MATE-CHOICE CRITERIA IN A PROTANDROUS SIMULTANEOUSLY HERMAPHRODITIC LAND SNAIL *ACHATINA FULICA* (FÉRUSSAC) (STYLOMMATOPHORA: ACHATINIDAE)

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ABSTRACT

The mate-choice behaviour of *Achatina fulica*, which is protandrous, was studied in the field. When snails were classified into two age classes, young adult and old adult, there was a clear mate-choice behaviour in *A. fulica*. Old adults, which are capable of producing both sperm and eggs, were more favoured as mating partners than young adults which produce only sperm. Size-assortative mating is clear in old adults but not in young adults. This species has two mate-choice criteria which are reproductive stage and body size. The reproductive stage-dependent mate choice is stronger than the body size-dependent mate choice

INTRODUCTION

Many animal species increase their fitness by choosing mates of better quality when individuals vary in their quality as potential mates (Fisher, 1958; Mayr, 1972). Mate choice by body size is common in many vertebrates and invertebrates, and size-assortative mating is considered to be the expression of mate choice by body size in many cases. If body size is positively correlated with male reproductive success and with female fecundity, positive size-assortative mating occurs (Ridley, 1983; Thornhill & Alcock, 1983; Ward, 1983).

Most land pulmonates are simultaneous hermaphrodites producing both sperm and eggs (Tompa, 1984; Leonard, 1991). Two individuals *in copula* are likely to exchange sperm. Some studies of pulmonates have shown that larger individuals produce more eggs in pulmonates (Wolda, 1963; Baur, 1988; Baur & Raboud, 1988). If sperm is much cheaper to produce than eggs, as assumed in many animals, there is a potential for land snails to evolve an optimal strategy of mate choice.

Individuals are expected to mate with larger individuals to maximize reproductive success. If larger individuals are more competitive or choosy in securing mates, size-assortative mating would be expected (Ridley, 1983). However, because there is little evidence of size-assortative mating in terrestrial pulmonates, it has been thought that they would show neither competition for mates nor mate choice (Baur, 1992; Leonard, 1991; Ridley, 1983). Baur (1992) suggested that size-assortative matings is rare in land snails because of time constraints of locomotory activity and high (time and/or energy) costs of searching for mates.

In simultaneously hermaphroditic land snails, there are three types of reciprocal mating systems: adichogamous hermaphrodite, protandrous hermaphrodite and protogynous hermaphrodite. In adichogamous hermaphroditism, each individual produces sperm and eggs from the beginning of maturation. In protandrous hermaphroditism, each individual first matures as a male, producing only sperm, and becomes truly hermaphroditic later. Protogynous hermaphrodites produce only eggs in the first stage of maturation. Protogynous hermaphroditism is, however, little known in land snails (Cook & Kondo, 1960). Although most land snails are adichogamous hermaphroditic, there are a number of protandrous hermaphroditic species (Lusis, 1961; Parivar, 1978; Runham & Hunter, 1970; Smith, 1966; Tompa 1984). Mate choice in hermaphrodites is more likely to evolve in protandry than adichogamy, because young male adults are likely to choose old adults which are complete hermaphrodites. It is clear that mate choice by reproductive stage differs from sexual selection for good genes, because differences between young and old adults are

developmental but not genetic. All young adults are able to become old adults.

Achatina fulica is a simultaneously hermaphroditic land snail and shows protandrous reproduction. Young adults produce only sperm, while old adults produce both sperm and eggs (Tomiyama, 1993). In the field, copulations between old adults were statistically more frequent than expected under random mating assumed in the same population (Tomiyama, 1994). About 90% of animals that began courtship were rejected by their opponents (Tomiyama, 1994). Thus, unlike many other land snails, *A fulica* would choose mates. For young adults to increase fitnesss, they need to copulate with old adults, which can produce eggs. For old adults, on the other hand, young adults would not be desirable mates, because young adults can be sperm donors for gynogenesis investment but not sperm acceptors for androgenesis investment. As long as there are these two modes of reproductive investment among individuals in populations, mate choice by reproductive stage would occur. In reproduction of *A. fulica*, the amount of sperm used is much smaller than the amount of eggs used (Tomiyama, 1993). Thus, the cost of male investment is smaller than that of female investment. The clutch size and egg volume of *A. fulica* are positively correlated with shell size (Tomiyama & Miyashita, 1992). Consequently, size-assortative mating is likely to occur by choosing large mates with larger fecundity in *A. fulica*

Therefore, the previous studies allow two predictions on the mating system of *A. fulica* First, they choose a mate by the reproductive stage, favouring old adults as mating partners rather than young adults. Second, size-assortative mating would occur. To test these predictions, I conducted the field observations of matings of *A. fulica*.

MATERIALS AND METHODS

Study site

The observation site was located on the northern part of Chichi-jima island in the Ogasawara (Bonin) Islands located in the northern Pacific Ocean, 27°N, 140°E. The climate of this island is subtropical, showing an annual mean temperature of 23 0°C No frost or snow has been recorded, and the temperature does not fall below 5°C throughout the year. The annual precipitation was less than 1300 mm for 10 years from 1980 to 1990. The study site was established on a northern slope, at an altitude of 70 metres. The forest at the site consists of broad-leaved evergreen trees, dominated by *Leucaena leucocephala* (L) The litter layer is thin (2–3 cm) and covered with a large number of fallen twigs and poor vegetation on the forest floor.

Maturation pattern and age determination of study animals

Achatina fulica shows protandrous development (Tomiyama, 1993) *A. fulica* becomes reproductively mature at about 5 months under laboratory conditions of 20–24°C and LD=12:12 h (Pawson and Chase, 1984). In the study site, where *A fulica* is a dormant in winter, development of the reproductive organs was observed about 12 months after hatching (Tomiyama, 1993) Many pulmonates end their shell growth with a reflected shell lip which is commonly considered to indicate sexual maturity (Wolda, 1970). Lip reflection, however, does not occur in *A fulica*, and the shell continues to grow for 3–6 months after the reproductive organs and genital atrium are fully formed. In *A fulica*, the peristome lip is usually very thin while the shell is still growing. In this period, *A fulica* begins to mate producing only sperm. Individuals in this reproductive stage are referred to below as young adults

Shell growth ends at the last stage of young adults. Then the animals become fully mature and produce both sperm and eggs. Thereafter, calcium deposition occurs on the inner surface of shell Thus even in fully matured animals the peristome continues to increase in thickness (Tomiyama, 1993). These animals are referred to below as old adults.

A fulica tends to produce egss after the peristome thickness exceeds 0.5 mm (Tomiyama & Miyashita, 1992) Thus the peristome thickness could be an useful index of the relative age and reproductive stage In this study, the animals were classified into 3 categories according to the formation of genital atrium and peristome thickness; juvenile the genital atrium was not formed; young adult: the genital atrium was formed and the lip was thin (thinner peristome than 0.5 mm); old adult: the genital atrium was formed and the lip was thick with calcium deposition (0.5 mm or thicker peristome).

Mating behaviour in the field

Copulation of *A. fulica* was observed at night time Mating behaviour of *A. fulica* can be divided into courtship (pre-copulation behaviour) and copulation. Courtship behaviour and mating of land snails often result in simultaneous exchange of sperm between mates. *A fulica* shows an elaborate mating behaviour with simultaneous reciprocal intromission. Courtship behaviour of *A. fulica* follows a fixed pattern. First, one animal (the initiator) approaches another from the back of the body and mounts on its shell. If the lower animal (the acceptor) accepts the courtship, courtship behaviour progresses to next step. After some reciprocal courtship behaviour, both animals insert their penes into the vagina of the

Table 1. The number of individuals and shell volume of young adults and old adults in the study site.

Reproductive stage	Young adults	Old adults	Mann-Whitney U-test
Whole population			
Number	729 (72.0%)	283 (28.0%)	
Shell volume (mm³)			
Mean ± SD	30486 ± 6980.9	37021.7 ± 10825.3	U = 14073.0***
Range	12149.5 – 52160.3	10986.4 – 96324.1	
Observed in courtship			
Number	62	90	
Shell volume (mm³)			
Mean ± SD	31426.8 ± 6917.4	39312.4 ± 10602.0	U = 1066.5***
Range	17484.9 – 46700.5	21497.4 – 74432.9	
Observed copulating			
Number	129	157	
Shell volume (mm³)			
Mean ± SD	30079.8 ± 6534.3	35884.7 ± 10238.9	U = 5923.5***
Range	17310.4 – 45877 3	15021.6 – 78884.8	

*** indicates a significance level of $P < 0.001$.

other. The sequence of behaviour from mounting to penis insertion takes about five minutes. The duration of the ensuing copulation averaged 4.6 hours with a range from 1.5 to 7.5 hours (Tomiyama, 1994).

In the field, it is easy to distinguish the initiator (= upper animal) and acceptor (= lower animal) in copulating pairs, because they do not change their positions during copulation even if they are poked Rejection of copulation was observed during courtship: 89 2% failed to complete penes insertion because of rejection (Tomiyama, 1994). It was clear from their behaviours which individuals rejected

In some early studies (Mohr, 1949; Ghose, 1959), it was thought that *A. fulica* is able to self-fertilize. Kekauoha (1966), however, found that isolated individuals never produce viable eggs, and Mead (1979) concluded that viable self-fertilisation does not take place in *A. fulica*

Observation

Mating behaviour of *A. fulica* was observed in a permanent 20 × 20 m quadrat at the study site. All individuals found between 6:00 p.m. and 6:00 a.m. on 14th to 15th July 1990 were recorded. The genital atrium of each animal found was inspected, then the peristome thickness, shell length and shell width were measured, and the shell marked by waterproof paint on the last whorl to identify the relative age, before returning the animal to the spot where it was found

The number of copulatory pairs rapidly increased till about 10-00 p m. and decreased after 3-00 a.m.(Tomiyama, 1994), so that courtship and copulation were observed between 9:00 p.m. and 3-00 a.m.

When a pair beginning courtship was found, their behaviour was observed until they completed reciprocal insertion of the penes into partner's vagina or copulation failed. The copulation position (upper or lower) of the rejected animal was recorded if copulation failed. Peristome thickness, shell length and shell width of snails were measured to the nearest 0 1 mm using calipers in both successful and unsuccessful matings. Newly discovered snails were marked by paint. The shell volume (V) was calculated by formula 4/3 π A²B, where A is 0.5 × shell width, and B is 0.5 × shell length. The relative difference of shell volume between two mates was calculated by the following formula: Difference index (DI = 100 × 2(|X – Y|)/(X + Y)), where X and Y are the shell volumes of two mates. When copulatory pairs (all are copulation succeeded pair) were discovered, three characters were also measured These observations were repeated for 14 nights on 15th to 28th July, 1990.

RESULTS

The number of young adults and old adults in the whole population at the study site and in observed mating pairs are shown in Table 1. In total, 1012 adult individuals were found at the study site: 729 (72.0%) were young adults and 283 (27.0%) were old adults. This difference is statistically significant (G-test, G_{adj} = 203.473, p<0.001). The proportions of young adults and old adults among animals observed courting was 40.8% (N = 62) and 59.2% (N = 90). There is a significant difference between this

Table 2. The number of pairs of courting adults observed, partitioned by reproductive stage of both partners All pairs were observed from the beginning of courtship behaviour to the end of courtship (penis insertion or rejection at a stage of courtship behaviour). The expected values were calculated from the ratio of young adults and old adults in the study site if there is random mating in the observed population.

Reproductive stage of Upper animal (courtship initiator)	Young	Young	Old	Old	
Reproductive stage of Lower animal (courtship acceptor)	Young	Old	Young	Old	
					total
Expected values	39.4 (51.9%)	15.3 (20.2%)	15.3 (20.2%)	6.0 (7.8%)	76
Observed pairs	13	31	5	27	76
Copulation succeeded	0	3	0	6	9
Copulation failed	13	28	5	21	67
Rejection by upper animals	1	1	5	11	18
Rejection by lower animals	12	27	0	10	49

observed frequency and that expected from the ratio of young and old adults in the population as a whole; 109 : 2.6 (G-test; G_{adj}=64.007, p<0.001). The proportions of young adults and old adults in the animals seen copulating were 45 1% (N = 129) and 54.9% (N = 157). The proportion of old adults was statistically larger than that of young adults (expected values from whole population; 205.9:80.1; G-test, G_{adj} = 0.519, p<0.001). These results indicate that old adults have more opportunities to mate compared with young adults and more young adults failed to copulate than old adults. There were also significant differences in the mean shell volumes of young adults and old adults in the whole population, and in those seen in courtship and in copulation (Table 1). However, the differences in shell volume of the whole population, and of those seen in courtship and in copulation, were not significant either for young adults (Kruskal-Wallis test; chi-square = 0.7746, dif = 1, p = 0.6789) or for old adults (Kruskal-Wallis test; chi-square = 3.0669, df = 1, p = 0.2158). This suggests that mating animals were not derived from a special fixed-size cohort of the adult animals in the population.

The number of courtships observed between pairs of young adults, mixed pairs (a young adult and an old adult), and pairs of old adults are shown in Table 2. If there is random mating in this population, the frequencies of courtships observed between pairs of young

upper/young lower, pairs of young upper/old lower, pairs of old upper/young lower and pairs of old upper/old lower, would be 51.9%, 20.2%, 20.2% and 7.8% respectively, calculated from Table 1. In fact, the observed ratios were 17.1% (13), 40.8% (31), 6.6% (5) and 35.5% (27) respectively (N = 76). Fewer pairs of young upper/young lower and old upper/young lower were observed than expected, and more young upper/old lower and old upper/old lower were observed than expected. These differences were statistically significant (G-test; G_{adj} = 83.522, p < 0.001).

Young adults were initiators (i.e. the upper partner) on 44 out of 62 matings (Table 2), significantly different (G-test; G_{adj} = 11.158, p < 0.001) from the expected ratio of 31 and 31, while old adults were initiators in only 32 of 100 matings, again a significant difference (G-test; G_{adj} = 13.190, p < 0.001) from the expected ratio (50 and 50). These results suggest that young adults tend to initiate courtship and old adults tend to accept courtship.

The acceptors of courtship (i.e. the lower animals) rejected courtship (N = 49; 73.1%) statistically (G-test; G_{adj} = 15.556, p < 0.001) more often than the initiators (i.e. the upper ones) (N = 18; 26.9%). There was also a significant difference (G-test; G_{adj} = 24.018, p < 0.001) between the rejections by young adults (N = 14; 20.9%) and old adults (N = 53; 79.1%). This suggests that old adults determine whether courtship is successful or not.

Table 3. The number of copulation pairs observed, partitioned by reproductive stage of both partners. The expected values were calculated from the ratio of young adults and old adults in the study site if there is random mating in the observed population.

Reproductive stage of Upper animal	Young	Young	Old	Old	
Reproductive stage of Lower animal	Young	Old	Young	Old	
					total
Expected values	74.2 (51.9%)	28.9 (20.2%)	28.9 (20.2%)	11.1 (7 8%)	143
Observed pairs	37	51	7	48	143

Table 4. The number of copulation successful and failing animals for young adults and old adults with restricted shell volume between 30,000 and 40,000 mm³.

	Copulation succeeded	Copulation failed
Young adults		
Number	9	21
Shell volume	34256.0 ± 2404.8	35357 6 ± 2336.8
Old adults		
Number	31	13
Shell volume	34312.7 ± 2689.6	34186.6 ± 3172.2

The number of copulations between pairs of young adults, mixed pairs of young and old adults, and pairs of old adults are shown in Table 3. There were significant differences between expected values under random mating and observed numbers (G-test; G_{adj} = 125.984, p < 0.001). The number of copulations between young upper/young lower and old upper/young lower (i.e. young acceptors) were less than expected, and that of young upper/old lower and old upper/old lower (i.e. old acceptors) were more than expected.

Young adults were initiators in 88 of 132 copulations (Table 3). This ratio is statistically different (G-test; G_{adj} = 14.895, p < 0.001) from the expected ratio of 66 and 66. Old adults were initiators in only 55 of 154 copulations, again a significant difference (G-test; G_{adj} = 12.707, p < 0.001) from the expected ratio of 77 : 77.

From the results of Tables 2 and 3, it is concluded that mating in *A. fulica* was not random, and that young adults showed active courtship and old adults showed passive courtship. These differences, however, may be due to size differences between young and old

adults. To eliminate the effect of body size, animals with a shell volume between 30,000 and 40,000 mm³ were selected, and the number of successfully and unsuccessfully copulating animals were compared between young and old adults (Table 4). Differences of shell volume among four groups was not significant (Kruskal-Wallis test; chi-square = 1.9605, df = 3, p = 0.5806). In young adults, there were fewer successful copulations than unsuccessful ones, on the other hand, in old adults, there were more successful copulations than unsuccessful ones. The difference between young adults and old adults was statistically significant (G-test; G_{adj} = 35.068, p < 0.001). This suggests that the difference of reproductive stage has a strong effect on mating behaviour even when differences in shell size are eliminated.

If there is mate choice in *A. fulica*, the first stage is when the courtship-initiating animals choose their mate (= courtship acceptor) before the beginning of courtship. The ratio between young and old adults for acceptor (= lower position) in the courtship and copulation are shown in Table 5. When the courtship initiator was a young adult, an old adult was

Table 5. The number of acceptor animals in matings between a young adult and an old adult. Expected values were calculated from the ratio of Table 1 under random mating in the population.

Reproductive stage of acceptor animal	Young	Old	Total
Courtship observed pairs			
initiator animal is young adult			
Expected values			
under random mating	31.7 (72.0%)	12.3 (28 8%)	44
Observed numbers	13	31	44
initiator animal is old adult			
Expected values			
under random mating	23.0 (72 0%)	9.0 (28.8%)	32
Observed numbers	5	27	32
Copulation observed pairs			
initiator animal is young adult			
Expected values			
under random mating	63.4 (72.0%)	24 6 (28.0%)	88
Observed numbers	37	51	88
initiator animal is old adult			
Expected values			
under random mating	39.6 (72.0%)	15.4 (28.0%)	55
Observed numbers	7	48	55

chosen as the acceptor statistically more often (N = 31; 70.5%) than a young adult (N = 13; 29.5%), compared with expected values under random mating (G-test; G_{adj} = 33.7529, P < 0.001). If initiator was an old adult, there was significant difference (G-test; G_{adj} = 43.387, p <0.001) between the number of young adults (N = 5; 15.6%) and old adults (N = 27; 84.4%) chosen as acceptors. These indicate that an old adult was more favoured as copulation partner than young adult by the courtship initiator in the first step of the mate choice.

Similar results were also observed in the case of copulation pairs. If the courtship initiator was a young adult, the number of old adults (N = 51; 58.0%) chosen as acceptor was statistically greater than the number of young adults (N = 37; 42.0%), compared with expected values under random mating (G-test; G_{adj} = 34.319, p < 0.001). When the initiator was an old adult, there was a significant difference (G-test; G_{adj} = 84.111, p < 0.001) between the number of young adults (N = 7; 12.7%) chosen as acceptors compared to the number of old adults (N = 48; 87.3%).

76 pairs were observed from the beginning to the end of courtship: only 9 pairs completed penes insertion, and the other 69 pairs failed because of rejection between mates (base of Table 2). These rejections of mating partners form the second stage of mate choice during courtship. With an old adult as the lower partner, courtships initiated by another old adults were accepted on 6 occasions out of 27; the 21 rejections were made equally by the upper partner (11 cases) or the lower partner (10 cases). Young adults initiated courtship with old adult partners on 31 occasions, but only 3 were successful. Of the 28 failed courtships, all were rejected by the old lower partner. The difference in the rejection of young and old courtship initiators by old partners is significant statistically (Fisher's exact probability test: p=0.034). This suggests that young partners are rejected by old partners in the second stage of mate choice during courtship. There are too few observations on rejection by young adults or by initiators to draw any conclusions.

The mean shell volumes for each of the four of pairs between young and old adults are shown in Table 6. There were no significant differences in the shell volumes of upper and lower animals for successfully copulating pairs. In pairs which were unsuccessful, when young adults were the upper animals, the lower animals were significantly larger than the upper animals. If old adults were upper animals, however, there was no significant difference in shell volume between upper and lower animals. This indicates that young adults failed when they try to mate with large animals.

The difference index (DI) of shell volume

Table 6. Shell volume (mm³, mean ± SD) of upper and lower animals for successful and unsuccessful between copulating young, mixed pairs and old pairs.

Upper animal Lower animal	Young Young	Young Old	Old Young	Old Old
Copulation successful				
Upper animals	27832.2 ± 6668.7	32160.5 ± 10849 5	58663.5 ± 43669 7	34322 8 ± 7608.7
(initiator)	(N = 37)	(N = 51)	(N = 7)	(N = 48)
Lower animals	30979 2 ± 6304 1	34487.4 ± 8491 6	50222.7 ± 31871.0	38962.9 ± 13162.6
(acceptor)	(N = 37)	(N = 51)	(N = 7)	(N = 48)
Mann-Whitney's U-test	U = 510.0, NS	U = 1002.5, NS	U = 21.0, NS	U = 904.5, NS
Copulation failed				
Upper animals	29260.8 ± 6237.1	29628.2 ± 6485.3	40647.0 ± 6898.2	35932.0 ± 5290.8
(initiator)	(N = 13)	(N = 28)	(N = 5)	(N = 21)
Lower animals	37466.6 ± 4597.4	42628.6 ± 10468.0	35741 3 ± 4909.0	38271.4 ± 13168.2
(acceptor)	(N = 13)	(N = 28)	(N = 5	(N = 21)
Mann-Whitney's U-test	U = 29 0**	U = 1117.0***	U = 7 0, NS	U = 206 0, N

Significance level; **$0.001 < P < 0.01$, ***$P < 0.001$; NS = not significant.

Table 7. Difference index (mean ± SD) of shell volume between upper and lower animals for successful and unsuccessful pairs of young adults, mixed pairs and pairs of old adults.

Upper animal Lower animal	Young Young	Young Old	Old Young	Old Old
Copulation successful				
Number of pairs	37	51	7	48
DI-value	22.8 ± 17 7	23.5 ± 17.5	105.1 ± 34.5	22.0 ± 18 2
Copulation failed				
Number of pairs	13	28	5	21
DI-value	28.1 ± 20.4	43.5 ± 25 7	89.1 ± 36 6	33.6 ± 22.0
(Mann-Whitney's U-test)	(U = 206.0; NS)	(U = 397 0**)		(U = 332.0*)

Significance level; *$0.01 < P < 0.05$, **$0.001 < P < 01$, NS = not significant.

between young pairs, mixed pairs and old pairs for successful and unsuccessful pairs are shown in Table 7. DI was low successful pairs, but high for failing pairs. The differences of DI between successful and failing pairs were significant (Mann-Whitney's U-test) for the pairs between young adult (initiator) and old adult (acceptor) (p = 0.0012) and that between old adult (initiator) and old adult (acceptor) (p = 0.0321). For the pairs between young adult (initiator) and young adult (acceptor), there was no significant differences of DI between successful and failing pairs. These results suggest that old adult pairs with a large difference in shell volume tended to fail to copulate. This tendency was not observed between young pairs.

Among pairs that copulated successfully, shell volumes of upper and lower animals were positively correlated between young (initia-

tors) and old (acceptors) and that between old (initiators) and old (acceptors) (Table 8) Between young (initiators) and young (acceptors), however, there was no correlation. There was a negative correlation among pairs which failed to mate between old (initiators) and old (acceptors). There were no significant correlations between young (initiators) and young (acceptors) and between young (initiators) and old (acceptors) when their mating failed. These results suggest that size assortative mating was occurring between old adults but not between young adults.

DISCUSSION

This study has clearly shown mate choice in *A fulica. A fulica* choose mates by reproductive

Table 8. Correlation of shell volume between upper and lower animals in successful and unsuccessful pairs of young adults, mixed pairs and pairs of old adults.

Upper animal Lower animal	Young Young	Young Old	Old Young	Old Old
Copulation successful				
Number of pairs	37	51	7	48
Correlation	r = 0 203 (p = 0 228)	r = 0.329 (p = 0.018)	—	r = 0.539 (p < 0.001)
Copulation failed				
Number of pairs	13	28	5	21
Correlation	r = 0.140 (p = 0.646)	r = −0.312 (p = 0 016)	—	r = −0.521 (p = 0.015)

stage. Old adults, who are capable of producing sperm and eggs, were more favoured as mating partners than young adults, who produce only sperm. It has also been shown that mating is positively size-assortative in old adults but not in young adults. Mate choice by size is age-dependent because the body size continues to increase with age after sexual maturing. Consequently, *A. fulica* have two mate choice criteria; reproductive stage and body size. The reproductive stage-dependent mate choice, which was observed in all mature animals, is stronger than the body size-dependent choice.

Mate choice of *A. fulica* occurs in the two stages during courtship behaviour. In the first stage, courtship-initiating snails choose partners. In the second stage, unattractive partners are rejected. In both steps, old adults were more favoured as mates than young adults.

A. fulica orientates towards conspecifics or chemicals extracted from their pedal glands (Chase *et al.*, 1978; Chase & Boulanger, 1978). Chase *et al.* (1980) showed that *A. fulica* has kin-specific chemical information. The courtship initiator approaches the courtship acceptor snail by following its mucus trail (Tomiyama, 1994). The mating snails frequently touched the soft bodies of partners by tentacles in the middle of courtship, and it is suggested that identification of mate quality depends on chemical information.

Mate choice behaviour has been observed in some species of simultaneously hermaphroditic marine gastropods (Crozier, 1918; Leonard, 1991; Leonard & Lukowiak, 1985; 1991). Ridley (1983) proposed that size-assortative mating was expected to occur in simultaneously hermaphroditic land snails. Assortative mating or mate choice, however, has not

been reported. On the contrary, most studies showed that terrestrial snails mate at random. *Cepaea nemoralis* (L.) performs random-mating for shell size and colour and banding patterns (Schindler, 1950; Schnetter, 1950; Wolda, 1963). Baur (1992) suggested that mating of *Arianta arbustorum* (L.) is random with respect to shell size. Takahashi *et al.* (1992) reported tht *Acusta despecta* (Sowerby) randomly copulates. Woyciechowski & Lomnicki (1977) showed that there is no difference of mating frequencies in *Helix pomatia* L. Although Clarke & Murray (1969) and Johnson (1982) reported that *Partula suturalis* Pfeiffer shows assortative mating with respect to coiling direction, mate choice by chirality has not been tested. Copulation between the opposite coiling morphs was less successful than that between the same coiling morphs, because of incompatible locations of genital organs (Lipton & Murray, 1979). Whether assortative mating by coiling direction in *Partula* results from mate choice has not been clear yet experimentally.

Why does *A. fulica* show clear mate choice unlike other terrestrial pulmonates? In *A. fulica*, mate choice by reproductive stage is closely associated with protandry. For a young adult, copulation with an old adult is indispensable for reproductive success. Therefore, mate choice by reproductive stage is important to increase their reproductive success. Consequently, *A. fulica* shows age-dependent mate choice and this choice is stronger than size-dependent mate choice.

Old adults simultaneously produce sperm and eggs, but they are not able to self-fertilize (Kekauoha, 1966; Mead, 1979). Hence, old adults need to copulate with others to fertilize their eggs. It is reasonable to call young adults

'male-behaving', and old adults 'female-behaving'. In dioecious animals, the inexpensiveness of male parental investment induces strong competition between males for access to females and leads to female's choice of mating partners if male parental investment is very small compared with female parental investment (Bateman, 1948). This theory of parental investment and sexual selection can be applied to the protandrous simultaneously hermaphroditic snails.

In *A. fulica*, the amount of injected sperm liquid in one copulation is less than 100 mg, while the weight of the protein gland in which all eggs are supplied with albumin fluid become about 3000 mg before egg formation (Tomiyama, 1993). Hence, male parental investment is meagre compared with female parental investment. Young adults are the dominant reproductive individuals (72.0%) in the field. Thus young adults encounter old adults less frequently than young adults. These encountered young adults are not favoured as mating partners and the rejection rate is very high. The dispersal range of old adults is smaller than that of young adults (Tomiyama & Nakane, 1993). In addition, courtship behaviour of *A. fulica* occurs exclusively during night-time and mating lasts for 4.6 hours on average with a range from 1.5 to 7.5 hours (Tomiyama, 1994). It is suggested that the operational ratio between young and old adults in natural populations is exclusively young adult bias, so that old adults are of great reproductive value in the population. Therefore, the male parental investment of *A fulica* becomes even cheaper than the female parental investment. Consequently, old adults have leeway to choose mates, in contrast to young adults which disperse widely searching for old adults, and many young adults fail to copulate in natural populations.

25.9% of copulatory pairs were between young adults. Because young adults are not able to produce eggs, copulation between young adults must be meaningless for reproduction. Copulation between young adults could be regarded as extraordinary behaviour caused by bachelorhood in young adults. However, some beneficial factors for copulation between young adults may exist. In pulmonates, only 0.1% of received sperm is used to fertilize eggs and the rest of sperm are digested as nutrition (Lind, 1973; Tompa, 1984). It is possible that *A. fulica* use received sperm as nutrition. A further explanation arises because *A fulica* can store received

sperm for up to 341 days (Raut & Ghose, 1982). Therefore young adults would be able to store received sperm until they are ready to produce eggs, because they become old adults in 3 to 6 months (Tomiyama, 1993).

If the reproductive value of old adults becomes very high, young adults will compete with each other for access to old adults. In land snail species, aggressive interactions to limit the access of courtship initiators to courtship acceptors have not been observed. There is no competition to disperse and find sexually receptive animals in *A fulica* (Tomiyama & Nakane, 1993)

Baur (1992) showed that *Arianta arbustorum* mate randomly with respect to body size To explain the absence of size-assortative mating in simultaneously hermaphroditic land snails, Baur (1992) proposed that, because of the time-constrained activity and the high costs of locomotion, the best strategy for land snails is to mate with any conspecific adult encountered to minimize the risk of complete failure in mating or to avoid desiccation during mate-hunting *A. fulica*, however, has some ecological peculiarities which are not observed in other land snail species. *A. fulica* prefers disturbed areas affected by humans, but is relatively rare in natural forest (Aoki, 1978) Usually, *A. fulica* undergoes repeated and explosive increases of population with high density in invaded areas (Mead, 1979). In addition, it shows high locomotory activity (Tomiyama & Nakane, 1993). For these reasons, old adults of *A. fulica* would not need to pay a high cost in searching for mates and time constraints would be weak compared with other land snails.

In old adults, the fecundity which is correlated with shell size shows great variability, ranging from 40.2 to 76.2 mm^3 for mean egg volume and from 13 to 137 for clutch size in the same population (Tomiyama & Miyashita, 1992) *A. fulica* shows large differences of reproductive value also among old adults. The difference of reproductive value among old adults enhances mate choice by size, so that the positive size-assortative mating occurs in old adults. For young adults, the costs of searching for an old adult is very high, so that young adults show random mating by size.

Fisher (1958) estimated that when there is much variation in individual quality as mates, mate choice evolves to gain better-quality mating partners to increase fitness. In many animal species, the evolution of mate choice has been

usually explained by selection for good genes (Andersson, 1994). In *A. fulica*, however, mate choice by reproductive stage differs from the selection for good genes, because differences between young and old adults are developmental but not genetic. It is considered that mate choice in *A. fulica* have been evolved by selection for good developmental stage to increase fitness.

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