

Social facilitation affects longevity and lifetime reproductive success in a self-fertilizing land snail

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Factors that reduce the reproductive output of self-fertilizing hermaphrodites are receiving increasing attention. The combined effects of reduced fecundity of selfing parents and inbreeding depression of the progeny have been referred to as self-fertilization depression. In isolated freshwater snails the reproductive output of selfing individuals also decreases due to the lack of social facilitation (absence of a conspecific). We examined the effect of social facilitation on lifetime reproductive success (number of young produced and longevity) over two generations in the simultaneously hermaphroditic land snail *Balea perversa*. In a parallel study we showed that *B. perversa* kept singly and in pairs reproduced exclusively by self-fertilization. In the parent generation, snails kept singly produced less offspring than snails kept in pairs. The difference in lifetime number of young was mainly due to differences in adult life span. Snails of the two groups did not differ in reproductive rate (number of young produced per 100 d of reproductive life) and hatchling size. In the offspring generation, snails kept singly did not differ from individuals kept in pairs in the lifetime number of young and hatchling survival. As in the parent generation, snails kept singly reproduced during a shorter period than snails kept in pairs. However, the shorter reproductive life span of snails kept singly was compensated for by a slightly (but not significantly) higher reproductive rate which resulted in a similar number of offspring produced for both groups. In both generations, snails of the two groups did not differ in size at first reproduction, adult growth rate and size at death. These findings suggest that social facilitation may affect longevity in selfing *B. perversa*.

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Among hermaphroditic animals, studies on the life history and population genetics of gastropods, mainly freshwater pulmonate snails, have contributed to our understanding of the evolution of selfing, and its biological causes and consequences (e.g. Jarne et al. 1993, Städler et al. 1995). Outcrossing and self-fertilization are common modes of reproduction in pulmonate gastropods (reviewed by Brown and Richardson 1988, Jarne 1995, Jarne and Städler 1995). Some species reproduce predominantly by self-fertilization, others are facultative self-fertilizers (selfing only occurs when no mating partners are available), and others reproduce exclusively by cross-fertilization.

Differences in survival rates between progeny of selfing and cross-fertilizing individuals have been found and interpreted as resulting from inbreeding depression (Jarne 1995). Selfing snails often have a lower fecundity than cross-fertilizing snails (but see van Duivenboden et al. 1985, Bayomy and Joosse 1987). The whole effect (fecundity of parents and inbreeding depression of the progeny) has been referred to as self-fertilization depression (Jarne et al. 1991). However, specific problems may arise when estimating self-fertilizing depression in animals (Doums et al. 1994). In experiments on hermaphroditic freshwater snails, selfed progeny have been produced usually by isolated virgin adults, and

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cross-fertilized progenies have been produced by paired/grouped adults (reviewed by Jarne et al. 1993). In these experiments the mode of fertilization (selfing versus cross-fertilization) is partly confounded with the snails' social environment (isolated versus paired/grouped), and the relevant controls have not been performed to disentangle these two possible effects on reproductive output. Doums et al. (1994) showed that grouping can have a negative effect on fecundity even in the absence of crowding suggesting 'social obstruction'. Vernon (1995) examined the potential of 'social facilitation' (i.e. the response of selfing individuals to the presence of conspecifics in the environment) in a freshwater snail. Detecting the presence of other conspecifics, presumably by some water-borne chemical communication, is known to influence feeding, growth, metabolism and reproduction in freshwater snails (Ritchie et al. 1966, Thomas and Benjamin 1973, 1974, Thomas et al. 1975). Vernon (1995) found that isolated, self-fertilizing individuals of *Biomphalaria glabrata* had a reduced reproductive output compared with paired, predominantly cross-fertilizing snails. However, the reproductive output of control snails (kept in pairs, but prevented from cross-fertilizing) was similar to that of paired, cross-fertilizing snails, suggesting that the low reproductive output of snails in isolation was not simply due to inbreeding depression with self-fertilization. Vernon (1995) suggested that an absence of social facilitation, caused by deprivation of social communication as a result of isolation, may reduce the reproductive output of isolated *B. glabrata*. Other studies have shown a higher fecundity in isolated freshwater snails compared with grouped snails as a consequence of crowding effects (e.g. Bayomy and Joosse 1987, Bohlken et al. 1987). These effects should be considered separately. Studies on social facilitation examine the effect of absence of partners in selfing animals, whereas studies on grouping examine the effect of crowding in selfing animals.

The present study investigates social facilitation in the land snail *Balea perversa*. Terrestrial gastropods detect the presence of conspecifics by chemical cues predominantly in mucus trails (Croll 1983, Chase 1986). Effects of grouping on reproductive output are well documented in land snails (e.g. Wolda 1972, Oosterhoff 1977, Baur and Baur 1990). However, the potential of social facilitation on both longevity and reproductive output has not been examined in terrestrial gastropods. The simultaneously hermaphroditic snail *B. perversa* reproduces predominantly by self-fertilization in natural populations (Wirth et al. 1997). On the Baltic island of Öland, individuals of *B. perversa* were frequently found attached to small pieces of lichens dispersed by wind (B. Baur unpubl.). In this way single, self-fertilizing individuals become founders of new populations. The absence or presence of conspecifics may affect the reproductive output of founder snails.

We designed a laboratory experiment to examine the effect of social facilitation on longevity and lifetime reproductive success in *B. perversa* over two consecutive generations. Parent-offspring analyses with molecular markers showed that *B. perversa* kept in the laboratory and fed on its natural diet (lichens and algae growing on pieces of limestone) reproduces exclusively by self-fertilization even snails kept in pairs (Wirth et al. 1997). We addressed the following questions: (1) does the presence of a conspecific affect longevity and lifetime reproductive success (lifetime number and viability of offspring) in selfing *B. perversa* from two generations? (2) do the different conditions of parental rearing (singly or in pairs) influence the lifetime fecundity of the progeny? and (3) how much of the interindividual variance in lifetime fecundity is attributable to different traits (reproductive life span, size at first reproduction and adult growth rate)?

Materials and methods

Study animals

Balea perversa is a land snail living in dry sites among rocks and on old stone walls, and occasionally, on tree trunks (Baur and Baur 1997). It is widely distributed in western Europe and in Scandinavia, where it occurs mainly along the coast as far north as 68°N in Norway (Kerney and Cameron 1979). *Balea perversa* has a narrowly conical shell, which in adults is 7–11 mm high. In the field individuals become sexually mature at an age of 3–5 yr (B. Baur and A. Baur unpubl.). *Balea perversa* is ovoviviparous, giving birth to single young with a shell height of approximately 1.4 mm (range 0.8–1.9 mm; Baur and Baur 1992). On rock-faces, *B. perversa* feeds on various species of epi- and endolithic lichens, algae and free-living cyanobacteria (Fröberg et al. 1993, Baur et al. 1994). In the heath-grassland Great Alvar on the Baltic island of Öland, *B. perversa* coexists with the land snail *Chondrina clienta* (Westerlund) on limestone walls (Baur 1988a). Experimental evidence indicates that both intra- and interspecific competition affect juvenile growth rate, age at first reproduction, adult shell size and survival in *B. perversa* and *C. clienta* (Baur 1990, Baur and Baur 1990).

Breeding experiment

Juvenile individuals of *B. perversa* (shell height 2–3 mm) were collected from a stone wall 10 km E of Mörbylånga in the heath-grassland Great Alvar on Öland, Sweden (56°33'N, 16°36'E). The snails were kept isolated in transparent plastic dishes (6.5 cm in diameter, 2 cm in height) until they reached sexual maturity as indicated by the formation of a thickened lip at the

shell aperture. To examine whether social facilitation affects lifetime reproductive success in *B. perversa*, virgin adults were randomly assigned to one of two groups: snails were kept either singly or in pairs throughout their reproductive life. Parent-offspring analysis using random amplified polymorphic DNA (RAPD) technique revealed that *B. perversa* collected as juveniles from the same population and kept under identical conditions as in the present experiment reproduced exclusively by self-fertilization, no matter whether they were kept singly ($N = 18$ individuals) or in pairs ($N = 14$ pairs; Wirth et al. 1997). In natural populations, however, the mating system of *B. perversa* includes both selfing (75–90%) and outcrossing (10–25%; Wirth et al. 1997).

To assess lifetime reproductive success, snails were kept in transparent plastic dishes as described above. The bottom of each dish was lined with paper towelling on which a piece of limestone (approximately 5 cm in diameter) densely covered with lichens and free-living cyanobacteria was placed. Pieces of limestone were obtained from an area adjacent to the snails' site of origin. Snails are active only during periods of high air humidity, when they graze lichens and free-living cyanobacteria (Schmid 1929, Neuckel 1981). To stimulate snail activity, the piece of limestone and paper towel were moistened and the dish covered with an acetate film; after 12 h, the waterproof cover was exchanged for a paper towel to dry out the dish. This procedure was carried out repeatedly at 48-h intervals, resulting in a rhythm of alternating 12 h activity and 36 h resting. Snails were kept at room temperature and under natural light conditions. For snails kept singly the piece of limestone was replaced every 72 d, for snails kept in pairs twice as frequently. The frequency of stone replacement provided the snails with food ad libitum (Baur and Baur 1990). The number of young produced in each dish was counted and the juveniles were removed every 18 d until the mother(s) died.

Size at first reproduction and size at death (shell height) of each snail and the size of the newborn offspring were measured to the nearest 1/12 mm using a binocular microscope with a stage micrometer. To identify individuals kept in pairs, one of the snails was marked on its shell with a spot of correction fluid (Tipp-Ex[®]) at the beginning of the experiment. The life span of each snail that died was recorded with an accuracy of 2 d. We defined adult life span as the period from first reproduction until death of a snail, reproductive lifespan as the time elapsed between production of the first and last young, and the post-reproductive life span as the period between last reproduction and death. Adult growth rate was defined as ((size at death – size at first reproduction)/adult life span) $\times 100$ d. Similarly, reproductive rate was defined as number of young produced per 100 d of reproductive life.

Data on size at first reproduction (= size at sexual maturity; see above), size at death, adult growth rate and adult life span were obtained for each individual. However, the number of young produced could only be assigned to individuals in snails kept singly. Therefore in snails kept in pairs the lifetime number of young was divided by two (as was done for estimates of reproductive rate). Reproductive life span and post-reproductive life span could accurately be determined in singles. In snails kept in pairs, however, the length of the reproductive life span could not be assessed accurately because the pair mate could continue to reproduce. This uncertainty leads to an underestimate of the length of the post-reproductive period of snails kept in pairs. On the other hand, snails kept in pairs had a significantly longer adult life span than snails kept singly both in the parent and offspring generation. This indicates that the uncertainty in the separation of reproductive and post-reproductive life span in snails kept in pairs does not affect our main results.

To assess whether offspring produced by snails kept singly differed in lifetime reproductive success from those deriving from snails kept in pairs, the same traits were recorded in snails of the consecutive generation. Two to three young born from snails kept isolated or from snails kept in pairs were raised in single dishes as described above. Virgin snails of the offspring generation were randomly assigned to one of five groups 2–4 weeks before they reached sexual maturity (Fig. 1). As in the parent generation, snails of the offspring generation were kept either isolated (groups $F_{1,s}$ and $F_{1,p}$) or in pairs ($F_{1,ss}$, $F_{1,sp}$ and $F_{1,pp}$) as described above. In addition to the traits listed above, we recorded the viability of newborn snails at an age of 2–16 d (hatchling size was only measured in the parent generation).

Statistical analyses

Mean values from pairs were used in all statistical analyses (i.e. pairs were considered as the experimental unit in comparison with snails kept singly). Data analysis was performed using the SAS program package

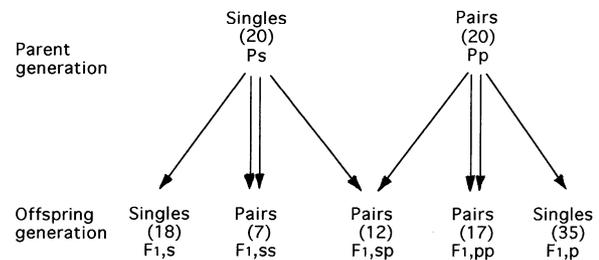


Fig. 1. Design of breeding experiment with sample size in parentheses.

Table 1. Lifetime fecundity, longevity and adult size of *B. perversa* kept singly ($N = 20$ individuals) or in pairs ($N = 20$ pairs) of the parent generation. Means \pm s.d. per individual with z - and P -values resulting from Mann-Whitney U -tests are shown.

Trait	Snails kept singly	Snails kept in pairs	z	P
Lifetime number of young	19.8 \pm 7.5	26.9 \pm 7.9	2.49	0.013
Hatchling size (mm)	1.79 \pm 0.23	1.76 \pm 0.17	0.60	0.549
Adult life span (d)	428.5 \pm 98.6	498.7 \pm 92.7	2.41	0.016
Reproductive life span (d)	322.2 \pm 112.6	422.1 \pm 105.5	2.18	0.030
Post-reproductive life span (d)	106.3 \pm 136.9	76.6 \pm 56.9	0.11	0.914
Reproductive rate (no. of young per 100 d reproductive life)	6.6 \pm 2.2	6.6 \pm 2.2	0.04	0.968
Size at first reproduction (mm)	9.3 \pm 0.5	9.2 \pm 0.2	0.68	0.498
Size at death (mm)	9.7 \pm 0.5	9.7 \pm 0.3	0.35	0.725
Adult growth rate (mm per 100 d adult life)	0.10 \pm 0.05	0.10 \pm 0.03	0.01	0.989

(SAS Institute 1991). Values are given throughout as mean \pm s.d.

Mann-Whitney U -test was used to compare traits of snails kept singly with those of snails kept in pairs. Kruskal-Wallis test was used to assess whether the condition of parental rearing affects the reproductive performance and longevity of their progeny. Sign-tests were applied to compare the number of hatchlings that died in the first half of the reproductive life of a snail (or pair) with the number of hatchlings that died in the second half of the reproductive life for single snails and snails kept in pairs.

Results

Lifetime reproductive success in the parent generation

Snails kept isolated throughout their life produced significantly less offspring than individuals kept in pairs (Table 1). Snails kept singly produced between 8 and 37 young ($\bar{x} = 19.8$) and thus showed a four- to five-fold intragroup variation in lifetime fecundity. Snails kept in pairs produced per individual between 11.5 and 44 young ($\bar{x} = 26.9$) and showed a four-fold variation in lifetime fecundity. The snails of both groups did not differ in the size of newborns (Table 1).

The difference in lifetime fecundity between the two groups was not due to differences in snail size or adult growth rate: snails from both groups differed neither in size at first reproduction nor in adult growth rate and size at death (Table 1). However, snails from the two groups differed in longevity (Table 1). Snails kept singly lived between 196 and 700 d as adults ($\bar{x} = 428$ d), snails kept in pairs between 354 and 792 days ($\bar{x} = 499$ d). Adult life span can be separated in a reproductive and a post-reproductive period. Snails kept in pairs reproduced over a significantly longer period than snails kept singly, but snails from both groups did not differ in the length of the post-reproductive period (Table 1). Furthermore, the snails in both groups did not differ in re-

productive rate (number of young produced per 100 d of the reproductive period; Table 1). These data indicate that reproductive life span was the most important factor determining lifetime fecundity of *B. perversa* in the parent generation.

The lifetime number of young was positively correlated with the length of reproductive life and negatively with post-reproductive life in snails kept singly (Table 2). In snails kept in pairs no significant correlation between lifetime number of young and any other trait was found (Table 2).

Conditions of parental rearing and offspring reproductive performance

The conditions of parental rearing did not influence the reproductive performance of their progeny. In offspring kept singly, individuals deriving from snails kept singly ($F_{1,s}$, $N = 18$) did not differ from individuals deriving from snails kept in pairs ($F_{1,p}$, $N = 35$) in lifetime number of young, hatchling survival, adult life span, post-reproductive life span, reproductive rate, size at first reproduction, adult growth and size at death (Mann-Whitney U -test, in all traits $P > 0.14$). Exceptionally, snails deriving from parents kept singly reproduced over a longer period than snails from parents kept in pairs (507.0 ± 162.9 d vs 406.3 ± 162.4 d; Mann-Whitney U -test, $P = 0.049$).

In offspring kept in pairs, no difference between individuals deriving from snails kept singly ($F_{1,ss}$, $N = 7$), those from snails kept in pairs ($F_{1,pp}$, $N = 17$), and those with one parent from either way of maintenance ($F_{1,sp}$, $N = 12$) were found in any of the traits measured, except for the length of the post-reproductive period (Kruskal-Wallis test, $P = 0.030$). Thus, a significant difference was found only in two of 18 comparisons. In a series of 18 tests, two significant differences can be obtained by chance. Consequently, we combined data on reproductive performance and longevity from the two groups of snails kept singly in the offspring generation ($F_{1,s}$ and $F_{1,p}$) as well as those from the three groups of snails kept in pairs ($F_{1,ss}$, $F_{1,sp}$ and $F_{1,pp}$) for further data analyses.

Lifetime reproductive success in the offspring generation

In contrast to the parent generation, snails from the offspring generation kept isolated or in pairs throughout their life did not differ in lifetime number of offspring (Table 3). Snails kept singly produced between 2 and 80 young ($\bar{x} = 29.5$), showing a 40-fold variation in lifetime fecundity. Snails kept in pairs produced per individual between 16 and 46 young ($\bar{x} = 30.8$) and thus showed a three-fold variation in lifetime fecundity. The snails in both groups did not differ in hatchling survival (Table 3).

As in the parent generation, snails in both groups did not differ in size at first reproduction, adult growth rate and size at death, but they differed in longevity (Table 3). Snails kept singly lived between 84 and 862 d as adults ($\bar{x} = 555$ d), snails kept in pairs between 352 and 777 d ($\bar{x} = 637$ d). Snails kept in pairs reproduced over a significantly longer period than snails kept singly, but did not differ in length of the post-reproductive period (Table 3). However, during the longer period of reproduction snails kept in pairs produced young at a slightly (but not significantly) lower rate than snails kept singly, which resulted in similar numbers of young produced during lifetime in both groups (Table 3).

The total number of young produced per snail was positively correlated with adult life span in snails kept singly and with length of the reproductive period in snails from both groups (Table 2). In contrast, lifetime number of young was not correlated with the length of post-reproductive life in either group. This suggests that post-reproductive life is in general not reduced as a cost of reproduction. Adult growth rate was negatively correlated with lifetime number of young produced (Table 2). This finding was not influenced by differences in size at first reproduction (partial correlation between lifetime fecundity and adult growth rate when size at first reproduction was kept constant; in snails kept singly: $r = -0.29$, $N = 53$, $P = 0.04$; in snails kept in pairs: $r = -0.30$, $N = 36$, $P = 0.08$). This suggests a trade-off between adult growth and reproduction in *B. perversa*

irrespective of the rearing condition. Lifetime number of young was also positively correlated with size at first reproduction in snails kept in pairs and with size at death in snails kept singly. Partial correlations between lifetime number of offspring and reproductive life span with keeping size at first reproduction (or size at death) constant revealed similar values as the correlation coefficients presented in Table 2.

Considering the two fitness components lifetime fecundity and reproductive life span in the parent generation, snails kept singly had a fitness of 0.74 and 0.76 relative to those of snails kept in pairs. In the offspring generation, the difference between the two groups was reduced. Snails kept singly had a lifetime fecundity of 0.96 and a reproductive life span of 0.85 relative to that of snails kept in pairs.

Age-specific fecundity

Snails kept singly did not differ in age-specific fecundity from snails kept in pairs (Kolmogorov-Smirnov test, parent generation $P > 0.1$; offspring generation $P > 0.7$). In the first 180 d of reproductive life, singles from the parent generation produced 63% of their lifetime progeny and pairs 55% (Fig. 2). The corresponding figures for the first 360 d of reproductive life were 96% in singles and 93% in snails kept in pairs. The slight (but non-significant) delay in reproduction by snails kept in pairs was due to the prolonged reproductive life span (see above).

In the offspring generation, singles produced 50% of their lifetime progeny in the first 180 d of reproductive life and snails kept in pairs 49%. The corresponding figures for the first 360 d of reproductive life were 82% in singles and 81% in pairs.

Hatchling survival did not change throughout the life of the mother(s). Hatchlings born in the first half of the reproductive life of the mother(s) did not differ in survivorship from those born in the second half of reproductive life (sign test; single snails: $P = 0.405$; pairs: $P = 0.238$).

Table 2. Pearson correlation coefficients between lifetime number of young and various life-history traits in *B. perversa* kept singly or in pairs over two generations

Trait	Parent generation				Offspring generation			
	Singles ($N = 20$)		Pairs ($N = 20$)		Singles ($N = 53$)		Pairs ($N = 36$)	
	r	P	r	P	r	P	r	P
Adult life span	0.04	0.878	0.15	0.516	0.58	<0.001	0.23	0.173
Reproductive life span	0.60	0.006	0.09	0.692	0.77	<0.001	0.39	0.020
Post-reproductive life span	-0.46	0.039	0.08	0.750	-0.23	0.105	-0.22	0.198
Adult growth rate	-0.41	0.075	0.02	0.942	-0.30	0.031	-0.41	0.013
Size at first reproduction	-0.48	0.031	0.14	0.548	0.16	0.248	0.43	0.008
Size at death	-0.54	0.013	0.20	0.410	0.28	0.041	0.13	0.448

Table 3. Lifetime fecundity, longevity and adult size of *B. perversa* kept singly ($N = 53$ individuals) or in pairs ($N = 36$ pairs) of the offspring generation. Means \pm s.d. per individual with z - and P -values resulting from Mann-Whitney U -tests are shown.

Trait	Snails kept singly	Snails kept in pairs	z	P
Lifetime number of young	29.5 \pm 15.3	30.8 \pm 8.0	0.55	0.581
Hatchling survival (%)	96.1 \pm 6.5	97.6 \pm 2.9	0.41	0.679
Adult life span (d)	555.2 \pm 180.0	637.0 \pm 92.4	2.36	0.018
Reproductive life span (d)	440.5 \pm 168.0	518.0 \pm 105.6	2.05	0.041
Post-reproductive life span (d)	114.7 \pm 112.1	119.0 \pm 87.3	0.95	0.343
Reproductive rate (no. of young per 100 d reproductive life)	6.6 \pm 2.4	6.1 \pm 1.6	1.45	0.146
Size at first reproduction (mm)	10.7 \pm 0.5	10.5 \pm 0.4	1.37	0.171
Size at death (mm)	11.3 \pm 0.6	11.4 \pm 0.5	0.63	0.530
Adult growth rate (mm per 100 d adult life)	0.12 \pm 0.08	0.13 \pm 0.05	1.60	0.109

Discussion

The present study shows that individuals of *B. perversa* kept singly throughout their life had a reduced lifetime fecundity (in the parent generation) and longevity (in both generations) compared with snails kept in pairs. The results of a parallel study showed that individuals of both groups reproduced exclusively by self-fertilization (Wirth et al. 1997). Thus, the lower reproductive output of isolated snails is not attributable to self-fertilization per se. If inbreeding would be the only factor reducing the reproductive output of isolated snails, then snails of both groups would be expected to have similar reproductive outputs. Another factor which could be important is the different social environment of isolated and paired snails. As a result of isolation, snails kept singly are prevented from communication with conspecifics. Similar reductions in fecundity of isolated individuals compared with selfing individuals kept in pairs or groups have been reported in the freshwater snails *Bulinus globosus* (Jarne et al. 1991) and *Biomphalaria glabrata* (Vernon 1995). Vernon (1995) suggested that an absence of social facilitation may play a role in reducing the reproductive output of isolated selfing snails, and that future studies using isolated and paired/grouped gastropods should be designed to control for possible effects of social facilitation. Individuals of *B. glabrata* are thought to be receptive to very low concentrations of chemicals that are released by nearby conspecifics (Thomas 1973). The exact nature of this communication substance is not yet known.

The present study is to our knowledge the first that demonstrates effects of social facilitation in a land snail. Land snails are able to detect the presence of conspecifics by chemical cues in mucus trails (Croll 1983, Chase 1986). In the present study the members of pairs were frequently observed to rest close to each other although we never observed any copulation in the course of the four-year breeding experiment (all dishes were checked on each day). The reason for the absence of mating behaviour under laboratory conditions is unknown. Most probably, the breeding conditions lack some essential stimuli to elicit mating behaviour in *B. perversa*. On the other hand, copulations have been

rarely observed in the field (B. Baur unpubl.). Frequent selfing may account for the low within-population level of genetic variability found in eight natural populations of *B. perversa* (Wirth et al. 1997). There is increasing evidence that in freshwater pulmonates self-fertilization may occur more frequently than formerly assumed (e.g. Jarne et al. 1993, Städler et al. 1995, Wethington and Dillon 1997). The same might be true for terrestrial pulmonates, particularly in species of small size (e.g. *Vallonia pulchella* (Whitney 1938); *Rumina decollata* (Selander and Hudson 1976); *Punctum pygmaeum* (Baur 1989); *Balea perversa* (Wirth et al. 1997)).

Available evidence indicates substantial differences in the reproductive behaviour and life history between basommatophoran (mainly freshwater) and stylomma-

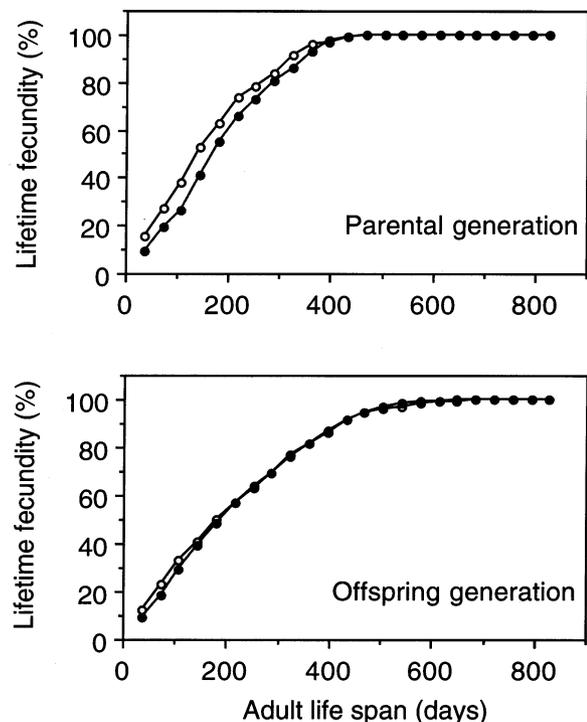


Fig. 2. Comparison of lifetime fecundity curves of *Balea perversa* kept singly (○) and in pairs (●) in the parental (above) and offspring generation (below).

tophoran (terrestrial) gastropods. In general, freshwater snails copulate more frequently than terrestrial snails (e.g. *Bulinus globosus* is able to copulate as male once per day for up to eight consecutive days; Rudolph 1983). In some experimental situations, copulation has been shown to occur so frequently that the reproductive output of paired snails was lower than that of selfing individuals (van Duivenboden et al. 1985, Bayomy and Joosse 1987). It has been argued that mating is energetically expensive and thus reduces the snails' reproductive output. In land snails mating is restricted to favourable weather conditions. Numerous land snails show elaborate courtship and copulation behaviour, which may last up to 24 h (e.g. in *Helix pomatia*; Baur 1998). In *Arianta arbustorum*, a predominantly outcrossing species, one copulation per year is enough for the fertilization of all eggs (Chen and Baur 1993).

Social facilitation may affect the reproductive output of single snails, which have been dispersed by wind (attached to leaves or pieces of lichens), floating or rafting on floating vegetation, and attached to insects, mammals and to the plumage or nest material of birds (Rees 1965, Dundee et al. 1967). On the Great Alvar of Öland, *B. perversa* has colonized almost all limestone walls that were built between 1820 and 1930. This can only be explained by passive dispersal and the snails' ability to reproduce by self-fertilization. The results of the present study suggest that social facilitation may reduce the reproductive success of single individuals which found new populations.

Previous studies showed that the density of conspecifics and the presence of another rock-dwelling land snail, *Chondrina clienta*, can influence growth, adult size and fecundity in *B. perversa* (Baur 1990, Baur and Baur 1990, 1992). Effects of intra- and interspecific competition may occur in high-density populations in the field. In the present study, ample food was provided to the snails and any effects of competition can be excluded (cf. Baur and Baur 1990). On stone walls in the Great Alvar of Öland, however, a huge variation in population density ranging from single individuals to more than 300 snails resting under single pieces of stone has been recorded (Baur et al. 1995, B. Baur unpubl.). These findings and the results of the present study suggest that fecundity in *B. perversa* might be optimal at low population density; the fecundity of single individuals might be affected by social facilitation, whereas that of snails living at high densities is influenced by intraspecific competition.

Jarne et al. (1993) suggested that gastropods with no mating opportunities should retard reproduction if selfing is connected to high inbreeding depression. We found no difference in the shape of the age-specific fecundity curves between snails kept singly and snails kept in pairs (Fig. 2). Thus, selfing *B. perversa* did not retard reproduction by waiting for a mating opportunity. However, selfing in *B. perversa* may be associated

with low levels of inbreeding depression (cf. Wirth et al. 1997).

Few studies have assessed the relative contributions of fitness components to total variation in lifetime reproductive success (Clutton-Brock 1988). In the context of population dynamics and selection acting on lifetime reproductive success it is important to identify the contributions made by different stages of the life span. Lifetime reproductive success is often partitioned into four components: survival to breeding age, reproductive life span, average fecundity per year of the reproductive life span, and offspring survival until reproduction (Brown 1988). One reason for partitioning variation in breeding success in this way is that different ecological and behavioural factors are likely to affect these four components in different ways.

In the present study, we measured reproductive life span and lifetime fecundity (as well as hatchling survival in the offspring generation). The lifetime number of young varied from 2 to 80 among individuals of *B. perversa* kept singly. Individual differences in offspring survival is one of the most important components of variation in reproductive success among breeding females in many birds and mammals (Clutton-Brock 1988). Studies of invertebrates have not yet been able to measure individual differences in offspring survival in natural populations (but see Prout 1965). In the present study, only a few stillborn young were observed and consequently hatchling survival was high (96.1–97.6%).

Lifetime fecundity of *B. perversa* was positively correlated with size at first reproduction only in snails kept in pairs of the offspring generation. In numerous species of oviparous terrestrial gastropods female fecundity (number of egg clutches, clutch size and egg size) is size-related (e.g., in *A. arbustorum* (Baur 1988b, Baur and Raboud 1988) and *Cepaea nemoralis* (Wolda 1963, Oosterhoff 1977)). In ovoviviparous gastropods like *B. perversa* the young hatch in the reproductive tract of the mother. The egg shell is resorbed by the parent or consumed by the embryo. It is possible that in ovoviviparous species the relation between female fecundity and shell size is confounded by the length of the period the young is retained in the reproductive tract (i.e. by environmental factors and the extent of parental care; Baur 1994).

In both groups of snails and in both generations reproductive life span was the best correlate of lifetime fecundity. Positive correlations between fecundity and longevity are common in both sexes of various taxa (e.g., in *Drosophila melanogaster*, Partridge et al. (1986); the dragonfly *Erythemis simplicicollis*, McVey (1988); great tits, *Parus major*, McCleery and Perrins (1988)).

Most interestingly, adult growth rate was negatively correlated with lifetime number of young. This suggests that individuals with a small lifetime fecundity invested some resources into additional shell growth. It is not known whether this type of growth occurs in the field

or whether it is an artifact of the favourable laboratory conditions. In a previous experiment, adult individuals of *B. perversa* kept under different conditions of competition for 450 d started to grow again when the competition pressure was relaxed most probably due to an increased food supply (Baur and Baur 1992).

Differences in reproductive traits between snails from the parent and offspring generation are difficult to explain. Snails from the parent generation were collected as juveniles in the field but otherwise kept under the same conditions as those of the offspring generation. Thus, the only difference was that snails from the parent generation spent approximately 20% of their growth period in the field. It is possible, however, that natural selection (e.g. abiotic factors such as cold) affects newly-hatched *B. perversa* to a different extent on the limestone walls of the Great Alvar. This could partly explain the differences between snails of the two generations observed in the present study.

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