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Reviews

Parental care in terrestrial gastropods

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Abstract. Parental care in terrestrial gastropods includes the preparation of oviposition sites, production of large, heavily-yolked eggs supplied with calcium carbonate, provisioning of hatchlings with eggs in species with facultative sibling cannibalism, egg retention, and ovoviviparity. Evidence for true viviparity is scarce in terrestrial gastropods, as it is for postlaying care of eggs, though external egg carrying on the shell occurs in a few species. Care of young has not been observed in any terrestrial gastropod species. Provisioning of eggs with nutrients and calcium carbonate might be the most common form of parental investment. Ovoviviparity allows terrestrial gastropods to persist in habitats otherwise unsuitable for oviparous species (e.g. exposed rock walls). An interspecific comparison demonstrates that egg-retaining and ovoviviparous species produce smaller clutches than oviparous species and suggests a cost of parental care.
Key words. Parental investment; juvenile survival; evolution; gastropods; molluscs; ovoviviparity; viviparity.

Introduction

Parental care has been defined as 'any form of parental behaviour that appears likely to increase the fitness of a parent's offspring'[34]. This descriptive term carries no implications about costs in terms of energy or fitness. In its broadest sense, parental care includes the preparation of oviposition sites, the production of large, heavily-yolked eggs and unfertilized nurse eggs, the care of eggs or young inside or outside the parent's body, and the provisioning of young before and after birth. In its narrowest sense, it refers only to the care of eggs or young when they are detached from the parent's body[34]. Parental investment measures the costs of parental behaviour to any component of the parent's fitness.

Parental care has evolved numerous times in animals. Clutton-Brock[34] has compiled an extensive review and critique on the origin and evolution of parental care. He applied evidence to current theory, and in doing so he uncovered huge gaps both in theory and empirical studies. Empirical studies on parental care have dealt mostly with vertebrates; in many other taxonomical groups not even the basic features of parental care are known.

Gastropods (snails and slugs) constitute by far the largest and most diverse class of Mollusca, with an estimated 40,000 marine, 3,000 freshwater and 24,000 terrestrial species[96]. Different forms of parental care in marine gastropods have been described by Fretter and Graham[51], Purchon[86] and Fretter[50]. This review examines parental care in terrestrial gastropods, a group of invertebrates whose behavioural ecology is not well known. The purposes of this review are 1) to describe different forms of parental care that occur in terrestrial gastropods, 2) to compare terrestrial and marine gastropods in their forms and frequencies of parental care, and 3) to evaluate the principle costs and benefits of parental care in terrestrial gastropods. Detailed information on parental care in terrestrial gastropods is sparse and often a by-product of studies with other aims. By compiling the existing information, this review should stimulate future studies on parental care in terrestrial gastropods.

Adaptation to terrestrial life

The pulmonates and prosobranchs are the two groups of gastropods that migrated onto land. Little[63,64] reviewed potential evolutionary routes from water to land. The changes in physical and chemical characters of the environment are immense for animal lines moving from aquatic to terrestrial environments. These changes affect all possible life processes, from respiration and excretion to methods of movement, the functioning of sense organs, and reproduction. Because gametes rapidly desiccate in air, internal fertilization is a prerequisite for a truly terrestrial existence. Gastropod eggs that are laid in an aquatic environment have direct access to water, calcium and trace elements. The majority of the land snail eggs are cleidoic; they contain all the nutrients and trace elements needed for a successful embryonic life[110]. Thus, in comparison to eggs of aquatic gastropod species, eggs of terrestrial species are in general supplied with all nutrients and trace elements required for a successful embryonic development. While indirect development with veliger larvae occurs in many marine gastropod species, with few exceptions all eggs of terrestrial gastropods have direct embryonic development[50, 51, 111].

Reproductive strategies in terrestrial gastropods

Among terrestrial gastropods, all pulmonates are hermaphroditic, whereas the majority of prosobranchs are gonochoristic[58]. Hence, no sex-specific pattern of reproductive behaviour and parental care can be expected in pulmonates (most of the terrestrial gastropods belong to this subclass).

The majority of land snails are oviparous with eggs laid singly or in batches; embryogenesis occurs after oviposition. All oviparous land snails thus far examined deposit individual eggs (i.e. each ovum is surrounded by its own egg shell or distinct jelly layer) and not egg masses or capsules, such as occur in the freshwater pulmonates and in most marine prosobranchs[107].

As a modification of simple oviparity, the eggs may be retained for periods of different length within the female reproductive tract, resulting in a shorter time from laying to hatching (hereafter called egg retention). In ovoviviparous species, eggs are retained within the female reproductive tract for the entire embryonic period. Hatching may occur just after oviposition, or young may hatch from the egg inside the female reproductive tract followed by birth. In viviparous species there is a transfer of nutritional material from the parent to the developing embryo, which is retained in the female reproductive tract until extrusion as free living young. Variations in pattern of egg retention and development are virtually continuous, but a division into oviparous species, species with egg retention, ovoviviparous and viviparous species is generally accepted[95].

Forms of parental care in terrestrial gastropods

Egg protection in oviparous snails

Numerous oviparous snail species deposit their eggs in excavations which they dig in moist soil[111]. In *Helix pomatia*, nest digging takes about 1 h at a site suitable for egg laying[81]. The cavity is lined with mucus (most probably to protect the eggs against bacteria and fungi). Egg laying lasts 35 h for a 70-egg clutch. After oviposition the nest is covered by soil and abandoned. Snails search actively for suitable oviposition sites. Not all nesting excavations that are initiated will be successfully filled with eggs; many holes are abandoned before one is finally considered suitable. In several populations *H. pomatia* makes seasonal migrations of up to 50 m from hibernating locations to sites that have soft soil and thus are suitable for egg laying[39, 62, 84]. Apart from suitable soil structure, soil moisture content is important for the choice of the oviposition site as indicated by choice experiments with *Arianta arbustorum*[9]. The desert snail *Sphincterochila boissieri* digs a 3-4 cm deep hole and lays its eggs in a mucid saccule which hangs in the cavity without touching the wall[115]. Most probably the mucid saccule decreases the risk of egg desiccation. The tropical snail *Archachatina* (*Calachatina*) *marginata* digs the 10–15 cm deep cavity for oviposition in the course of one night[82]. Sometimes it takes two nights to complete the preparation of the oviposition site and egg laying, most probably due to the hardness of the soil or to disturbance by other snails.

Individuals of the West African tree snail *Pseudachatina downesii* and those of other arboreal species lay their eggs in the axils of branches of the tree upon which they live[102]. Several species of tree-living snails lay their eggs in brood chambers made by leaves. In Celebes, snails of the genus *Cochlostyla* deposit their eggs in leaves rolled up into a cornucopia, stuck together with mucus and lined with mucus[89]. The Javan tree snail *Amphidromus purus* also forms nests for their eggs by plastering leaves together[75]. Nest preparation and oviposition lasts 4–8 days in this species. Having finished egg-laying (up to 234 eggs of 3 mm diameter are put in one nest), the envelope is sealed with mucus and the snail drops from the tree.

The survival prospects of eggs may depend not only on the suitability of the oviposition site chosen and on protective cover, but also on the spatial pattern in which the eggs were deposited. For example, the predatory snail *Zonitoides arboreus* typically lays single eggs scattered in maple and beech leaf litter[59]. This egg-laying strategy might have evolved to minimize cannibalism among offspring in this predatory species.

Egg provisioning

The majority of land snails produce eggs that vary little in size within species. The species vary mostly in clutch size and in the number of clutches[23, 30, 52, 72, 77, 113, 114]. The among-species variation in egg size ranges from 0.5 mm to 50 mm in maximum diameter. The largest eggs belong to *Strophocheilus* (*Borus*) *popelairianus*, a snail with a shell length of 15–23 cm that occurs in Colombia and Ecuador; their oval, hard-shelled eggs are up to 51 mm long and 28–35 mm wide[27]. The litter-dwelling *Punctum pygmaeum* with a shell diameter of 1.5 mm produces the smallest eggs with an average size of 0.41×0.50 mm[6, 13]. In *Arianta arbustorum*, hatchling size is positively correlated with egg size[29]. Thus, a larger investment of a parent snail in single eggs results in larger hatchlings. Large hatchlings, in turn, may enjoy an enhanced survival compared to small hatchlings. For example, large hatchlings of *Strophocheilus oblongus* more frequently survived immediate posthatching starvation than small ones kept under identical conditions[111]. However, hatchlings of *A. arbustorum* emerging from larger eggs have also a longer developmental period than those from smaller eggs[29].

Snail eggs are rich in energy and nutrients (proteins, mucopolysaccharides, calcium)[38,111]. For example, the protein concentration in freshly-laid eggs of *Helix pomatia* averages 14.2% of their dry weight[2], 26.7% in *Trochoidea* (*Xerocrassa*) *seetzeni*[115], 38.8% in *Sphincterochila boissieri*[115], and 25.6% in *Arianta arbustorum* (A. Baur, unpublished data). In *A. arbustorum*, the concentrations of energy and nutrients vary little among eggs of single batches (A. Baur, unpublished data). In addition to the provisioning of energy and nutrients to the embryo, terrestrial gastropods deposit calcium carbonate in the eggs. This calcium is used for the calcification of the embryonic shell (hatchlings have a well calcified shell) and for the deposition of calcium reserves in the first calcium cells which differentiate during the embryonic life[48,110]. The calcium requirements for embryonic life explain the considerable amount of calcium that the adult gastropod loses during the oviposition period[48]. For example, *Anguispira alternata* mobilizes 10–25 mg of calcium for one egg batch in less than a day[106], and the slug *Deroceras reticulatum* looses 65% of the total calcium measured in the whole animal just before the egg-laying period to produce a batch of 100 eggs[48]. In several species of terrestrial gastropods, a significant amount of calcium carbonate in embedded in the egg shell. Some species have partly calcified eggs, with discrete crystals of calcium carbonate in a jelly matrix (e.g. *H. pomatia*, *A. arbustorum*). Other species produce heavily calcified eggs, with an outer shell consisting of a layer of fused calcium carbonate crystals, making the egg shell hard and brittle like a bird's egg (e.g. *Cepaea nemoralis*)[24,107]. The developing embryos resorb calcium from their egg shells[107], and in some species the hatching young eat their own egg shell[17]. Egg shells containing calcium carbonate occur in at least 36 of the approximately 80 families[28,42] of stylommatophoran land snails[107].

The snails' shell growth and reproductive output are affected by the availability of calcium. For example, egg production of *Helix aspersa* exposed to acid soils was doubled when calcium carbonate was supplied during the experiment[37].

Many terrestrial and amphibious prosobranchs, such as *Cochlostoma septemspirale* and *Pomatia elegans*, cover their eggs with soil particles[36,60,85]. Attaching soil to the egg surface protects the egg against predators and desiccation and, most important, allows the uptake of calcium carbonate from the soil, which is crucial for the development of the embryo (compared with eggs of terrestrial pulmonates those of prosobranchs do not contain calcium carbonate[110]). Indeed, embryos of *P. elegans* develop when the eggs are kept in water with a high concentration of calcium carbonate, but not in distilled or tap water[36]. Species such as *P. elegans* lay their eggs singly in order to coat each one with soil (calcium). If the animals deposited their eggs in batches, most of the eggs would not be in direct contact with the soil calcium, especially in large batches. In *C. septemspirale*, a snail of 7 mm shell height living on soil with a high calcium carbonate content, a special method of egg calcification has evolved. This snail ingests large amounts of soil and forms chalky faecal pellets. At egg laying, the mother holds each egg by the foot while using her mouth to transfer and fix the calcium rich faecal pellets to the surface of each egg[85].

Trophic eggs and egg cannibalism

Apart from increasing egg size, maternal nutrition can be enhanced by providing hatchlings with food. Alexander[1] suggested that if parents are unable to increase their investment in young through increasing egg size, an alternative strategy is to increase clutch size and allow some siblings to consume others (the icebox effect). The optimum clutch size can be found by calculating the clutch size leading to maximum brood productivity, taking into account the effects of sibling cannibalism and possible trade-offs.

Maternal provision of trophic eggs of different types to hatchlings is widespread among marine gastropods. Numerous species of prosobranch snails normally produce trophic eggs, which serve as the first food for their progeny[44–46,92]. The consumption of trophic eggs can be facultative (may not occur in all egg capsules of a species) or obligate. In several species the larvae consume still unhatched embryos as well as 'abnormally' developing embryos. Furthermore, cannibalism among embryos (siblings) within an egg capsule occurs both in species with trophic eggs and in species without.

Embryos only have access to nurse eggs that occur in the same egg capsule. Nurse eggs, initially indistinguishable in size from normally-developing eggs, can occur in large numbers. For example, the eggs of the marine prosobranch *Colus islandicus* are 200–210 μm in diameter, but of 7,350 in a capsule only 1–5 hatch[104]. When a species provides trophic eggs to its offspring, some embryos typically reach much larger sizes than others. For example, hatchling size ranges from 0.54 to 1.83 mm in *Murex virgineus*[69] and from 0.66 to 1.84 mm in *Murex brandaris*[44]. An interspecific comparison indicates that hatchling size in prosobranch species with trophic eggs is more variable than in species without trophic eggs, and that shell length of hatching snails is positively correlated with the average trophic-egg supply for each embryo[44,45].

A similar form of food provision has evolved in terrestrial gastropods. Hatchlings of various species of herbivorous land snails cannibalize sibling eggs[10,14,17,41]. Emerging *Arianta arbustorum* first eat their own egg shells and then the eggs of unhatched siblings, including those with fully developed embryos[21]. Under natural conditions hatchlings were also observed to cannibalize eggs from neighbouring batches[7]. Thus, in stylommatophoran land snails, egg cannibalism occurs within and between clutches, in contrast to marine prosobranch gastropods, in which the consumption of trophic eggs and cannibalism are restricted to embryos within a capsule.

In *A. arbustorum*, egg cannibalism occurs exclusively during the hatchling stage (due to an age-specific occurrence of digestive enzymes), juvenile and adult snails being herbivorous[8]. Cannibalistic hatchlings eat only conspecific eggs[11] and do not discriminate between sib and non-sib eggs (i.e. eggs from neighbouring batches[7]). Furthermore, newly-hatched snails discriminate neither between fertilized and unfertilized conspecific eggs nor between eggs with well-developed embryos and eggs with less advanced embryos[19]. However, cannibalistic hatchlings preferentially eat large conspecific eggs[19].

Significant benefits accrue to cannibalistic hatchlings of *A. arbustorum*. Laboratory experiments demonstrated that newly-hatched snails fed a cannibalistic diet during their first 10 days of life increased in wet weight 2.6 times as much as siblings fed on lettuce[15]. In this experiment, egg consumption within 10 days ranged from 0.7 to 4.0 eggs per individual and weight increase of cannibalistic hatchlings was positively correlated with the number of eggs consumed. Diet did not affect hatchling survival during the first 10 days, but it did influence future survival: 66.6% of the individuals initially fed on eggs attained adulthood compared to 38.0% of those fed on lettuce. Cannibalistic hatchlings tended to complete shell growth more rapidly and thus became sexually mature earlier than non-cannibalistic ones, but the two groups did not differ in adult shell size. Thus, a cannibalistic diet during the hatchling stage will give accelerated growth and higher survival.

The extent of within-batch egg cannibalism depends primarily on the hatching asynchrony of the eggs and on the hatchlings' propensity for cannibalism[20,21]. Within populations, the extent of cannibalism is not influenced by clutch size[21]. Snails that emerged from relatively small eggs of a lowland population exhibited a higher propensity for cannibalism than hatchlings from relatively large eggs of mountain populations[20]. The great variation between populations in propensity for cannibalism suggest different costs and benefits of egg cannibalism in different situations. Under natural conditions, the hatching asynchrony and, as a result, the extent of egg cannibalism will depend also upon the type of oviposition (batches or scattered eggs), on the spatial heterogeneity of egg-laying sites and on climatic conditions. For example, in egg batches of the terrestrial slug *Deroceras agreste* the hatching asynchrony increases as the temperature decreases[31,32].

Selection may favour egg cannibalism if the potential reduction of the mother snail's total fecundity due to sibling cannibalism is compensated for by the increased survival of her cannibalistic progeny. In *A. arbustorum*, not all eggs within a batch hatch; indeed, some eggs are not fertilized and in others the embryos die during development. Under natural conditions, eggs that fail to hatch can serve as trophic eggs. The proportion of fertilized eggs within batches in *A. arbustorum* decreases towards the end of the reproductive season[16], which means enhanced opportunities of egg cannibalism for newly hatched snails. Due to the short time until first hibernation, snails hatching late in autumn have the lowest propects of survival and, consequently, cannibalism may be most profitable for these hatchlings. It is not known, however, whether an ovipositing snail is indeed able to manipulate the proportion of fertilized eggs within a batch or whether the lower hatching success observed at the end of the breeding season is simply a result of various environmental factors.

Cannibalism among offspring can also be influenced by parental manipulation[1,40,49,83]. A mother snail could manipulate the extent of within-batch cannibalism by altering the degree of hatching asynchrony in the batch, for example, by her choice of the oviposition site. An oviposition site that provides equal humidity and temperature conditions for all eggs in the batch synchronizes hatching[25]. In choice experiments, *A. arbustorum* prefers to oviposit in soil of higher moisture content and thus reduces the risk of later egg desiccation[9]. Both the type and spatial distribution of oviposition sites in natural populations suggest that abiotic factors, such as permanent moisture, exert a strong influence on the choice of the oviposition site.

Sibling cannibalism directly affects the fitness of both the cannibal and the victim[40,83]. Natural selection will favour cannibalistic behaviour if (cost to victim) $\times\, r/$(benefit to cannibal) < 1, where r is the degree of relatedness[57]. The selective advantage to cannibalism will increase either as the benefit of the cannibal increases or the cost to the victim and/or relatedness decreases. Thus, cannibalism will be favoured by natural selection when it increases an individual's fitness through direct, immediate gains. Due to multiple mating and sperm storage, batches of *A. arbustorum* mainly consist of half-siblings (B. Baur, unpublished data). Calculations based on survival from egg to maturity recorded in natural populations[3] and potential benefits to the cannibals (see above) indicate that egg cannibalism in *A. arbustorum* is adaptive among half-sibs and under harsh environmental conditions even among full-sibs[7].

Multiple mating has been observed in several species of land snails including *Theba pisana*, *Helix aperta*, *Helix pomatia*, *Cepaea nemoralis* and *Arianta arbustorum*[18,55,61,67]. Repeated mating in simultaneously hermaphroditic gastropods is adaptive both for male function to inseminate several 'females' and for female function to increase fertility and fecundity (the latter by stimulating egg production via hormones) and serving as a hedge against sterile mates[12,22,33]. Multiple mating with different partners might also provide genetic benefits for the female function of a hermaphrodite. Using sperm from more than one mate will result in genetically more diverse offspring. Moreover, multiple mating by females may promote sperm competition in certain situations[76]. Multiple paternity has been demonstrated in clutches of multiply mated *C. nemoralis*[67] and *A. arbustorum* (B. Baur, unpublished data).

Egg retention and ovoviviparity

Egg-retaining snails can keep their eggs for any (longer) period of time in the female reproductive tract after they are formed. If the conditions for oviposition become favourable (e.g. the soil is moist or soft enough to allow a hole to be excavated for a nest), then the snails release their eggs immediately, as any oviparous snails would do. For example, *Limicolaria martensiana* retains its eggs when it aestivates during the dry season in central Africa[74]. At the beginning of the rainy season, eggs and young are immediately deposited, ensuring them the best prospects of survival. Thus, parental care of young by retaining them in the reproductive tract occurs when the environmental conditions are unfavourable for eggs and juveniles[74].

Egg-retaining snails can also hibernate while gravid (e.g. *Pupa muscorum*[111]). They can deposit their eggs with partly-developed embryos early in the reproductive season, providing the emerging young with a prolonged period of growth compared to those of oviparous species living in the same habitat. Thus, egg retention allows a successful reproduction in harsh environments such as alpine and subarctic regions, where the reproductive season is short and often interrupted by unfavourable weather. In temperate regions, egg-retaining snails may be able to produce an additional brood each year[111]. However, besides these advantages, egg retention might bear significant costs to the parent snail (see below).

In ovoviviparous species the eggs are arranged in succession in the reproductive tract. The egg shell becomes resorbed by the parent or is consumed by the embryo, which uses the calcium carbonate to build up its own shell. Thus, ovoviviparity is an extreme form of egg retention (the young hatch in the reproductive tract). In some species, reproduction can be oviparous, egg-retaining or ovoviviparous[73,74,77]. For example, individuals of *Lacinaria biplicata* are usually ovoviviparous, but under favourable environmental conditions they lay eggs with well-developed embryos[43]. Similarly, the South African snail *Achatina* (*Cochlitoma*) *zebra* can be oviparous or ovoviviparous[65]. Partulidae are ovoviviparous snails that occur on the Society Islands. In these snails the egg shell is resorbed by the parent before birth[68]. Gravid animals contain anything from 1 to 10 (usually 2–3) eggs or juveniles in the brood pouch[35].

In general, the number of eggs held by egg-retaining and ovoviviparous snails is variable. The most common cases involve the retention of 2–6 eggs in the reproductive tract[109]. However, several species produce a single egg at a time (e.g. *Punctum pygmaeum*[13]).

Viviparity

One of the most sophisticated forms of parental care in gastropods is viviparity. In viviparous species nutrients are passed from the mother to the developing embryo. This reproductive strategy can be found in various families of marine and freshwater gastropods[50,51,86], but there are relatively few reports on viviparity in terrestrial gastropods. In the pulmonate land snail *Tekoulina pricei*, that occurs in the Cook Islands, 5–7 embryos of increasing size were found in the uterine oviduct[95]. The size increment from the smallest to the largest embryo was 55–70 times. Similarly, based on size differences of embryos in the female reproductive tract, the two African snails *Pseudoveronicella zootoca* and *P. pauliani* are considered as viviparous[47], but details on the mechanism of nutrition are unknown. In *Achatinella*, the largest embryo found in the female reproductive tract was 92 times the size of a fertilized egg and 11 times that of the smallest embryo, suggesting a form of supplement nutritive transfer[95].

Postlaying care of eggs

In contrast to marine prosobranchs (see below 'Distribution of parental care'), postlaying care of eggs might not be highly developed in terrestrial gastropods. Exceptions are several Endodontid species, which exhibit a most-sophisticated form of parental care. On Polynesian islands, *Libera fratercula* and its congeners brood 4–6 eggs in the umbilicus of the shell, which forms a pouch-like cavity[97,102]. In some species of this genus eggs and newly-hatched snails are retained by a temporary shell plate, which partly covers the umbilicus. This plate is broken away or absorbed by the mother to release the young under favourable environmental conditions.

A kind of egg grooming was described in *Vallonia pulchella*, a small snail with an adult shell diameter of 2–2.5 mm living in grasslands[56]. Adult snails moved with their head and radula over the surface of an egg as they were feeding. Gugler assumed that the snails removed fungi from the surface of the egg shells. However, such a grooming behaviour could only evolve if the snails are able to recognize their own eggs. So far, no evidence for an ability to recognize own eggs is available in terrestrial gastropods[9]. The observed behaviour could be a result of overcrowding in the breeding container and thus needs experimental evaluation.

Distribution and frequency of parental care

The existing information suggests that sophisticated forms of preparation of egg-laying sites in terrestrial gastropods are restricted to arboreal species and to a few families of ground-dwelling species. The majority of terrestrial gastropods lay their eggs at presumably suitable sites and abandon them without providing any further care.

Egg provisioning could be considered as the most common form of parental care in terrestrial gastropods. In comparison to aquatic species, terrestrial gastropods produce in general larger but fewer eggs. However, the provisioning of nutrients and calcium carbonate to the eggs is a prerequisite for terrestrial life (see above 'Adaptation to terrestrial life'), and therefore may have evolved independently of selection for enhanced juvenile survival through parental care. However, this does not explain the enormous interspecific variation in egg size observed in terrestrial gastropods, which may be related to different levels of parental investment (see 'Discussion').

Food provisioning in the form of nurse eggs and egg cannibalism is widespread among prosobranch marine snails[44–46,92]. In terrestrial gastropods, facultative egg cannibalism has so far been recorded in 15 species belonging to 6 families[17]. Present evidence suggests that egg cannibalism tends to occur in terrestrial gastropod species that have multiple paternity in their broods, produce small eggs in relation to their shell size, and have hatchlings that eat their own calcified eggshells[17]. Available information on parental care in marine gastropods suggests that food provisioning in form of nurse eggs (see above 'Trophic eggs') and postlaying care in form of external egg carrying are more common in marine[50,51 86] than in terrestrial gastropods. For example, the marine prosobranch *Clanculus bertheloti* has a shell which is ornamented with spiral grooves within which the eggs are deposited and covered with a thin layer of mucus[86]. Eggs are deposited on the shells of both females and males. The young snails develop in the grooves of the parental shell and with the protective veil of mucus which covers most of the shell. The whelk *Neptunea despecta* often attaches clusters of egg capsules to its own shell, and carries them about, although it may alternatively deposit them on the substratum[86]. The proximate reason for the switching between these two reproductive strategies is unknown. Terrestrial gastropods aestivate during periods of drought, often exposed to wind and insolation. In these species eggs carried on the shell would desiccate[88]. In terrestrial habitats, the low moisture content of the air may select against egg carrying behaviour. Instead it may select for strategies protecting eggs such as egg retention and ovoviviparity. Although most pulmonate land snails are oviparous, in 30 of the approximately 80 families[28,42] there is at least one species with egg retention or ovoviviparity[109]. Tompa[108,109] suggested that egg retention and ovoviviparity have evolved independently several times in terrestrial gastropods. In the basommatophoran pulmonates (mainly freshwater snails) and in terrestrial slugs egg retention and ovoviviparity are absent[54,109].

Brooding of eggs is also common in marine habitats[50,51,86]. Many marine gastropods protect the egg capsules by retaining them within the mantle cavity or in the pallial oviduct until they hatch. Some sedentary marine prosobranch (Mesogastropoda) attach their eggs to the inner side of the shell, as in the Vermetidae, and the young emerge at the crawling stage. In *Pyxipoma*, there is a special brood chamber which opens to the exterior just below the right margin of the foot and this may contain 100 to 150 small embryos[66]. In the Iranian Gulf, the embryos of *Planaxis sulcatus* break out of the egg membrane, but remain in the pallial oviduct where they feed on other developing eggs and finally emerge as young crawling snails at a much greater size than from the egg[105]. In New Caledonia, the same species was observed to produce free swimming veliger larvae, which is probably the original condition.

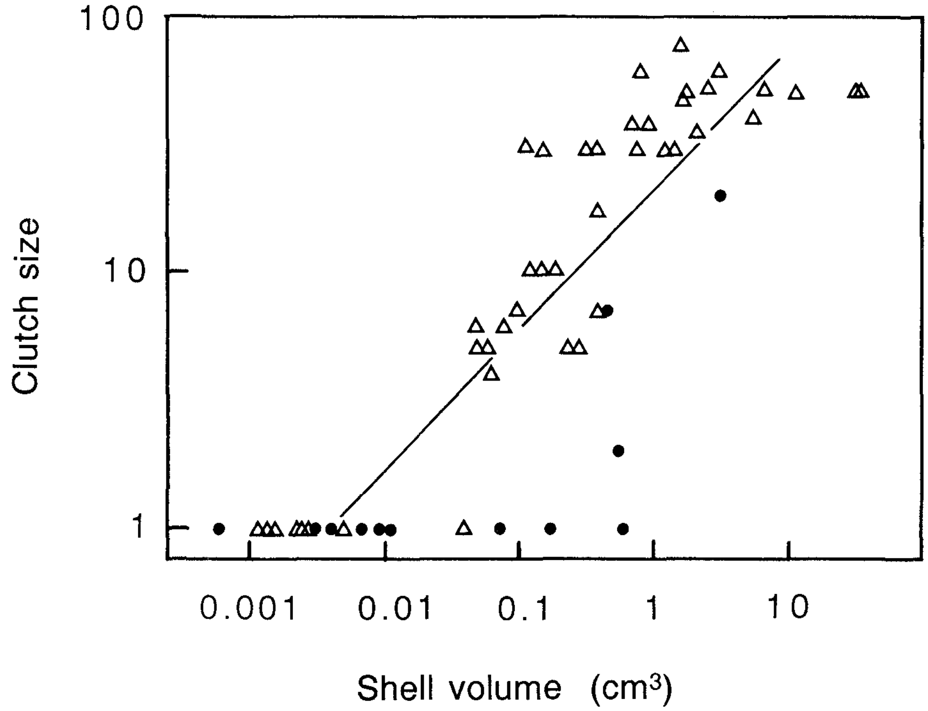
Viviparity appears to be rare in terrestrial gastropods. In contrast, viviparity has been reported in several species of freshwater prosobranchs (e.g. *Viviparus ater*[53,87]).

Costs and benefits of parental care

Evidence for costs and benefits of parental care in terrestrial gastropods is indirect. Nest digging may represent a form of parental investment. Compared to snails that deposit their eggs beneath leaf litter or in moss, individuals that dig a nest for oviposition need significantly more time during which they are susceptible to predation and exposed to severe water loss. In natural populations of *Arianta arbustorum* in Sweden, egg batches were deposited in decaying grass, in moss, under leaf litter or buried in the soil[9]. It is, however, unknown whether the eggs of the latter group enjoyed increased survival as a result of parental investment. In a laboratory experiment, buried eggs of *A. arbustorum* were less affected by inter-clutch cannibalism than eggs deposited in decaying grass and moss, indicating a benefit of nest digging (B. Baur, unpublished data).

The search for suitable oviposition sites may signify an increased risk of predation and desiccation for the parent snail. However, no empirical data concerning potential costs and benefits for this behaviour are available for terrestrial gastropods.

The energetic costs of egg production are substantial in terrestrial gastropods. For example, the reproductive investment per year in *A. arbustorum* (measured as total dry weight of the eggs produced in a field cage experiment) was 1.6 times as large as the dry weight of the snail's soft body[23]. Assuming 3–4 reproductive seasons as the average lifetime of a snail[23], the reproductive allocation of an individual is 5–6 times as large as its body weight in this species. In the terrestrial slug *Deroceras reticulatum*, the hermaphrodite gland shows a



Relationship between clutch size and shell volume in land snails from northwestern and central Europe. Egg-retaining and ovoviviparous species (filled circles) have smaller clutches than oviparous species (triangles) when differences in shell size are taken into account (comparison of residuals to the regression line: $t = 5.28$, d.f. $= 57$, $p < 0.001$).

200%-decrease between the mature-unmated and the senescent stage[98,99]. An adult gastropod invests considerable calcium carbonate in the production of an egg batch (see above 'Egg provisioning').

The main benefit of egg retention and ovoviviparity might be a minimization of potential egg mortality caused by drought and predators. In fact, ovoviviparity is common in species living in habitats with extreme environmental conditions such as exposed rock-walls or stone walls which provide no suitable oviposition sites (e.g. *Pyramidula rupestris*, *Balea perversa*[4]) and in species living in tropical regions[73,74,77]. For example, desiccation of eggs causes most of the mortality in the tropical snail *Limicolaria martensiana*[74]. In this case ovoviviparity could have evolved in response to selection pressures such as irregular starts of the rainy season[77].

Egg-retention and ovoviviparity also represent costs to the animals. Clutch size and hatchling size scale allometrically with shell size in land snails from northwestern and central Europe[26]. When the potentially confounding effects of shell size are removed (by considering the residuals from clutch size-shell volume and hatchling size-shell volume regressions), egg-retaining and ovoviviparous species produce significantly smaller clutches than oviparous species (fig.). On the other hand, hatchling size did not differ between egg-retaining/ovoviviparous and oviparous species ($t = 0.79$, d.f. $= 36$, $p = 0.43$). This indicates a cost of retaining eggs or young in the reproductive tract in terms of a reduced fecundity.

Discussion

The present review indicates that the majority of terrestrial gastropods provide no form of parental care in its narrow sense. Instead they rely on other strategies to maximize their reproductive success. Many marine prosobranchs produce huge numbers of small eggs or provide nurse eggs to embryos[50,51]. Compared with marine snails, terrestrial snails often specialize in quality rather than quantity of the eggs they produce. The majority of the extant land snails produce during their lifetime 100–500 relatively large eggs (B. Baur, unpublished data). In small-sized land snail species the lifetime reproductive output is even smaller, ranging from 5–30 eggs[13].

Several models have been developed to explain the evolution of egg size under parental care[91,93,103]. The 'safe-harbour' hypothesis suggests that, all other things being equal, natural selection is expected to maximize the amount of time that developing organisms spend in the safest stages of development and minimize time spent in those where the instantaneous rate of mortality is highest[70,71,90,91,112]. For example, when mortality of eggs is high and that of juveniles is low, selection should minimize the time spent in the egg and maximize the proportion of developmental time spent as juvenile. According to the safe-harbour hypothesis, egg size is likely to increase with increasing quality of parental care. However, the safe-harbour hypothesis does not allow us to distinguish whether increased egg size results from selection pressures other than parental care.

In *Arianta arbustorum*, egg size increases and clutch size decreases in populations living in harsh environments with short reproductive periods[5]. Individuals of *A. arbustorum* living at an altitude of 2600 m in the Swiss Alps produce eggs that are (in relation to their mother's soft body weight) 1.7 times as heavy as those from snails living under more benign conditions in the valley at 1220 m[23]. This suggests that in *A. arbustorum* the level of parental investment per offspring increases in physically harsh environments. In other extreme environments, egg retention and ovoviviparity may have evolved as an increased level of parental care.

Apart from parental care, different behavioural strategies of the parent snails may enhance the survival of their offspring. Little is known concerning physical and chemical defense mechanisms that might have evolved in eggs and juveniles of terrestrial gastropods. Aposematic eggs have been described in prosobranch apple snails that are amphibious[94]. In Florida, *Pomacea paludosa* deposits eggs on a stem of emergent aquatic vegetation or on the trunk of a cypress. The eggs are very conspicuous (pale orange) and unpalatable for many predators[94]. Many marine gastropods enclose their eggs in protective capsules[78,79,100,101]. Perron[80] determined the physical strength and energetic cost of egg capsules belonging to 10 species of Hawaiian *Conus*. Protective capsules accounted for up to 50% of the total reproductive energy devoted to ova and capsules. Strong capsules produced by species with large ova may have evolved as a result of selection for improved protection of embryos from predation and physical stress. No similar information is available for eggs of terrestrial gastropods.

As in many other animal groups, there is a need for experimental studies on different aspects of parental care in terrestrial gastropods. Several snail species may be well-suited for these kinds of studies (e.g. species in which both oviparity and ovoviviparity occur), but their potential as experimental organisms has not yet begun to be exploited by evolutionary biologists.

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1 Alexander, R. D., The evolution of social behaviour. A. Rev. Ecol. Syst. *4* (1974) 325–383.
2 Alyakrinskaya, I. O., Egg nutrient content in gastropods. Dokl. Akad. Nauk SSSR *260* (1981) 245–248.
3 Andreassen, E. M., Population dynamics of *Arianta arbustorum* and *Cepaea hortensis* in western Norway. Fauna norv. Ser. A *2* (1981) 1–13.
4 Baur, A., Intra- and interspecific influences on age at first reproduction and fecundity in the land snail *Balea perversa*. Oikos *57* (1990) 333–337.
5 Baur, B., Shell size and growth rate differences for alpine populations of *Arianta arbustorum* (L.) (Pulmonata: Helicidae). Revue suisse Zool. *91* (1984) 37–46.
6 Baur, B., The minute land snail *Punctum pygmaeum* (Draparnaud) can reproduce in the absence of a mate. J. moll. Stud. *53* (1987) 112–113.
7 Baur, B., Can cannibalistic hatchlings of the land snail *Arianta arbustorum* distinguish between sib and non-sib eggs? Behaviour *103* (1987) 259–265.
8 Baur, B., Effects of early feeding experience and age on the cannibalistic propensity of the land snail *Arianta arbustorum*. Can. J. Zool. *65* (1987) 3068–3070.
9 Baur, B., Do the risks of egg cannibalism and desiccation influence the choice of oviposition sites in the land snail *Arianta arbustorum*? J. Zool. *216* (1988) 495–502.
10 Baur, B., Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism. Oecologia, Berl. *77* (1988) 390–394.
11 Baur, B., Egg-species recognition in cannibalistic hatchlings of the land snails *Arianta arbustorum* and *Helix pomatia*. Experientia *44* (1988) 276–277.
12 Baur, B., Repeated mating and female fecundity in the simultaneously hermaphroditic land snail *Arianta arbustorum*. Invert. Reprod. Develop. *14* (1988) 197–204.
13 Baur, B., Growth and reproduction of the minute land snail *Punctum pygmaeum* (Draparnaud). J. moll. Stud. *55* (1989) 383–387.
14 Baur, B., Egg cannibalism in hatchlings of the land snail *Helix pomatia*: nutritional advantage may outweigh lack of kin recognition. Malacol. Rev. *23* (1990) 103–105.
15 Baur, B., Possible benefits of egg cannibalism in the land snail *Arianta arbustorum*. Funct. Ecol. *4* (1990) 679–684.
16 Baur, B., Seasonal changes in clutch size, egg size and mode of oviposition in *Arianta arbustorum* (L.) (Gastropoda) from alpine populations. Zool. Anz. *225* (1990) 253–264.
17 Baur, B., Cannibalism in gastropods, in: Cannibalism: Ecology and Evolution among Diverse Taxa, pp. 102–127. Eds M. A. Elgar and B. J. Crespi. Oxford University Press, Oxford 1992.
18 Baur, B., Random mating by size in the simultaneously hermaphroditic land snail *Arianta arbustorum*: experiments and an explanation. Anim. Behav. *43* (1992) 511–518.
19 Baur, B., Intraclutch egg cannibalism by hatchlings of the land snail *Arianta arbustorum*: non-random consumption of eggs? Ethol. Ecol. Evolution *5* (1993) 329–336.
20 Baur, B., Interpopulation differences in propensity for egg cannibalism in hatchlings of the land snail *Arianta arbustorum*. Anim. Behav. (1994) in press.
21 Baur, B., and Baur, A., Proximate factors influencing egg cannibalism in the land snail *Arianta arbustorum* (Pulmonata, Helicidae). Oecologia, Berl. *70* (1986) 283–287.
22 Baur, B., and Baur, A., Effect of courtship and repeated copulation on egg production in the simultaneously hermaphroditic land snail *Arianta arbustorum*. Invert. Reprod. Develop. *21* (1992) 201–206.
23 Baur, B., and Raboud, C., Life history of the land snail *Arianta arbustorum* along an altitudinal gradient. J. Anim. Ecol. *57* (1988) 71–87.
24 Bayne, C., Histochemical studies on the egg capsules of eight gastropod molluscs. Proc. malacol. Soc. Lond. *38* (1968) 199–212.
25 Bayne, C., A study of the desiccation of egg capsules of eight gastropod species. J. Zool. *155* (1968) 401–411.
26 Bengtsson J., and Baur, B., Do pioneers have r-selected traits? Life history patterns among colonizing terrestrial gastropods. Oecologia, Berl. *94* (1993) 17–22.
27 Bequaert, J., Monography of the Strophocheilidae, a neotropical family of terrestrial mollusks. Bull. Mus. comp. Zool. Harv. *100* (1948) 1–210.
28 Bieler, R., Gastropod phylogeny and systematics. A. Rev. Ecol. Syst. *23* (1992) 311–338.
29 Birchler, T., Mehrfache Vaterschaft und phänotypische Variabilität bei der Landschnecke *Arianta arbustorum*. Diplom-Thesis, University of Basel, 1992.
30 Cain, A. J., Ecology and ecogenetics of terrestrial molluscan populations, in: The Mollusca, vol. 6, pp. 597–647. Ed. W. D. Russell-Hunter. Academic Press, London 1983.

31 Carrick, R., The life-history and development of *Agriolimax agrestis*, the grey field slug. Trans. R. Soc. Edinb. *59* (1938) 563–597.
32 Carrick, R., The grey field slug, *Agriolimax agrestis* L., and its environment. Ann. appl. Biol. *29* (1942) 43–55.
33 Chen, X., and Baur, B., The effect of multiple mating on female reproductive success in the simultaneously hermaphroditic land snail *Arianta arbustorum*. Can. J. Zool. (1994) in press.
34 Clutton-Brock, T., The Evolution of Parental Care. Oxford University Press, Oxford 1991.
35 Cowie, R. H., Evolution and extinction of Partulidae, endemic Pacific island land snails. Phil. Trans. R. Soc. B *335* (1992) 167–191.
36 Creek, G., The reproductive system and embryology of the snail *Pomatias elegans*. Proc. zool. Soc. Lond. *121* (1951) 228–240.
37 Crowell, H. H., Laboratory study of calcium requirements of the brown garden snail, *Helix aspersa* Müller. Proc. malac. Soc. Lond. *40* (1973) 491–503.
38 Duncan, C. J., Reproduction, in: Pulmonates, vol. 1, pp. 309–365. Eds V. Fretter and J. Peake. Academic Press, London 1975.
39 Edelstam, C., and Palmer, C., Homing behaviour in gastropods. Oikos *2* (1950) 259–270.
40 Elgar, M. A., and Crespi, B. J. (eds). Cannibalism: Ecology and Evolution among Diverse Taxa. Oxford University Press, Oxford 1992.
41 Elmslie, L. J., Studies on the feeding of newly hatched *Helix aspersa*. Snail Farming Research *2* (1988) 45–48.
42 Emberton, K. C., Kuncio, G. S., Davis, G. M., Phillips, S. M., Monderewicz, K. M., and Guo, Y. H., Comparison of recent classifications of stylommatophoran land-snail families, and evaluation of large-ribosomal-RNA sequencing for their phylogenetics. Malacologia *31* (1990) 327–352.
43 Fechter, R., and Falkner, G., Weichtiere. Mosaik Verlag, München 1990.
44 Fioroni, P., Zur Morphologie und Embryogenese des Darmtraktes und der transitorischen Organe bei Prosobranchiern (Mollusca, Gastropoda). Revue suisse Zool. *73* (1966) 621–876.
45 Fioroni, P., Die Prosobranchier-Entwicklung mit Nähreiern. Zool. Anz *221* (1988) 201–247.
46 Fioroni, P., and Schmekel, L., Die nährstoffreiche Gastropoden-Ontogenese. Zool. Jb. Abt. Anat. Ontog. Tiere *96* (1976) 74–171.
47 Forcart, L. The Veronicellidae of Africa. Annls. Mus. r. Congo belg. Sér. Zool. *23* (1953) 1–110.
48 Fournié, J., and Chétail, M., Calcium dynamics in land gastropods. Am. Zool. *24* (1984) 857–870.
49 Fox, L. R., Cannibalism in natural populations. A. Rev. Ecol. Syst. *6* (1975) 87–106.
50 Fretter, V., Prosobranchs, in: The Mollusca, vol. 7, pp. 1–45. Eds A. S. Tompa, N. H. Verdonk and J. A. M. van den Biggelaar. Academic Press, London 1984.
51 Fretter, V., and Graham, A., British prosobranch molluscs: their functional anatomy and ecology. Rep. Ray Soc. 1962.
52 Frömming, E., Biologie der mitteleuropäischen Landgastropoden. Duncker und Humblot, Berlin 1954.
53 Gebhardt, M., and Ribi, G., Reproductive effort and growth in the prosobranch snail, *Viviparus ater*. Oecologia, Berl. *74* (1987) 209–214.
54 Geraerts, W. P. M., and Joosse, J., Freshwater snails (Basommatophora), in: The Mollusca, vol. 7, pp. 141–207. Eds A. S. Tompa, N. H. Verdonk and J. A. M. van den Biggelaar. Academic Press, London 1984.
55 Giusti, F., and Andreini, S., Morphological and ethological aspects of mating in two species of the family Helicidae (Gastropoda, Pulmonata): *Theba pisana* (Müller) and *Helix aperta* Born. Monitore zool. ital. *22* (1988) 331–363.
56 Gugler, C. W., The eggs and egg-laying habits of some Midwestern land snails. Trans. Kansas Acad. Sci. *66* (1963) 195–201.
57 Hamilton, W. D., The genetical evolution of social behaviour I, II. J. theor. Biol. *7* (1964) 1–51.
58 Heller, J., Hermaphroditism in molluscs. Biol. J. Linn Soc. *48* (1993) 19–42.
59 Ingram, W. I., Observations of egg laying habits, eggs, and young of land mollusks on the Edmund Niles Huyck Preserve, Rensselaerville, New York. Am. Midl. Nat. *32* (1944) 91–97.
60 Kilian, E. F., Untersuchungen zur Biologie von *Pomatias elegans* (Müller) und ihrer "Konkrementdrüse". Arch. Molluskenk. *80* (1951) 1–16.
61 Lind, H., The behaviour of *Helix pomatia* L. (Gastropoda, Pulmonata) in a natural habitat. Vidensk. Meddr dansk naturh. Foren. *147* (1988) 67–92.
62 Lind, H., Homing to hibernating sites in *Helix pomatia* involving detailed long-term memory. Ethology *81* (1989) 221–234.
63 Little, C., The colonisation of land. Origins and adaptations of terrestrial animals. Cambridge University Press 1983.
64 Little, C., The terrestrial invasion: an ecophysiological approach to the origins of land animals. Cambridge University Press 1990.
65 Longstaff, J., Observations on the habits of *Cochlitoma zebra*, var. *fulgurata* (Pfeiffer), and *Cochlitoma zebra*, var. *obesa* (Pfeiffer), in confinement, Proc. zool. Soc. Lond. *26* (1921) 379–387.
66 Morton, J. E., The structure and adaptations of the New Zealand Vermetidae. Trans. R. Soc. N. Z. *79* (1951) 1–51.
67 Murray, J. J., Multiple mating and effective population size in *Cepaea nemoralis*. Evolution *18* (1964) 283–291.
68 Murray, J., and Clarke, B. C., The inheritance of polymorphic shell characters in *Partula* (Gastropoda). Genetics *54* (1966) 1261–1277.
69 Natarajan, A. V., Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. Proc. Indian Acad. Sci. *46* (1957) 170–228.
70 Nussbaum, R. A., Parental care and egg size in salamanders: an examination of the safe harbor hypothesis. Res. popul. Ecol. *29* (1987) 27–44.
71 Nussbaum, R. A., and Schultz, D. L., Coevolution of parental care and egg size. Am. Nat. *133* (1989) 591–603.
72 Oosterhoff, L., Variation in growth rate as an ecological factor in the land snail *Cepaea nemoralis*. Neth. J. Zool. *27* (1977) 1–132.
73 Owen, D. F., A population study of an equatorial land snail, *Limicolaria martensiana* (*Achatinidae*). *Proc. zool. Soc. Lond.* *144* (1965) 361–382.
74 Owiny, A. M., Some aspects of the breeding biology of the equatorial land snail *Limicolaria martensiana* (Achatinidae: Pulmonata). J. Zool. Lond. *172* (1974) 191–206.
75 Paravicini, E., Die Eiablage zweier Javanischer Landschnecken. Arch. Molluskenk. *53* (1921) 113–116.
76 Parker, G. A., Sperm competition and its evolutionary consequences in the insects. Biol. Rev. *45* (1970) 525–568.
77 Peake, J. F., Distribution and ecology of the Stylommatophora, in: Pulmonates, vol. 2A: Systematics, evolution and ecology, pp. 429–526. Eds V. Fretter and J. F. Peake. Academic Press, London 1978.
78 Pechenik, J. A., The role of encapsulation in invertebrate life histories. Am. Nat. *114* (1979) 859–870.
79 Pechenik, J. A., The encapsulation of eggs and embryos by molluscs: an overview. Am. malacol. Bull. *4* (1986) 165–172.
80 Perron, F. E., The partitioning of reproductive energy between ova and protective capsules in marine gastropods of the genus *Conus*. Am. Nat. *118* (1981) 110–118.
81 Perrot, J.-L., La confection du nid et la ponte chez l'*Helix pomatia*. Revue suisse Zool. *45* (1938) 221–235.
82 Plummer, J. M., Observations on the reproduction, growth and longevity of a laboratory colony of *Archachatina*

(*Calachatina*) *marginata* (Swainson) subspecies *ovum*. Proc. malacol. Soc. Lond. *41* (1975) 395–413.
83 Polis, G. A., The evolution and dynamics of intraspecific predation. A. Rev. Ecol. Syst. *12* (1981) 225–251.
84 Pollard, E., Aspects of the ecology of *Helix pomatia* L. J. anim. Ecol. *44* (1975) 305–329.
85 Prince, G., Über Lebensweise, Fortpflanzung und Genitalorgane des terrestrischen Prosobranchiers, *Cochlostoma septemspirale*. Arch. Molluskenk. *96* (1967) 1–18.
86 Purchon, R. D., The Biology of the Mollusca. Pergamon, New York 1977.
87 Ribi, G., and Gebhardt, M., Age-specific fecundity and size of offspring in the prosobranch snail, *Viviparus ater*. Oecologia Berl. *71* (1986) 18–24.
88 Riddle, W. A., Physiological Ecology of Land Snails and Slugs, in: The Mollusca, vol. 6, pp. 431–461. Ed. W. D. Russell-Hunter. Academic Press, London 1983.
89 Sarasin, P., and Sarasin, F., Die Landmollusken von Celebes. Wiesbaden, 1899.
90 Sargent, R. C., Taylor, P. D., and Gross, M. R., Parental care and the evolution of egg size in fishes. Am. Nat. *129* (1987) 32–46.
91 Shine, R., Propagule size and parental care: the 'safe harbor' hypothesis. J. theor. Biol. *75* (1978) 417–424.
92 Smith, B. J., Black, J. H., and Shepherd, S. A., Molluscan Egg Masses and Capsules, in Marine Invertebrates of Southern Australia, part II, pp. 841–891. Eds S. A. Shepherd and I. M. Thomas. South Australian Government Printing Division, Adelaide 1989.
93 Smith, C. S., and Fretwell, S. D., The optimal balance between size and number of offspring. Am. Nat. *108* (1974) 499–506.
94 Snyder, N. F. R., and Snyder, H. A., Denfenses of the Florida apple snail *Pomacea paludosa*. Behaviour *40* (1971) 175–215.
95 Solem, A., *Tekoulina*, a new viviparous tornatellinid land snail from Rarotonga, Cook Islands. Proc. malac. Soc. Lond. *40* (1972) 93–114.
96 Solem, A., The Shell Makers Introducing Mollusks. Wiley, New York 1974.
97 Solem, A., Endodontoid Land Snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra), part I, Family Endodontidae. Field Museum of Natural History, Chicago 1976.
98 South, A., A comparison of the life cycles of *Deroceras reticulatum* (Müller) and *Arion intermedius* Normand (Pulmonata: Stylommatophora) at different temperatures under laboratory conditions. J. moll. Stud. *48* (1982) 233–244.
99 South, A., A comparison of the life cycles of the slugs *Deroceras reticulatum* (Müller) and *Arion intermedius* Normand on permanent pasture. J. moll. Stud. *55* (1989) 9–22.
100 Spight, T. M., Factors extending gastropod embryonic development and their selective cost. Oecologia (Berl.) *21* (1975) 1–16.
101 Spight, T. M., Do intertidal snails spawn in the right places? Evolution *31* (1977) 682–691.
102 Standen, R., On calcareous eggs of terrestrial Mollusca. J. Conch. *15* (1917) 154–164.
103 Taylor, P. D., and Williams, G. C., Demographic parameters in evolutionary equilibrium. Can. J. Zool. *62* (1984) 2264–2271.
104 Thorson, G., Studies on the egg-capsules and development of Arctic marine prosobranchs. Meddr Grønland *100* (1935) 1–71.
105 Thorson, G., Studies on the egg masses and larval development of Gastropoda from the Iranian Gulf. Dan. Sci. Invest. Iran *2* (1940) 159–238.
106 Tompa, A. S., Embryonic utilization of egg shell calcium in a gastropod. Nature *255* (1975) 232–233.
107 Tompa, A. S., A comparative study of the ultrastructure and mineralogy of calcified land snail eggs (Pulmonata: Stylommatophora). J. Morph. *150* (1976) 861–888.
108 Tompa, A. S., Studies on the reproductive biology of gastropods: part 1. The systematic distribution of egg retention in the subclass Pulmonata (Gastropoda). J. Malac. Soc. Aust. *4* (1979) 113–120.
109 Tompa, A. S., Oviparity, egg retention and ovoviviparity in pulmonates. J. moll. Stud. *45* (1979) 155–160.
110 Tompa, A. S., Studies on the reproductive biology of gastropods: part 3. Calcium provision and the evolution of terrestrial eggs among gastropods. J. Conch. *30* (1980) 145–154.
111 Tompa, A. S., Land snails (Stylommatophora), in The Mollusca, vol. 7, pp. 47–140. Eds A. S. Tompa, N. H. Verdonk and J. A. M. van den Biggelaar. Academic Press, London 1984.
112 Williams, G. C., Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton 1966.
113 Wolda, H., Natural populations of the polymorphic land snail *Cepaea nemoralis* (L.). Archs néerl. Zool. *15* (1963) 381–471.
114 Wolda, H., and Kreulen, D. A., Ecology of some experimental populations of the landsnail *Cepaea nemoralis* (L.). II. Production and survival of eggs and juveniles. Neth. J. Zool. *23* (1973) 168–188.
115 Yom-Tov, Y., The biology of two desert snails *Trochoidea (Xerocrassa) seetzeni* and *Sphincterochila boissieri*. Israel J. Zool. *20* (1971) 231–248.