

Inter-population differences in propensity for egg cannibalism in hatchlings of the land snail *Arianta arbustorum*

BRUNO BAUR

Institute of Zoology, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland

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Abstract. Under natural conditions hatchlings of the land snail *Arianta arbustorum* cannibalize unhatched sibling eggs. Newly hatched *A. arbustorum* from different populations (from a lowland forest, a subalpine forest and an alpine pasture in Switzerland) differed significantly in the frequency of cannibalistic attacks on conspecific eggs. The percentage of cannibalistic hatchlings ranged from 50.0% in a subalpine forest to 87.8% in a lowland forest. Two populations were consistent in the proportion of cannibalistic hatchlings over 3 years, while in a third population the proportion of cannibalistic hatchlings varied between years. Hatchlings from populations with a high frequency of cannibals also began to eat eggs at an earlier age. In two populations, the proportion of cannibalistic hatchlings per batch increased over the course of the season, while in a third population the proportion of cannibals per batch was constantly high. Propensity for egg cannibalism was not correlated with absolute egg size, suggesting that the amount of energy and nutrients received during embryonic development did not affect cannibalistic behaviour during the hatchling stage. Differences in the investment in single eggs could explain the inter-population variation in propensity for egg cannibalism in *A. arbustorum*.

The evolution of patterns of behaviour cannot be understood fully without examining critically the nature of individual and geographical variation in natural populations (Arnold 1992). Where different populations are exposed to differential mortality, food availability and recruitment rates, one would expect to find inter-population differences in both behavioural and life-history traits in response to the prevailing local conditions (e.g. Horn & Rubenstein 1984; Stearns 1992).

Sibling cannibalism directly affects the fitness of both the cannibal and the victim (Polis 1981; Elgar & Crespi 1992). Natural selection will favour cannibalistic behaviour if $(\text{cost to victim}) \times r / (\text{benefit to cannibal}) < 1$, where r is the degree of relatedness (Hamilton 1964). 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, usually nutritional, and therefore may be associated with poor environments and/or physiological stress. Hence, inter-population differences in the extent of sibling cannibalism should be associated either with differences in the average degree of relatedness or

with different stress situations at hatching (e.g. differences in the nutritional state of hatchlings, or differences in juvenile mortality). For example, when juvenile mortality rates are high for other reasons, the benefit necessary for cannibalism to be favoured by natural selection can be small (Eickwort 1973).

Hatchlings of various species of herbivorous terrestrial gastropods cannibalize sibling eggs (Baur 1988a, b, 1992a; Elmslie 1988). Emerging *Arianta arbustorum* first eat their own egg shells and then the eggs of unhatched siblings, including those with fully developed embryos (Baur & Baur 1986). In *A. arbustorum*, egg cannibalism occurs exclusively during the hatchling stage, juvenile and adult snails being herbivorous (Baur 1987a). Cannibalistic hatchlings eat only conspecific eggs and do not discriminate between sibling and non-sibling eggs (i.e. eggs from neighbouring batches; Baur 1987b, 1988c, 1993). In previous studies I recorded differences in the propensity to eat sibling eggs among hatchlings from different batches (Baur 1987b). In some batches all hatchlings were cannibalistic, in others none or only a few hatchlings consumed an egg. Thus, the extent of intra-clutch egg cannibalism in a population may depend on the hatchlings' propensity for egg

cannibalism and on the hatching asynchrony of the young within batches, which in turn is influenced by environmental factors (e.g. microhabitat differences in temperature and moisture). Under unfavourable environmental conditions, hatching asynchrony increases and thus provides a few of the hatchlings with the opportunity for egg cannibalism, thereby significantly enhancing their survival chances (Baur 1990a, b, 1992a).

My aims in this study were (1) to examine whether hatchlings of *A. arbustorum* from different populations differ in their propensity for egg cannibalism, (2) to examine whether these possible differences in propensity to eat conspecific eggs were consistent over a period of 3 years, and (3) to test whether differences in cannibalistic behaviour are related to differences in egg and hatchling size (and thus to differences in the nutritional state of hatching snails) both within and between populations.

METHODS

Study Organism

Arianta arbustorum is a simultaneously hermaphroditic land snail, which is common in moist habitats of north-western and central Europe (Kerney & Cameron 1979). The snail has determinate growth; individuals become fully grown and sexually mature at an age of 2–4 years. Adults measure 16–20 mm in shell diameter and reproduce during 3–4 years (maximum 14 years; Baur & Raboud 1988). In the field, snails deposit one to three clutches consisting of 20–50 eggs in each reproductive season. *Arianta arbustorum* mates repeatedly in the course of a reproductive season and stores viable sperm for periods of more than 1 year (Baur 1988d, 1992b). The eggs of a single batch are often fertilized by sperm from two or more individuals (unpublished data). In the Swiss Alps, the snails show a profound altitudinal variation in life-history traits (Baur 1984, 1990c; Baur & Raboud 1988). Adult size, number of egg batches produced, clutch size, egg size and reproductive investment per year decrease with increasing altitude, while age at maturity and reproductive investment per egg increase.

General Methods

Eggs and newly hatched snails for the tests were obtained from adult *A. arbustorum* which had

been collected at four sites (for convenience referred to as populations) in Switzerland: (1) Aesch is a grass-covered clearing in a coniferous forest 10 km south of Basel (47°28'N, 7°34'E; 360 m above sea level); (2) Amden in the eastern Swiss Alps is a belt of nettle, *Urtica dioica* L., along a scree band in an alpine pasture (47°10'N, 9°11'E; 1430 m), 125 km south-east of Aesch; (3) Gurnigel A is an embankment of a track in a small pine wood 20 km south of Bern (46°44'N, 7°27'E; 1440 m), approximately 80 km south of Aesch and 140 km west of Amden; and (4) Gurnigel B is a track embankment in a subalpine pine forest 1 km east of Gurnigel A at an altitude of 1430 m.

In 1989–1991, adult snails were collected at each site as soon as the snow had melted. Owing to clear cutting at Gurnigel A, I could collect snails from there only in 1989. In 1990 and 1991 I used animals from Gurnigel B. Snails from Gurnigel A and B are completely isolated by distance and unsuitable habitat and thus belong to separate populations.

The snails were transported to Basel, where they were kept in transparent plastic containers (measuring 14 × 10 × 5 cm) lined with moist soil at 19°C and on a light:dark cycle of 18:6 h. They were fed fresh lettuce ad libitum. Containers were checked for eggs weekly during the snails' reproductive period, deposited eggs being collected and counted. Approximately half of the eggs of each batch were incubated at 19°C in petri dishes lined with damp paper towelling. Newly hatched snails were removed from the remaining eggs and tested for their cannibalistic propensity (see below). The remaining eggs were offered as food in tests.

I determined the size of the nearly spherical eggs by measuring the diameter of 20 randomly chosen eggs from several batches to the nearest 0.04 mm using a binocular microscope with a stage micrometer. Egg volume was calculated using the formula of a sphere: egg volume = $(\pi/6) \times (\text{egg diameter})^3$. To relate egg size to the size of the mother, I also measured the size (shell breadth and height) of the mother to the nearest 0.1 mm using vernier calipers and calculated the shell volume using the following formula: shell volume = $0.312 \times (\text{breadth})^2 \times (\text{height}) - 0.038$ (all measurements in mm; unpublished data). Shell volume is a more reliable measurement of snail size than weight, because weight depends on the state of hydration and, thus, is highly variable in terrestrial gastropods.

Table I. Duration of test periods and number of batches and hatchlings tested for each population and year

Population	Year	Test period (length in days)	Number of batches tested	Number of hatchlings tested
Aesch	1989	9 June–17 September (100)	20	150
	1990	23 May–6 August (75)	16	124
	1991	7 May–28 August (113)	69	458
Amden	1989	23 June–17 September (86)	13	75
	1990	6 May–15 August (101)	38	443
	1991	24 May–23 August (91)	77	450
Gurnigel A	1989	6 June–22 September (108)	80	514
Gurnigel B	1990	25 May–9 June (15)	30	237
	1991	21 June–27 August (67)	75	514

Test period refers to the time interval in which tests were conducted.

To examine whether within-batch differences in propensity for egg cannibalism are associated with hatchling size, the shell diameter of 20 newly hatched snails was measured to the nearest 0.04 mm in each of five batches from the Amden population using a binocular microscope with a stage micrometer before the individuals were tested (see below).

Test Procedure

Newly hatched snails (younger than 1 day) with no prior feeding experience were placed in the centre of a 65-mm-diameter petri dish lined with moist soil. Six conspecific eggs were arranged at equal distances in a circle of 2 cm radius from the test animal. Tests were run at room temperature (20–23°C) and under natural light conditions. Each dish was checked twice per day for wholly or partially eaten eggs. When a developing embryo became visible through the egg shell of a 'food egg', it was replaced by a newly laid egg to avoid hatching during the test period. Tests were terminated as soon as the hatchlings started to eat their first egg and the time was recorded. Trials lasted up to 4 days, and each hatchling was tested only once. Hatchlings that started to eat an egg within 4 days were considered as cannibalistic and those that did not as non-cannibalistic. Testing was restricted to 4 days because older snails rarely eat eggs (Baur 1987a). If available, eight hatchlings were tested from each batch. With a few exceptions, only one batch per mother snail was used. Table I gives the periods during which

the tests were conducted for each population and year, and the number of hatchlings tested. In all, 2965 hatchlings from 418 batches were tested during the 3 years.

I measured the propensity for egg cannibalism in two ways. First, I assessed for each batch the proportion of hatchlings that consumed a conspecific egg in individual tests. Second, I recorded the time elapsed until a single hatchling began to eat an egg in the test. Consequently, broods can be characterized by the proportion of cannibalistic hatchlings and the average time elapsed until hatchlings began to eat eggs (latency of egg cannibalism).

Data Analysis

Between-year variation in frequency of cannibalistic hatchlings was examined using the chi-squared test of independence. Chi-squared tests were used to compare the observed proportions of cannibalistic hatchlings in single batches with binomial distributions based on population mean values. Expected frequencies were calculated for each population using the proportions of all batches from which eight hatchlings were tested. Some classes were pooled in order to avoid small expected frequencies in the calculations of χ^2 . Correlation analysis was used to examine whether the propensity for egg cannibalism changes over the course of the reproductive season. In the latter analysis the frequency data were transformed (arcsine square-root) to meet the parametric assumptions of normality (Sokal & Rohlf 1981).

Table II. Percentage of cannibalistic hatchlings for each population and year

Population	Percentage of cannibalistic hatchlings			χ^2	df	P
	1989	1990	1991			
Aesch	89.3	87.1	86.9	0.62	2	0.75
Amden	61.3	69.8	80.9	21.62	2	<0.001
Gurnigel A	50.0	—	—	—	—	—
Gurnigel B	—	85.7	87.7	0.63	1	0.45

The number of hatchlings and batches tested is given in Table I. Between-year variation was evaluated using a chi-squared test of independence.

RESULTS

Frequency of Cannibalistic Hatchlings

The populations differed significantly in percentage of cannibalistic hatchlings ($\chi^2=299.43$, $df=3$, $P<0.001$; Table II). On average 87.8% of hatchlings from the Aesch population were cannibalistic. Corresponding figures for Gurnigel A were 86.7%, for Amden 70.7% and for Gurnigel B 50.0% (Table II). The Aesch and Gurnigel B populations were consistent in the percentage of cannibalistic hatchlings between years (Table II). In Amden, the frequencies of cannibalistic hatchlings did not differ between 1989 and 1990 ($\chi^2=2.11$, $df=1$, $P>0.15$), while in 1991 significantly more hatchlings were cannibalistic than in the preceding years (Table II).

Variation in Latency of Egg Cannibalism

The populations also differed significantly in the distribution of time until cannibalistic hatchlings started to eat an egg (combined data of 3 years: contingency test, $\chi^2=40.41$, $df=9$, $P<0.001$; Fig. 1). Hatchlings from the Aesch population initiated egg cannibalism most rapidly: $52.3 \pm 7.4\%$ ($\bar{X} \pm SD$ of 3 years) of the cannibals began to consume an egg in the first day of the test (Fig. 1). Corresponding figures for cannibalistic hatchlings from Gurnigel B were $48.5 \pm 9.3\%$, for Amden $44.5 \pm 11.0\%$, and for Gurnigel A 35.8% (Fig. 1). The percentage of hatchlings that initiated egg cannibalism in the first day of the test was positively correlated with the percentage of cannibalistic hatchlings in a population ($r=0.98$, $N=4$, $P=0.02$). Thus, populations with a high proportion of cannibalistic hatchlings consisted of snails that rapidly began to eat an egg.

Distribution of Cannibalistic Hatchlings within Batches

If the probability of eating an egg were constant throughout the tests and the same for all egg batches (=mother snails) in a population, then the number of cannibalistic hatchlings in a batch should be binomially distributed. To compare the observed proportion of cannibalistic hatchlings in a batch with a binomial distribution I used only batches from which eight hatchlings were tested (thus the probability of eating an egg in a population can slightly differ from that presented in Table II).

The results are summarized in Fig. 2. In the Aesch and Gurnigel B populations data from 3 and 2 years were pooled because the average proportion of cannibalistic hatchlings did not differ between years (Table II). In the Amden population data from 1990 look very similar to those from 1991 and thus are not shown.

In the Aesch, Gurnigel A and Gurnigel B populations, the distributions of the proportion of cannibalistic hatchlings of single batches deviated significantly from binomial distributions (Aesch 1989–1991: $\chi^2=25.72$, $df=2$, $P<0.001$; Gurnigel A 1989: $\chi^2=15.67$, $df=3$, $P<0.01$; Gurnigel B 1990–1991: $\chi^2=21.51$, $df=2$, $P<0.001$). There were more batches with either a few or eight cannibalistic hatchlings than expected. Similarly, snails from the Amden population showed an excess of batches with none, a few or eight cannibalistic hatchlings. In the Amden population, however, the distributions of the proportion of cannibalistic hatchlings within batches did not differ significantly from binomial distributions (1989: too small sample size for data analysis; 1990: $\chi^2=5.00$, $df=3$, $P>0.1$; 1991: $\chi^2=4.56$, $df=3$, $P>0.2$). The finding that offspring from a single snail tend to be

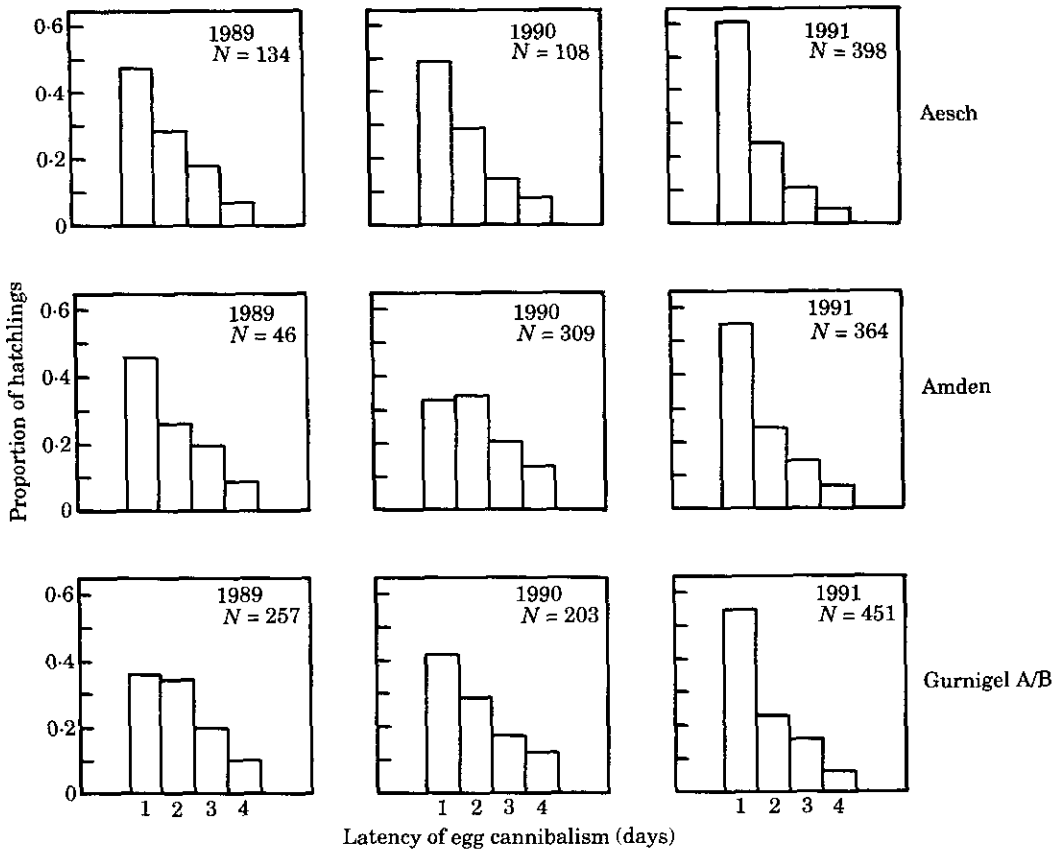


Figure 1. Distributions of latency of egg cannibalism in *A. arbustorum* from different populations. *N* indicates the number of cannibalistic hatchlings for each population and year. The number of snails tested is given in Table I.

more or less prone to eat conspecific eggs than the average of the population suggests either a genetic component in the determination of egg cannibalism in *A. arbustorum*, or a variable probability of eating an egg (e.g. a seasonal change).

Seasonal Variation in Cannibalistic Propensity

In the Gurnigel A and B populations (in all years) and the Amden population (only in 1989 and 1990), the proportion of cannibalistic snails per batch was positively correlated with the time of the year (Table III). In these populations the propensity for cannibalism was higher towards the end of the reproductive season than at the beginning. No similar tendency was found in hatchlings from the Aesch population in any year (Table III). In contrast to the increased

proportion of cannibalistic snails, the hatchlings did not start to eat conspecific eggs earlier towards the end of the reproductive season than at the beginning (correlation analysis, in all populations and years, $P > 0.1$).

Effects of Clutch Size, Egg and Hatchling Size

Table IV gives data on the shell size of fully grown snails, clutch size, and absolute and relative egg size (egg volume/shell volume of mother) for each population. Snails from any one population did not differ in shell breadth, clutch size and egg diameter between years (one-way ANOVA or *t*-test; in all cases $P > 0.1$). Snails from the Aesch population produced batches that contained 2.4 times more eggs than those from the Gurnigel A and B populations; they also produced the largest

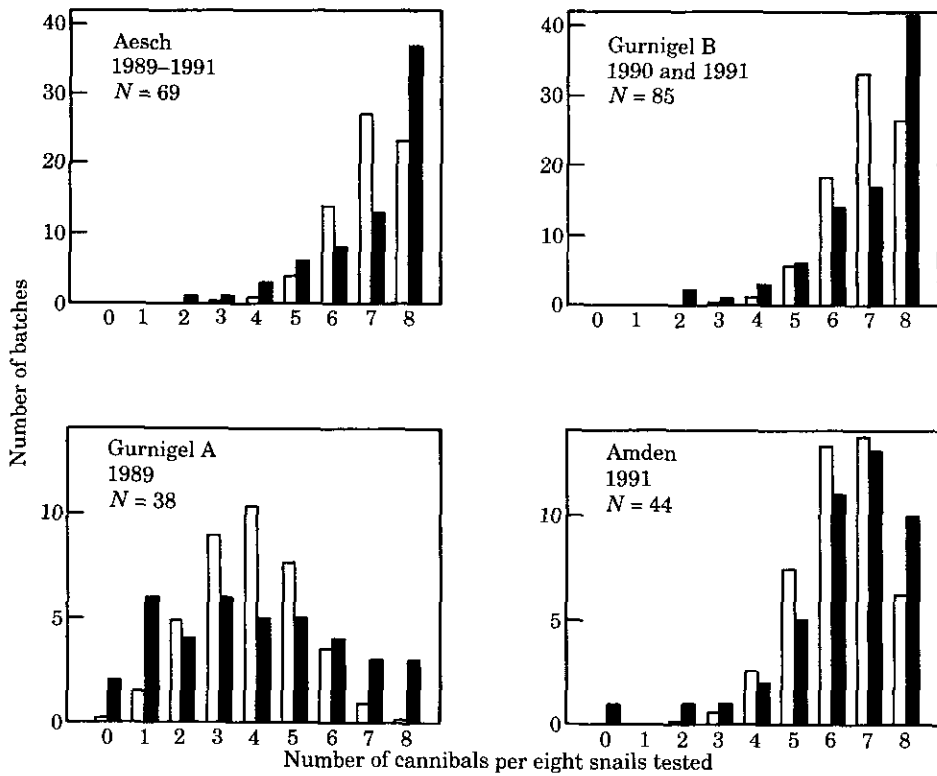


Figure 2. Observed numbers of cannibalistic hatchlings in individual batches of *A. arbustorum* (■) compared with those expected if the probability of eating an egg is the same for all batches in a population (binomial distribution; □). *N* indicates the number of batches, from each of which eight hatchlings were tested.

Table III. Correlation coefficients of the proportion of cannibalistic hatchlings per batch with the time of the year (1 January=day 1)

Population	Year		
	1989	1990	1991
Aesch	0.60 (7) <i>P</i> =0.151	0.32 (15) <i>P</i> =0.250	0.05 (47) <i>P</i> =0.717
Amden	0.91 (6) <i>P</i> =0.011	0.72 (32) <i>P</i> =0.001	0.22 (44) <i>P</i> =0.156
Gurnigel A	0.61 (38) <i>P</i> =0.001	—	—
Gurnigel B	—	0.60 (29) <i>P</i> =0.001	0.41 (56) <i>P</i> =0.002

The number of batches from which eight hatchlings were tested is given in parentheses.

eggs. When egg size is controlled for differences in mother size, however, snails from both Gurnigel populations and the Amden population laid relatively larger eggs than those from the Aesch

population (Table IV). These results confirm previous studies on the altitudinal variation of reproductive traits in *A. arbustorum* (Baur & Raboud 1988; Baur 1990c).

Table IV. Shell size of fully grown individuals, clutch size and egg size in *A. arbustorum* from four populations

Population	Shell breadth (mm)		Clutch size		Egg diameter (mm)		Relative egg size ($\times 10^3$)	
	$\bar{X} \pm \text{SD}$	(N)	$\bar{X} \pm \text{SD}$	(N)	$\bar{X} \pm \text{SD}$	(N)	$\bar{X} \pm \text{SD}$	(N)
Aesch	21.1 \pm 1.1	(138)	71.9 \pm 27.7	(140)	3.11 \pm 0.16	(61)	7.10 \pm 1.35	(61)
Amden	18.5 \pm 0.9	(108)	39.4 \pm 19.0	(171)	2.94 \pm 0.13	(14)	8.15 \pm 1.62	(14)
Gurnigel A	17.5 \pm 0.6	(128)	28.8 \pm 11.6	(141)	2.91 \pm 0.18	(125)	9.67 \pm 2.05	(117)
Gurnigel B	17.5 \pm 0.8	(102)	28.2 \pm 12.5	(98)	2.94 \pm 0.19	(40)	9.83 \pm 1.29	(40)

Relative egg size refers to egg volume/shell volume of the mother.

No association between clutch size, absolute or relative egg size and frequency of cannibalistic hatchlings is evident. Within populations, the proportion of cannibalistic hatchlings per batch was not correlated with either egg size (absolute and relative) or clutch size (in all populations, $P > 0.1$).

Within-batch differences in cannibalistic propensity were not associated with differences in hatchling size. Hatchling size and cannibalistic propensity were determined in each of 20 individuals from five batches of the Amden population. Shell breadth of cannibalistic hatchlings averaged 2.61 ± 0.16 mm ($\bar{X} \pm \text{SD}$; $N=75$), that of non-cannibalistic hatchlings 2.56 ± 0.13 mm ($N=25$). In neither batch did cannibalistic and non-cannibalistic snails differ in shell size when they emerged from their own egg (t -test, in four batches: $P > 0.3$, in one batch $P = 0.084$). Furthermore, in neither batch was hatching size of individuals that became cannibalistic correlated with the time until they began to eat an egg (Spearman rank correlation, in four batches: $P > 0.2$, in one batch $P = 0.095$).

DISCUSSION

Differences in propensity for cannibalism have been reported among laboratory strains in mice, *Mus musculus*, and flour beetles, *Tribolium confusum* (Polis 1981; Stevens 1992). The present study is one of the first to provide evidence for differences in the propensity for sibling cannibalism in natural populations. Studies of intraspecific geographical variation may provide insight into the evolution of cannibalistic behaviour. I suggest three (not mutually exclusive) hypotheses to explain inter-population differences in the propensity for egg cannibalism in hatchlings of *A. arbustorum*: they may evolve in response to

inter-population differences in (1) the average degree of relatedness, (2) the nutritional state of hatching snails, and/or (3) the maternal investment in single eggs.

Relatedness is a key variable in the evolution of sibling cannibalism. Hamilton's (1964) theory predicts that the extent of cannibalism should decrease through kin selection as a function of the relatedness between cannibal and victim. In an earlier study, I estimated that when cannibalism is directed towards full-siblings, an increase in survivorship from egg to maturity from 0.69 to 1.04% will be enough to favour its evolution (Baur 1987b). If half-siblings are the victims, an increase in survivorship to just over 0.86% is sufficient (cannibalistic *A. arbustorum* do not discriminate between eggs of different degrees of relatedness: Baur 1987b). Owing to multiple mating and sperm storage, the eggs of a batch are fertilized by sperm from two or more individuals (unpublished data) and consequently within-batch egg cannibalism in *A. arbustorum* may more often affect half-siblings than full-siblings.

In the flour beetle, the rate of cannibalism in larvae was significantly lower if they were fed related rather than unrelated eggs after only three generations in a controlled laboratory experiment (Wade 1980). Similarly, one might expect that the propensity for egg cannibalism is lower in very small and thus highly inbred populations of *A. arbustorum* than in large populations.

No data on the average degree of relatedness are available for the different snail populations. Detailed experiments are needed to examine whether relatedness can affect the propensity for egg cannibalism in *A. arbustorum*. Furthermore, the genetic component of this behaviour should be assessed. Experimental evidence from several studies indicates that there is a strong genetic component to cannibalism in many species:

breeding strains with different cannibalistic tendencies have been observed in rotifers (Gilbert 1980), flour beetles (Stevens 1992) and rodents (Polis 1981; Elwood 1992).

Differences in the propensity for egg cannibalism could reflect differences in the nutritional state of hatching snails (Fox 1975; Polis 1981). In *A. arbustorum*, the within-batch variation in energy and nutrient content of eggs is significantly smaller than that of egg size (A. Baur, unpublished data). Size at hatching, on the other hand, is positively correlated with egg size (Birchler 1992). Thus, the size of an emerging snail may indicate its nutritional state; however, size at hatching appeared to have no influence on whether or not an individual became cannibalistic. Furthermore, size at hatching did not affect the time until cannibalistic individuals began to eat an egg. Within populations, the proportion of cannibalistic hatchlings per batch did not depend on the mean egg size of that batch. The frequency of cannibalistic hatchlings in different populations was not associated with the mean egg size of the populations. These different lines of evidence suggest that the hatchlings' propensity for egg cannibalism is not affected by egg size or by hatching size.

Snails from the Aesch population produced the largest eggs. In relation to the mother's size, however, a single egg represented a smaller investment compared with eggs from snails of the Amden, Gurnigel A and B populations (absolute egg size may be limited by morphological and physiological constraints on the mother or by prolonged embryonic development). Alexander (1974) 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. In *A. arbustorum* and several other species of terrestrial gastropods, egg cannibalism can be considered as a kind of facultative food provision that becomes most important in stress situations. In this way some of the offspring may have a chance to survive even under severe conditions. This (facultative) food provision might occur most frequently in broods of the Aesch population, whose snails produce

significantly more eggs than those in Amden and Gurnigel A and B. As an adaptation to the relatively small investment in a single egg, a pronounced propensity for egg cannibalism may have evolved in hatchlings of the Aesch population. This could be a response to other predators causing a high juvenile mortality rate. In lowland populations, juvenile *A. arbustorum* are exposed to more potential predators (e.g. shrews, toads and ground beetles) than juveniles living in sub-alpine habitats. This suggests a strong selection for rapid juvenile growth in lowland populations, which could be achieved by an increased food provision.

Maternal provision of nurse eggs of different types to hatchlings may be more widespread than is currently realized (in amphibians: Crump 1992; in social insects: Crespi 1992; Kukuk 1992). Numerous species of marine prosobranch snails normally produce nurse eggs, which serve as the first food for the offspring (Fioroni 1966, 1988; Smith et al. 1989). In some other species the larvae additionally consume siblings (Hoagland 1986; Fioroni 1988).

Juvenile mortality in *A. arbustorum* is size-dependent, being highest in the smallest individuals. Andreassen (1981) found a survivorship from egg to maturity of 0.69% in a natural population of *A. arbustorum* near Bergen, Norway. Experimental evidence indicates that cannibalistic *A. arbustorum* have a significantly higher survivorship than non-cannibalistic individuals (Baur 1990a). Furthermore, cannibalistic hatchlings tend to complete shell growth more rapidly than non-cannibalistic ones, which may lead to a greater seasonal and lifetime reproductive output in cannibalistic snails.

Intraspecific variation in cannibalistic behaviour could be influenced by proximate factors, such as the consumption of a particular diet during the juvenile stage (e.g. in anuran tadpoles: Pfenning 1992; Pfenning et al. 1993). Two lines of evidence suggest that this is not the case in hatchlings of *A. arbustorum*. First, in the present study the mother snails as well as their eggs were kept under identical conditions, but the emerging hatchlings differed in their propensity for cannibalism. Second, siblings fed either a cannibalistic or a vegetarian (lettuce) diet did not differ in their food preference in choice tests; both ate lettuce when they were older than 8 days (Baur 1987a).

Shell size at first hibernation is of critical importance in land snails, because winter mortality acts most strongly on the smallest individuals (Oosterhoff 1977; Baur & Baur 1991). Assuming equal hatchling size, snails hatched early in the breeding season may have higher prospects of survival than those hatched later in the season, because the former have more time for growth (Wolda 1963; Wolda & Kreulen 1973). It follows that egg cannibalism is most beneficial later in the season. In fact, in two populations of *A. arbustorum* the proportion of cannibalistic hatchlings per batch increased in the course of the season. The mechanism for this increase in cannibalistic propensity is unknown, because I kept all the mother snails and eggs during incubation under constant environmental conditions.

To sum up, the present study provides evidence for inter-population variation in propensity for egg cannibalism in hatchlings of *A. arbustorum*. Differences in the hatchlings' propensity to eat sibling eggs depended neither on egg nor on hatchling size. Different degrees of relatedness and/or different investments in single eggs could explain the evolution of differences in propensity for egg cannibalism among populations. However, these hypotheses need experimental evaluation.

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