Anim. Behav., 1992, **43**, 511–518

Random mating by size in the simultaneously hermaphroditic land snail *Arianta arbustorum*: experiments and an explanation

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*(Received 7 March 1991; initial acceptance 4 April 1991;
final acceptance 23 August 1991; MS. number: 3737)*

Abstract. It has been proposed that size-assortative mating should occur in simultaneous hermaphrodites with reciprocal fertilization and size-related fecundity because all individuals invest substantially in mating. Mating patterns were recorded in two species of simultaneously hermaphroditic land snails. In a natural population of *Helix pomatia*, snails showed a slight (but non-significant) tendency towards size-assortative mating, whereas mating in a population of *Arianta arbustorum* was random with respect to size. Laboratory experiments were conducted to test (1) whether individuals of *A. arbustorum* discriminate between mating partners of different size, and (2) whether a large shell might be of advantage during courtship to increase mating success. In mate-choice tests with individuals of different shell size, pairs formed randomly with respect to size. Courtship was neither hindered nor prolonged in pairs with large size differences. In the second experiment, a large snail was placed close to two courting conspecifics (both smaller). The larger snail interfered with the courting snails, but in general did not displace one of them. Courtship progressed to copulation only if one of the three snails ceased to court; this was independent of the size of that individual. Thus, a large shell did not increase mating success. It is suggested that time-constraints of locomotory activity and high costs of searching for a mate can explain the prevalence of random mating patterns in simultaneously hermaphroditic land snails.

Size-assortative mating is a common mating pattern in natural populations of many invertebrate and vertebrate species (e.g. Bateson 1983; Ridley 1983; Crespi 1989). Among molluscs, size-assortative mating has been observed in marine gastropods (Crozier 1918; Edwards 1968). In simultaneously hermaphroditic terrestrial gastropods, however, mating has been reported to be random with respect to shell size (*Cepaea nemoralis*: Wolda 1963), shell colour and banding pattern (*C. nemoralis*: Schilder 1950; Schnetter 1950; Lamotte 1951; Wolda 1963), as well as between resident and introduced individuals (*Helix pomatia*: Woyciechowski & Lomnicki 1977). An exception is *Partula suturalis*, in which assortative mating with respect to dextral and sinistral shell coiling has been observed in the wild (copulation is hindered but not prohibited by opposite coil in this species; Clarke & Murray 1969; Johnson 1982). Hermaphroditic land snails would greatly enhance their reproductive success by choosing large mates since female fecundity (number of clutches, clutch size and egg size) is positively correlated with shell size (Wolda 1963; Baur 1988a; Baur & Raboud 1988).

Ridley (1983) proposed that three conditions are necessary and sufficient for the development of size-assortative mating in natural populations. These factors are (1) a correlation between male size and success in competition for mates (intrasexual selection), (2) a correlation between female size and fecundity, and (3) prolonged pairing. Ridley (1983) suggested that size-assortative mating should also occur in simultaneous hermaphrodites with reciprocal fertilization and size-related female fecundity. He argued that all individuals invest substantially (all their eggs) in mating, so there will be selection for careful mate choice. Specifically, a land snail should choose a mate as large as possible.

In another approach, Parker (1983) proposed a model for indiscriminate mate choice (random mating). This should occur when there is little variance in mate quality in both sexes, and/or when search costs for mates are high (e.g. low encounter rates due to low population densities or low mobility).

Here I present data on mating patterns in natural populations of two species of hermaphroditic land

0003–3472/92/030511+08 $03.00/0

snails. I also present experiments designed to test whether courting individuals of the land snail *Arianta arbustorum* discriminate between potential mates of different size and whether large individuals have any way of increasing mating success during courtship. Based on field observations and experimental results, I propose a hypothesis to explain the absence of size-assortative mating in simultaneously hermaphroditic land snails.

STUDY ANIMALS

Arianta arbustorum is a simultaneously hermaphroditic, self-incompatible helicid land snail, which is common in moist habitats of northwestern and central Europe. Individuals become sexually mature at an age of 2–4 years. Adult snails live on average 3–4 years (maximum 14 years; Baur & Raboud 1988). In the field, snails deposit one to three clutches each consisting of 20–50 eggs in each reproductive season (Baur & Raboud 1988; Baur 1990).

Mating behaviour in *A. arbustorum* includes introductory behaviour (foreplay) with reciprocal tactile and oral contacts, and curving turns to reach an optimal position with respect to the genital opening of the partner (Hofmann 1923; B. Baur, unpublished data). This is followed by dart shooting, the pushing of a calcareous dart into the mating partner's body, which is assumed to facilitate mating by increasing behavioural synchrony (Adamo & Chase 1988). Finally, the copulation is reciprocal; spermatophores are transferred after simultaneous intromission. *Arianta arbustorum* mates repeatedly in the course of a reproductive season and viable sperm can be stored for more than a year (Baur 1988b).

Helix pomatia, also a simultaneously reciprocal hermaphrodite, has elaborate mating behaviour (for detailed descriptions see Meisenheimer 1907; Lind 1976). Mating is followed by an obligatory post-copulatory pause which lasts up to 8 h and is essential for the internal transport of the spermatophore (Lind 1973, 1976). In the field, mating can last up to 36 h (Tischler 1973; Lind 1988). Periods of mating activity alternate with periods without mating activity. In the latter phase a snail will not mate even in the company of a sexually active snail (Jeppesen 1976). Individuals mate two to six times per year, and viable sperm are stored for up to 4 years (Tischler 1973; Duncan 1975; Lind 1988).

MATING PATTERNS IN NATURAL POPULATIONS

Observations on mating *A. arbustorum* were made in a natural population in a subalpine forest near Gurnigel, 30 km south of Bern, Switzerland (46°44′N, 7°27′E; altitude 1430 m above sea level). Snails were abundant on the embankment of a track (population size approximately 300 sexually mature individuals). On 3 May 1990, snails were creeping in patches free of snow. Thirty-five mating pairs were found between 1200 and 1400 hours. I measured the size (shell breadth and height) of mating and non-mating snails to the nearest 0·1 mm using a vernier caliper and calculated shell volume following Rensch (1932): shell volume = $(\text{breadth})^2 \times (\text{height}/2)$. 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.

Mating patterns are usually quantified by the product–moment correlation coefficient (r) for the sizes of mating pairs (Ridley 1983). In simultaneously hermaphroditic animals r can be distorted by the way the animals' sizes are assigned to the axes. To overcome this problem, I used a randomizing method to assign the larger or smaller individual of a mating pair first to the X-axis, the other to the Y-axis. Having calculated the correlation coefficient r, the individuals of each mating pair were again randomly assigned to the axes. This procedure was repeated 100 times and r is presented as the mean value of 100 runs. Correlations are presented for shell volume; body size expressed by linear dimensions (shell breadth and height) yielded lower r-values throughout. Deviations from random mating ($r=0$) were tested using a two-sided t-test (Sokal & Rohlf 1981).

Mating and non-mating snails did not differ in size ($\bar{X} \pm \text{SD}$; shell volume of mating snails: $2{\cdot}28 \pm 0{\cdot}31$ cm^3, $N=70$; non-mating snails: $2{\cdot}30 \pm 0{\cdot}33$ cm^3, $N=188$; $t=0{\cdot}397$, $P>0{\cdot}7$). Mating *A. arbustorum* varied in shell volume from 1·65 to 2·96 cm^3, but pairs were formed randomly with respect to size ($r=0{\cdot}245$, $N=35$, $P=0{\cdot}16$; range of r in the 100 runs: 0·228–0·305). None of the 100 randomized runs revealed any significant correlation coefficient (for $df=33$ the critical value of r is 0·334 at the 5% level).

Observations on mating *H. pomatia* were made in a natural population near Uppsala, central

Sweden (59°50′N, 17°40′E) in the late afternoon of 10 June 1988. This population lives on the northern periphery of the species distribution (*H. pomatia* was originally brought to Sweden during medieval times; Kerney & Cameron 1979). The snails were abundant (700–1000 sexually mature individuals) in a clearing of a pine-dominated forest. The temperature was 18°C and the vegetation was drying up after a rain shower the previous night. Many snails were active, most of them grazing. Approximately 20% of the active snails were courting or copulating. The sizes of mating and non-mating snails were measured and examined for deviation from random mating as described above.

Mating *H. pomatia* did not differ in shell volume from non-mating individuals ($\bar{X} \pm$ SD; mating snails: $33{\cdot}7 \pm 3{\cdot}6$ cm^3, $N = 166$; non-mating snails: $33{\cdot}7 \pm 4{\cdot}3$ cm^3, $N = 51$; $t = 0{\cdot}036$, $P > 0{\cdot}9$). Variation in size of mating *H. pomatia* represented a two-fold range of shell volume (24·3–43·3 cm^3). The correlation coefficient for the sizes of the 83 mating pairs was 0·190 ($P = 0{\cdot}09$; range of r in the 100 runs: 0·185–0·240). Two of the 100 randomized runs revealed a correlation coefficient larger than the critical value (0·217) at the 5% level. Thus, there was a weak tendency for size-assortative mating in this population of *H. pomatia.*

The following day was warm, the vegetation dry and no snail was active, except that many pairs were still in copulation (snail activity is determined by particular combinations of environmental conditions such as water availability, temperature and time of day: Bailey 1975, 1989a, b; Prior 1985; Ford & Cook 1987). Thus, mating exceeded the period favourable for activity, and exposed copulating pairs to severe water loss.

GENERAL METHODS

Sexually mature individuals (indicated by a reflected lip at the shell aperture) of *A. arbustorum* were collected from the Gurnigel population (see above) on 3 May 1990. Snails were marked individually on their shells with numbers written with a waterproof felt-tipped pen on a spot of correction fluid (Tipp-Ex). The animals showed no visible reaction to the marking procedure. Individuals were kept isolated in plastic beakers (6·5 cm diameter) lined with moist soil. Lettuce was available ad libitum. The snails were kept outdoors in a shaded place (natural temperature and photoperiod) for at least 2 weeks before being used in the tests. Based on their shell size (measured as described above), the individuals were divided into three groups: small snails (shell volume 1·60–2·10 cm^3, $N = 61$); medium-sized snails (2·11–2·45 cm^3, $N = 62$) and large snails (2·46–3·50 cm^3, $N = 65$). Hereafter these groups are referred to as small, medium and large snails. Half of the snails of each group were used in the size-discrimination experiment, the other half in the size-advantage experiment (see below).

SIZE-DISCRIMINATION EXPERIMENT

This experiment was designed to test whether individuals of *A. arbustorum* discriminate between mating partners of different size.

Methods

Three active snails (individuals with an extended soft body and everted tentacles), one from each size group, were placed in a test arena (transparent plastic container measuring 14 × 10 × 7 cm). The bottom of the test arena was covered with moist paper towelling to maintain snail activity. Snails were chosen randomly except that the size differences were at least 25% between members of the different groups. Tests ($N = 40$) were initiated in the evening and run during the night in May and June 1990. This period is the time of maximum mating activity in natural snail populations (Cain & Currey 1968; Wolda & Kreulen 1973). Furthermore, the snails are most active at dusk and in the first half of the night (Cameron 1970; Bailey 1975). Test boxes were kept outdoors to expose test animals to natural temperature and light conditions.

I observed the snails' behaviour at intervals of 15 min (at night using a torch). Records included time until initiation of courtship (courtship latency), courtship duration (time interval from courtship initiation to copulation) and the type of pair formation (small–medium, small–large and medium–large). The initiation of courtship was defined as the first simultaneous oral contact (which was usually accompanied by a slight eversion of the penial lobe in one of the snails). The beginning of copulation was defined as the first simultaneous intromission. Observation sessions were terminated either when two snails mated or

Table I. Pair formation and time until copulation in mate-choice tests with *A. arbustorum* of different shell size

Pair formation	Expected under random mating	Observed (N)	Time until copulation (h)	
			Mean ± SD	Range
Small–medium	8	10	9·3 ± 4·3	2·5–15·5
Small–large	8	7	10·2 ± 3·6	5·6–14·2
Medium–large	8	7	12·0 ± 2·6	8·1–15·2

after 8 h if no snail initiated courtship behaviour. Snails involved in matings were excluded from further tests. Snails that did not initiate courtship behaviour were tested again 10–14 days later in a new set of animals.

Results

Snails mated in 24 out of 40 trials. Pairs of different size composition were formed in frequencies expected under random mating (Table I; $\chi^2 = 0{\cdot}75$, $df = 2$, $P > 0{\cdot}7$). Courtship duration ranged from 2·5 to 15·5 h but did not differ between pairs of different size composition (Table I; Kruskal–Wallis test, $P > 0{\cdot}7$). This indicates that snails do not discriminate between partners of different size and that courtship is neither hindered nor prolonged in pairs with large size differences.

The latter finding is supported by the results of another experiment, in which mate choice in trios of *A. arbustorum* of equal shell size as well as in trios of snails of different size was examined (the experimental procedure was as described above, except that the tests were run at 22°C and during the day). Time until copulation did not differ between the groups ($\bar{X} \pm$ SD; snails of equal size: 7·1 ± 1·3 h), $N = 4$ pairs; snails of different size: 7·9 ± 2·9 h, $N = 8$; Mann–Whitney U-test, $P > 0{\cdot}3$).

SIZE-ADVANTAGE EXPERIMENT

This experiment examined whether a large shell size provides any kind of (fighting) advantage in groups of courting *A. arbustorum* to increase mating success.

Methods

Twelve snails (four from each size group) were placed together in a plastic container measuring 19 × 14 × 9 cm with a damp towel substrate. Snails that began to court (as indicated by a slight eversion of the penial lobe) were noted and pairs consisting of a small and a medium-sized individual were transferred to a test arena (transparent plastic container measuring 14 × 10 × 7 cm and lined with moist paper towelling). In the test arena they were allowed to court for 15 min before a large snail, also stimulated for courtship, was placed close to the pair. I recorded the snails' behaviour as described in the first experiment. Trials were terminated when two snails mated or when all three snails ceased to court. Snails involved in matings were excluded from further tests. Snails that did not mate were tested again as described above. Tests were carried out simultaneously with those of the first experiment.

A large individual should dislodge one of the smaller snails if it has any kind of fighting advantage during courtship. Hence, one would expect large snails to be engaged in all matings.

Results

In 16 out of 30 trials (53·3%) no mating occurred. In these trials the snails courted for between 8·7 and 19·9 h ($\bar{X} \pm$ SD = 13·8 ± 3·3 h) but failed to copulate. A copulation occurred only if one of the snails ceased to court; this was independent of the size of that individual. Courtship progressed to copulation in 14 trials (Table II). A large snail displaced a smaller individual in 8 of the 14 cases. Thus, mating pairs were formed randomly with respect to shell size (Table II, $\chi^2 = 1{\cdot}00$, $df = 2$, $P > 0{\cdot}5$). Courtship duration ranged from 2·0 to 14·4 h, but did not differ between pairs of different size composition (Table II; Kruskal–Wallis test, $P > 0{\cdot}3$). This suggests that courting tenacity rather than shell size may be important for mating success in *A. arbustorum*.

Table II. Mate displacement by large individuals of *A. arbustorum* in courting groups of three snails of different size

Pair formation	Displacement by a large snail	(N)	Courtship duration (h)	
			Mean ± SD	Range
Small–medium	No	6	6·3 ± 3·6	2·0–10·7
Small–large	Yes	5	8·7 ± 5·3	2·5–14·4
Medium–large	Yes	3	9·8 ± 4·3	4·9–12·9

DISCUSSION

Understanding the underlying causes of mating patterns is necessary to assess their relation to sexual and natural selection. Mating patterns can vary from random to assortative mating between populations of the same species (cf. Lewontin et al. 1968). Mating patterns may be influenced by social and environmental variables such as sex ratio, population density and length of periods favourable for activity, which in turn may vary widely among populations.

In one of the natural snail populations a slight (but non-significant) tendency for size-assortative mating was recorded, in the other population mating was random with respect to size. According to Ridley (1983), size-assortative mating should occur in simultaneous hermaphrodites because they invest substantially in mating. In a detailed review of the literature across taxa, he found support for his hypothesis in several animal groups, but not in all (e.g. insects). The disagreement between observation and prediction in insects may have been due to small sample sizes and/or inappropriate experimental design in the particular studies cited, as suggested by Ridley. However, it may also indicate that the processes leading to assortative mating in a particular animal group can differ quantitatively from those that predominate in most other taxa. Other factors, such as physical or temporal constraints may contribute to the evolution of mating patterns in other species (see below).

In simultaneous hermaphrodites there may be a conflict between female and male 'interests' with respect to mating frequency and mate choice. From the point of view of female fecundity, a snail should mate more than once during the egg-laying period (May–July) because individuals denied further copulations produce smaller egg clutches (Baur 1988b). Snails should primarily choose high quality mates, but these (so far unknown) qualities might not coincide with mate size. From the point of view of male fecundity, a snail should mate with a large partner to provide its sperm access to many eggs (clutch size is size-related in *A. arbustorum*). Furthermore, to increase male fecundity, a snail should mate as many times as possible, even after the egg-laying period (relatively little energy is required for the production of spermatophores and sperm in comparison with eggs: the dry weight of one spermatophore of *A. arbustorum* is less than that of one egg; B. Baur, unpublished data). On the other hand, mating incurs substantial risks for terrestrial gastropods (drying-out during copulation (see below), predation (Pollard 1975) and transmittance of parasites). These partially counteracting selection pressures, together with physical and temporal constraints, may vary among different populations, resulting in different mating patterns.

The size-discrimination experiment indicated that individuals of *A. arbustorum* from the Gurnigel population do not distinguish between potential mates of different size, a result supported by field observations. The visual capacity of helicid snails may not allow them to discriminate between different shell colours (although cues from different pheromones associated with different genotypes (shell colours) cannot be excluded; Hamilton & Winter 1984). However, the snails are able to distinguish between obstacles of different shape and size (Hamilton & Winter 1984). Furthermore, the snails' courtship involves intensive body contact, giving them an opportunity to estimate the size of the potential mating partner.

Terrestrial gastropods locate potential mates by chemical cues (Croll 1983; Chase 1986). Courting individuals of *A. arbustorum* attract other conspecifics, which then interfere with the courting pair

(Baur 1991). The formation of courting groups involving three individuals has been observed in natural populations of *A. arbustorum* (B. Baur, unpublished data). Lind (1988) recorded in a natural population of *H. pomatia* that in 86 of 981 cases more than two individuals were involved in courtship behaviour, the maximum being five. However, the displacement experiment demonstrated that large shell size does not provide any advantage during courtship to increase mating success.

Size-assortative mating has been reported in the marine nudibranch *Chromodoris zebra* (Crozier 1918). Sexually mature individuals of this hermaphroditic slug range in body length from 4 to 18 cm and can copulate at all hours of the day throughout the year. Size-assortative mating in *C. zebra* can be explained by a physical constraint: two individuals that differ greatly in size are unable to bring the reproductive organs together. Mating duration in this species is not constrained by diurnal fluctuations of the environment; individuals have plenty of time to match the size of a potential mate and if they are unequal in size they move apart to search for another mate (Crozier 1918).

In contrast to many species of marine gastropods, mating in terrestrial gastropods often exceeds the period favourable for locomotory activity (courtship and mating duration ranges from a few to more than 36 h; Duncan 1975; Giusti & Lepri 1980; Chung 1987; Adamo & Chase 1988; Giusti & Andreini 1988). In *H. pomatia*, the duration of mating is determined by physiological constraints (Lind 1973, 1976; Jeppesen 1976). During courtship and copulation land snails are exposed to severe water loss (cf. Prior 1985). Furthermore, they are more susceptible to predation than single adults (Pollard 1975). Considering the risks of desiccation and predation, selection probably acts to minimize time spent in copula. Members of at least 10 families of terrestrial gastropods push calcareous darts into their partner during courtship (Tompa 1980). It is assumed that dart shooting synchronizes courtship behaviour and thus minimizes courtship duration (Adamo & Chase 1988). In *Helix aspersa*, the dart injects a pheromone that decreases courtship duration (Adamo & Chase 1990). Consequently, there are time constraints on mating in terrestrial gastropods.

Population density of terrestrial gastropods varies enormously both among sites and in time (e.g. Andreassen 1981; Baur 1986). Many snail populations are characterized by extremely low densities of sexually mature individuals ($<0{\cdot}01$ snails/m^2), leading to low mate encounter rates. Considering the low mobility of snails (mucus has to be secreted in locomotion, which contributes to the high energy costs of gastropod crawling; Davies et al. 1990), costs of searching for a mate may be high, reducing the number of matings.

Thus, I propose, because of the time-constrained activity and high costs of locomotion, the best strategy for a land snail is to mate with the first mating partner available to minimize the risk of ending up without any mate at all or to dry up during mating. The resulting random mating pattern does not necessarily imply random fertilization of eggs, because multiple mating and sperm storage offer opportunities for sperm competition (B. Baur, unpublished data). For example, individuals of *H. pomatia* mated two to six times per year in a Danish population, but laid only one clutch of eggs during that period (Lind 1988). Differential sperm utilization resulting in multi-paternal broods have been demonstrated in *C. nemoralis* (Murray 1964) and in *A. arbustorum* (B. Baur, unpublished data). Random mating due to time constraints has been found in other taxa; e.g. in a natural population of common toads, *Bufo bufo*, with a short breeding period (Höglund 1989).

According to Parker (1983), random mating should occur when there is little variance in mate quality, and/or when search costs for mates are high. The lack of data on search costs does not allow any quantitative test of Parker's model (1983). However, search costs may, as a result of low encounter rates, increase with decreasing population density. This suggests that random mating may occur especially in low-density populations. However, the mating patterns described in this paper relate to high-density populations suggesting that mating with the first partner available may be beneficial even under conditions of high population density, most probably because of the time-constraints for locomotory activity.

ACKNOWLEDGMENTS

I thank A. Baur for field assistance and I. Ahnesjö, A. Baur, A. Cook, J. Höglund, S. C. Stearns, S. Ulfstrand and A. van Noordwijk for constructive comments on the manuscript. Financial support was received from the Swiss National Science Foundation (grant No. 31-26258.89).

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