, 2002), most of which are simultaneous hermaphrodites.

Within gastropods, one can distinguish internal or external fertilization, but the first type is more frequent among terrestrial gastropods (Nakadera and Koene, 2013). External fertilization occurs in some primitive species of archaeogastropods (Jarne and Auld, 2006). Fertilization is affected by many factors, such as the quality and size of sperm (Werner and Simmons, 2008; Birkhead *et al*., 2009; Pizzari and Parker, 2009), which is selected by sperm competition and fertilization success (Pitnick *et al*., 2009). Schmera *et al*. (2016) compared the data on sperm length in 57 stylommatophoran species from 23 families (Succineidae - 1 species, Chondrinidae - 3, Lauriidae - 1, Orculidae - 1, Pyramidulidae - 1, Vertiginidae - 2, Enidae - 1, Clausiliidae - 8, Bothriembryontidae - 2, Odontostomidae - 2, Strophocheilidae - 1, Discidae - 1, Oxychilidae - 3, Zonitidae - 1, Limacidae - 3, Agriolimacidae - 1, Vitrinidae - 2, Arionidae - 3, Helicidae - 10, Bradybaenidae - 1, Cochlicellidae - 1, Helicodontidae - 1, Hygromiidae - 7) from Europe and South America, taking into account the breeding systems in order to test the hypothesis that sperm competition can favor the evolution of longer sperm (Parker, 1993; Parker and Begon, 1993). Their results indicate that in stylommatophorans, simultaneous hermaphrodites' sperm length can be influenced by the breeding system, the age of sexual maturity, and shell size. Moreover, they showed that sperm length increases with shell size (Schmera *et al*., 2016).

Courtship and copulation can be done unilaterally, which means that one partner plays a specified role (male or female), while the other individual plays a reverse role during copulation, and usually, after one round of copulation the roles are changed, or reciprocally (both individuals play the male or female role at one time during copulation) (Tompa, 1984; Heller, 2001). Moreover, mating can be done in different positions, such as shell-mounting or face-to-face. In their review, Davison and Mordan (2007) pay attention to the fact that the mating position within terrestrial stylommatophorans is constant across the evolution of most lineages. They focused on the mating behavior within land stylommatophorans (snails and slugs) and classified the genera into four categories: 1) face-to-face, simultaneous reciprocal, 2) face-to-face, unilateral, 3) shell-mounting, simultaneous reciprocal and 4) shell-mounting, unilateral. They summed up the data on the mating behavior and presence of love darts in 93 genera from 35 families of terrestrial gastropods. The comparison of the data suggests that the face-to-face, simultaneous reciprocal behavior is the most common mating behavior within stylommatophorans (Davison and Mordan, 2007).

Terrestrial gastropods are able to reproduce by cross-fertilization, which means that gametes from different individuals are necessary for insemination, or by self-fertilization - insemination can be done by a fusion of gametes produced by one specimen, but the first type is more frequent among terrestrial snails and slugs, whereas self-fertilization is more widespread in freshwater species and bivalves (Duncan, 1975; Peake, 1978; Heller, 1993, 2001; Jarne *et al*., 1993). Usually, cross-fertilization is the preferred type of insemination, but self-fertilization gives them the opportunity to reproduce when mating is not possible, allowing them to occupy and colonize new areas due to the ability of reproduction even at low population density, and it also reduces the costs of male allocation (Heller, 2001). Self-fertilization has also some disadvantages, such as low genetic diversity caused by limited recombination and possible inbreeding depression (Chen, 1993, 1994; Heller, 2001).

Self-fertilization evolved several times in few independent phylogenetically lines, it occurs in different species of terrestrial gastropods. Heller (1993) summarized data about presence of this type of fertilization in 19 genera from 12 families, in Veronicellidae (*Filicaulis*, *Vaginulus*), Vertiginidae (*Vertigo*, *Truncatellina*), Vallonidae (*Vallonia*), Partulidae (*Partula*), Achatinidae (*Achatina*, *Archachatina*), Subulinidae (*Rumina*), Chondrinidae (*Chondrina*), Arionidae (*Arion*), Philomycidae (*Philomycus*), Succineidae (*Catinella*, *Omalonyx*, *Oxyloma*, *Succinea*), Limacidae (*Deroceras*, *Agriolimax*) and Polygyridae (*Triodopsis*) (Heller, 1993). In some cross-fertilizer species (e.g. *Arianta arbustorum*, *Bradybaena fruticum*) also self-fertilization is possible, but fitness reduction is observed as a consequence (Chen 1993, 1994; Kuźnik-Kowalska *et al*., 2013).

One of the most interesting families in the context of fertilization is Arionidae, belonging to Stylommatophora. A typical genus for this family is *Arion* which has the most species. In Europe, 35 *Arion* species (Welter-Schultes, 2012) occur and in these species both cross-fertilization and self-fertilization are present, depending on the species. *A*. *lusitanicus*; *A*. *hortensis*; *A*. *distinctus* and *A*. *owenii* reproduce by cross-fertilization, whereas *A*. *circumscriptus*; *A*. *silvaticus* and *A*. *intermedius* reproduce frequently by self-fertilization. *A*. *ater* and *A*. *subfuscus* are able to cross- and self-fertilize (Foltz *et al*., 1982).

Love darts

Some terrestrial gastropods are able to produce love darts called *gybsobelum* or shooting darts (Koene and Schulenburg, 2005), which are hard, pointed structures composed of calcium carbonate, chitin or cartilage (Hasse *et al*., 2002). The size of the darts varies from 1 to 30 mm, but usually is less than 5 mm and always correlated with the size of the animal. Apart from *radula* and jaws, love darts and their shape can be used for the identification and classification of gastropods (Chung, 1986). Some species have one or more love darts which is an effect of repeatable evolutionary events (Koene and Schulenburg, 2005). Presence of these structures is connected with face-to-face mating behavior and low-spired shape of the shell (Davison *et al*., 2005; Jordaens *et al*., 2009). Davison and Mordan (2007) summarize data about presence of love darts in particular families in Helicoidea and Limacoidea superfamilies, they occur in Bradybaenidae, Helicidae, Helminthoglyptidae, Hygromiidae, Ariophantidae, Urocyclidae, Vitrinidae, Zonitidae, Philomycidae and Dyakiidae families (Davison and Mordan, 2007; Koene *et al*., 2013). Among terrestrial slugs and snails can be observed diversity in dart structures. Some species produce single dart which stays in body of dart receiver, then dart is rebuilt by dart shooter, as in the case of *C*. *aspersum* or *H*. *pomatia* (Chung, 1987; Chase, 2007). In other species, *e.g.*, *Polymita muscarum*, *P. picta, Euhadra subnimbosa*, dart is retracted and reused, it does not remain in the partner's body (Koene and Chiba, 2006; Reyes-Tur and Koene, 2007; Koene *et al*., 2013). Love darts contain gland products which cause changes in female reproductive system after entering to the haemolymph (Kimura *et al*., 2014). Sticking darts into the body of the gastropod causes contraction, retraction of the shell, and inhibition of sexual behavior, or escape. It appears that the firing of darts stimulates the dart shooter and it is a discharge of aggressive behavior (Chung, 1987). Dart donor is disadvantaged because of exposed on possible infections resulting from skin damages and process of sperm storage is modified (Rogers and Chase, 2002).

According to the functions of love darts, there were many hypotheses which tried to explain their significance. Adamo and Chase (1988) postulated that the main function of love darts were encouragement the partner to mate, whereas Diver (1940) claimed that these structures were involved in recognizing of individuals which belong to the same species. Another explanation of their presence was the gift of calcium for the partner. All these hypotheses have been rejected. The function of love darts is not fully understood, but it is believed that they play a stimulating role during mating and they increase fertilization success of the dart receiver by enhancing the possibility of fertilizing eggs. Lodi and Koene (2016) in their review combined physiological, morphological and behavioural data about love darts in 23 species belonging to the Helicoidea superfamily (Helicidae, Bradybaenidae, Helminthoglyptidae). They reported that the common characteristic of dart shooting is increasing of male reproductive success by moving the mucus to dart receiver (Lodi and Koene, 2016).

Reproductive strategies in gastropods: semelparity and iteroparity

In the case of each reproductive strategy, the most important aspect is the trade-off between fecundity, growth, and survivorship of individuals (Perron, 1983). Among molluscs, not only in terrestrial gastropods, there are two different reproductive strategies, namely semelparity and iteroparity, which differ from each other, but these are not alternative strategies (Heller, 2001). An essential factor is the survival of adults in relation to the survival of juveniles (Heller, 2001). Semelparity means that an animal accedes to the reproduction only once during its life and after that it dies and the death is considered to be part of this strategy. An animal puts all its resources to maximize its reproductive success at the expense of its lifespan. In semelparous species, the cost of offspring production increases, while the cost of offspring decline decreases. In case of iteroparity, an animal reproduces many times during its life, which means in practice that it is able to reproduce every year (Rantes *et al*. 2002). In iteroparous species, the cost of offspring production decreases and each additional offspring is less expensive. An animal allocates some resources to reproduction and spends the rest of them on growth and survivorship, which allows it to reproduce many times during its lifetime (Roff, 1992). For molluscs iteroparous species are the most common; this strategy is identified with K-selection, while semelparity is linked to r-selection (MacArthur and Wilson, 1967). The r-selected species are characterized by production of numerous small offspring, high mortality among juveniles, and a short lifespan of an animal. Juveniles mature quickly and are able to reproduce, but only a small percentage of them survive. K-selection is based on a small number of offspring as well as the comprehensive care of them. Most juveniles survive until the reproductive age, and produce the next generation of animals (MacArthur and Wilson, 1967; Begon *et al*., 2006).

Semelparity is usually connected with the annual lifespan and occurs in many families within Heterobranchia clade, in Succineidae (*Succinea putris*; *Oxyloma retusum*), Euconulidae (*Habroconus semenlini*), Milacidae (*Milax gagates*), Agriolimacidae (*Deroceras reticulatum*), Vitrinidae (*Semilimax semilimax*, *S. kotulai*, *Vitrina pellucida*), Arionidae (*Arion ater*, *A. subfuscus*, *A. fuscus*, *A. lusitanicus*, *A. intermedius*), Limacidae (*Bielzia coerulans*), Helicidae (*Theba pisana*), Hygromiidae (*Xeropicta vestalis*, *Monacha cartusiana*, *M. haifaensis*, *Cernuella virgata*, *Helicella itala*, *Trochulus hispidus*), and many others (Runham and Laryea, 1968; Heller, 1982, 2001; Barker, 1988, 1991; South, 1989; Lazaridou-Dimitriadou and Sgardelis, 1995; Silva *et al*., 2009; Örstan, 2010; Welter-Schultes, 2012; Kuźnik-Kowalska *et al*., 2013; Proćków *et al*., 2013).

An example of semelparous terrestrial gastropods is *Arion vulgaris* accepted as one of the 100 most invasive species in Europe (Rabitsch, 2006). It is a serious threat to agricultural and horticultural crops, causing their damage (Gren *et al*., 2009). This species lives about one year, but some slugs can live longer, and most of them die after laying eggs (Davies, 1987; Kozłowski, 2008). Each individual in its lifetime lays between 240 and 540 eggs, from 12 to 124 white, round eggs per clutch (Kozłowski, 2000; Kozłowski and Kozłowski, 2000), and after a month juveniles hatch. Hatching can be spread over time and depends on the temperature; it takes place from September until the air temperature falls to 5 ºC (Kozłowski, 2000).

Many slug species are considered to be invasive species (Kozłowski *et al*., 2010). Among them, many have a life cycle and are semelparous (Heller, 2001). Kozłowski *et al*. (2010) showed the alien invasive slug species which are threat to crop plants. The biggest pests are *A. distinctus*, *A. vulgaris*, *A. rufus*, *Deroceras panormitanum*, *Limax maximus* and *Tandonia budapestensis* (Kozłowski *et al*., 2010). These species have economic importance causing crop damages, mainly fruits and vegetables. For example, *A. vulgaris* reduce strawberry yields in Sweden by half (Gren *et al*., 2009). These pest species lay a large number of eggs, for example *A. distinctus* lays 200 eggs, and *A. rufus* - 415 eggs, from 8 to 229 per clutch. *A. fasciatus* poses a relatively small threat to crops, perhaps because of its life expectancy (15 - 25 months) and the number of produced eggs (104 - 123 eggs, from 10 to 30 per clutch) (Welther-Schultes, 2012).

Reproductive modes in gastropods: oviparity, ovoviviparity and viviparity

Among terrestrial gastropods, three different reproductive modes occur, that is oviparity, ovoviviparity and viviparity. The first one is the most common mode, which means that an animal is capable of laying eggs (Heller, 2001). Lodé (2012) proposed to replace the term ‘oviparity’ with ‘ovuliparity’ in the case of molluscs and arachnids

(Lodé, 2012). The term 'ovoviviparity' can be defined as a special case or modification of viviparity. This way of reproduction is based on laying eggs by the mother, but the embryonic development proceeds inside the mother's body in the egg shell at the expense of egg yolks. Juvenile offspring destroys egg shells before hatching or just after egg laying (Meier *et al*., 1999; Markow *et al*., 2009). Within this concept, one can distinguish ovoviviparity *sensu lato,* which means that incubation of eggs takes place in the reproductive tract at any time of the embryonic development of an animal. Moreover, a part of the embryonic development takes place after laying eggs in the environment. Ovoviviparity *sensu lato* is identified with egg retention. Ovoviviparity *sensu stricto* lies in the fact that the embryonic development takes place in the parent's body and juveniles are born or hatch immediately after laying eggs. This mode of reproduction has many advantages, and the main ones are: 1) decrease in the offspring mortality due to drought or predation, 2) increase in the offspring chances in food competition with juveniles hatched from eggs, 3) this mode of reproduction gives a chance to reproduce in unstable conditions, where it is difficult to predict the beginning of a rainy season during the year (Tompa, 1979a; Sulikowska-Drozd, 2009). In some papers one can find the term 'brooding', which means that the embryonic development occurs wholly or partially inside the parent's body, not necessary inside the genital tract (Heller, 1993). Among ovoviparous terrestrial gastropods, one can mention *Ferussacia folliculum* (Ferussaciidae), *Pupilla muscorum*, *P*. *sterrii* (Pupillidae), *Leptinaria unilamellata* (Subulinidae), *Pyramidula pusilla*, *P*. *umbilicata* (Pyramidulidae), *Balea biplicata*, *B*. *perversa* (Clausiilidae) and all species of *Lauria* (Lauriidae) (Pokryszko, 2001; Carvalho *et al*., 2009; Welter-Schultes, 2012), and many others.

Sulikowska-Drozd and Maltz (2012) studied the reproduction of ovoviviparous clausiliid *Balea fallax* under laboratory conditions. Layed eggs of this clausiliid hatch earlier than in other clausiliid species, and adult specimens preserve eggs for short periods. The size of the eggs of this species suggests that parents invest more in offspring, and some part of parental care is used to increase offspring fitness (Sulikowska-Drozd and Maltz, 2012). Sulikowska-Drozd *et al.* (2012) showed that *B*. *fallax* is capable of egg-retention and there is no correlation between the body size of individuals and the number of preserved eggs (Sulikowska-Drozd *et al*., 2012). Other ovoviviparous clausiliids are: *Vestia gulo*, *V*. *elata*, *V*. *turgida* (Sulikowska-Drozd, 2009) and *Ruthenica filograna* (Szybiak, 2010; Szybiak *et al*., 2015).

Sulikowska-Drozd (2009) studied egg retention and ovoviviparity in three clausiliids, *Vestia gulo*, *V*. *turgida* and *V*. *elata*. Differences in number of retained eggs in *V*. *gulo* and *V*. *turgida* were observed. Sulikowska-Drozd (2009) claimed, that the number of produced eggs depends on the season of the year, whereas number of juveniles is probably connected with the habitat preferences. Cannibalism has been observed in *V*. *gulo* and *V*. *elata*, but not in *V*. *turgida* (Sulikowska-Drozd, 2009). Detailed knowledge about ovoviviparous gastropods is crucial in the understanding of the reproductive success of each species, especially in the context of endangered species.

An example of ovoviviparity among terrestrial gastropods is the study carried out by Heller *et al*. (1997), in which scientists worked on the reproductive biology and population dynamics of a minute snail *Lauria cylindracea*. This species is characterized by low fecundity, but this type of reproduction is advantageous because of offspring survival. After hatching, juveniles are able to feed, grow and cope with flooding, drowning and drought. Ovoviviparous gastropods can survive more easily in unfavorable environmental conditions, such as excess of water in some habitats (Heller *et al*., 1997).

Viviparity is a mode of reproduction which consists in producing living offspring. In other words, viviparity means that ova are fertilized in the reproductive tract and stored inside the reproductive system of an animal, and juveniles are born fully formed. Tompa (1979b) suggested that viviparity occurs very rarely among terrestrial gastropods, but it is possible in some cases. There is evidence that viviparity may be present in vaginulid *Pseudoveronicella zootoca*, achatinellid *Tekoulina pricei* and in acavid *Stylodon studeriana* (Solem, 1972; Tompa, 1979a, b, 1984; Heller, 2001).

Eggs and egg cannibalism

Among terrestrial gastropods, a common reproductive mode is oviparity, as mentioned in the previous chapter. Gastropods can lay eggs in different places, such as in the forest litter, inside excavated holes or in arboreal places, and their size varies depending on the species (Heller, 2001). The smallest eggs are laid by *Opisthostoma retrovertens*, *Carychium tridentatum*, *Vertigo pusilla*, *Vallonia costata*, *V*. *pulchella*, *Cecilioides acicula*, *C*. *genezarethensis*, *Punctum pygmaeum*, *Succinea oblonga*, whereas the largest ones are produced by *Acavus haemastoma*, *A*. *waltoni*, *Megalobulimus bronni*, *M*. *capillaceus*, *M*. *oblongus*, *M*. *popelairianus*, *M*. *rosaceus*, *M*. *terrestris*, *Stylodon studeriana*, *Powelliphanta superba*, *Limax flavus* (Frömming, 1954; Berry, 1964; Baur, 1989; Pokryszko, 1990; Heller *et al*., 1991; Heller, 2001). There is a correlation between the body size expressed as shell height and the size of the egg produced by an animal. For example, a small gastropod *C*. *tridentatum* (2 mm) produces small eggs of 0.4x0.3 mm, and similarly *V*. *pusilla* (2 mm) produces eggs of 0.6x0.3 mm (Baur, 1989; Pokryszko, 1990), whereas large *M*. *popelairianus* (230 mm) produces eggs of 51x28 mm (Heller, 2001). Bigger juveniles hatch from larger eggs, which means that egg size determines the size of juveniles and also their growth, survivorship and possible future reproductive success. Bigger juveniles, which come from bigger eggs, are more resistant to starvation (Tompa, 1984) and have longer development (Baur, 1994a). Gastropods with larger sizes can lay more eggs, *A*. *circumscriptus* (25 - 32 mm long) deposits 104 - 123 eggs, *A*. *hortensis* (30 - 40 mm long) - up to 200 eggs, whereas *A*. *vulgaris* (70 - 140 mm long) lays up to

400 eggs and *A. rufus* (150 mm long) - up to 500 eggs (Welter-Schultes, 2012). Production of larger eggs has many advantages: hatched juveniles are bigger and have a higher growth rate and survivorship, acquiring food is easier, and bigger juveniles have higher chances of successful reproduction. On the other hand, bigger eggs require longer incubation and the risk of mortality before hatching increases (Clutton-Brock, 1991). Heller (2001) presented a summary on animal and egg size on the basis of literature data, which shows that there is a correlation between these two properties (Heller, 2001). Laying eggs is part of life reproductive strategy, and interest in this subject has increased recently, especially in relation to life cycles.

In the case of terrestrial gastropods, egg cannibalism can sometimes be observed, especially in the case of many stylommatophonan species. Egg cannibalism delivers calcium to juveniles, and this component has great importance for snails during all their life, especially affecting their growth during the early stages of development (Oosterhoff, 1976). Baur (1994a) discovered that this phenomenon occurs in helicid *A. arbustorum*. Newly hatched juveniles cannibalize deposited eggs, which are derived from the same parent. Cannibalistic behavior occurred with varying frequency depending on the type of population. Baur (1994a) showed that cannibalistic behavior was observed in 50 % of hatched offspring in subalpine forest, and in 87.8 % in lowland forest. Moreover, it has been shown that the occurrence of cannibalism among juveniles is not connected with the egg size. The amount of energy and nutrients obtained by a snail during embryonic development does not cause cannibalistic behavior in juveniles of *A. arbustorum* (Baur, 1994a).

Ożgo and Bogucki (2006) showed that juvenile specimens of *Cepaea nemoralis* in natural habitats radulated shells of live snails. The authors linked this behavior with pH and calcium content in the soil. In *C. nemoralis* cannibalism has also been observed. Shell predation and cannibalism were present on acid soils or with low content of calcium. The occurrence of these effects can be explained as an adaptation to life in adverse conditions of the environment (Ożgo and Bogucki, 2006).

Conclusions

Studies on reproduction systems of terrestrial gastropods provide new, original data, which fill the gap in the current state of the knowledge. The main significance of this type of research is possibility of population management, what is very important in the context of the control of pests which can cause serious damages in agriculture, conservation of endangered and rare species or in the case of gastropods farming for culinary and other purposes. Many papers concern about morphology of reproductive systems of species belonging to Arionidae, Agriolimacidae, Limacidae, Helicidae families, but other species should be explored additionally. Studying reproductive systems with combination of phylogenetic data among many species will allow to obtain new information about reproductive strategies in terrestrial gastropods.

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