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Heritability of Reproductive- and Growth-related Traits in the Apple Snail *Pomacea canaliculata*

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Summary

In order to estimate the relative importance of heredity in determining the phenotypic value of several quantitative traits, 9 family populations (brothers and sisters) of the apple snail *Pomacea canaliculata* were examined for reproductive- and growth-related traits.

Compared with the original population, the average phenotypic value of the traits decreased in family populations, and the degree of decrease varied among the traits. Higher heritability was estimated in growth-related traits than in reproductive-related traits. This differences between reproductive-and growth-related traits suggested the relationship between heritability and inbreeding depression.

The apple snail, *Pomacea canaliculata*, is useful as an experimental organism for genetics and breeding studies, due to its special biological characteristics : a short life cycle (around 6 months), high fertility rate (200-700 eggs/female), large egg size (about 2 mm), short hatching time (12 days), and high hatching rate (around 50%) (1, 2). Adult apple snails show a chromosome number of $2n=28$ and male heterogamety (XX) (3). A pure mating system i.e. 1 female with only 1 male, was suggested by analysis of isozyme for one egg lump (1). Female reproductive behavior of laying egg lumps consisting of 200 to 700 eggs each and keeping the siblings together, makes this organism interesting for quantitative genetics.

Quantitative characters are said to show polygenic inheritance if their variation depends on allelic differences at more than just a few loci. In genetical analysis of quantitative characters, however, genotypic-environmental interaction can be an important factor. The partitioning of phenotypic variance into genotypic and environmental components is necessary to estimate the relative importance of the various determinants of the phenotype, in particular the role of heredity versus environmental factors. Estimation of the relative importance of heredity in determining phenotypic value (heritability) is relevant to genetic improvement of cultured aquatic organisms.

In the present work, using family comparisons of the apple snail, the heritability of reproductive- and growth-related traits was estimated and differences between reproductive- and growth-related traits were discussed.

Materials and Methods

Animals

The apple snails, *Pomacea canaliculata*, were maintained in a closed colony in this laboratory. Separate egg lumps, deposited on the aquarium wall, were taken at random, weighed, and individually transferred to one petridish. Incubation temperature of eggs was 28°C, in an incubator with controlled humidity. After 12 days, the snails hatched. Newly hatched snails were reared for 30 days at a water temperature of 26°C using 2.8 l aquarium with 500 ml water. The snails were fed on cabbage and pelletized carp diet once daily.

Measurement of traits

Nine family populations were produced from separated 9 egg lumps from the original population. Each family population was placed in a separate 60 l aquarium and reared for a year. So, each family population consisted of brothers and sisters. The following traits of the egg lumps and hatched snails were measured :

(1) The egg lumps, laid on the aquarium wall, were weighed to determine the mean egg weight per egg.

(2) Egg number per lump was determined.

(3) The number of hatched snails were counted and also the unhatched, to determine the hatchability.

(4) Body weight of the pooled snails at hatch was measured to determine the mean body weight at hatch.

(5) Survival rate at day 15 was calculated.

(6) Body weight of each snail was measured on day 15 and day 30. Twenty snails were reared each 2.8 l vessel with 500 ml water from day 0 to day 30.

Traits (1)-(4) reflected the reproductive capacity of the female, and (5) and (6) were growth-related characters. Means and standard deviations of family traits were calculated.

Heritability

Heritability was estimated by standard analysis-of-variance techniques (4). The expected mean square between-family is equal to $\sigma_E^2 + k\sigma_G^2$. σ_E^2 and σ_G^2 are the environmental and genetic components of variance, respectively, k is the number of individuals measured per family (or the harmonic mean of the numbers in the family if sample sizes are not equal). The expected mean square within-family is equal to σ_E^2.

Results and Discussion

1. Differences of quantitative parameters between original and family populations

Table 1 shows the parameters related with reproductive and growth traits in the original population of the apple snail *Pomacea canaliculata.* Parameters (1)-(3) related to hatchability were measured for 47 egg lumps, excluding unhatched egg lumps. Each parameter varied widely, for example, hatchability ranged from 16.4% to 87.8% with mean value of 51.7%, and body weight at day 15 ranged from 23.9 mg to 95.3 mg with a mean value of 48.0 mg.

Table 2 shows the parameters in family populations prepared from the original population. Since each family population consisted of brothers and sisters, the laid egg lumps were produced by full-sib mating and offspring represented a coefficient of inbreeding (F) of 0.250. Weight of egg and survival rate at day 15 were similar to those of the original population. Egg number per lump, hatchability, weight of hatched snails were smaller than those of the original population, while body weight at day 15 and 30 were larger in family populations than in the original population. Mean weight of egg, egg number per lump, hatchability, and body weight at hatch indicated a significant decrease of variance in comparison with that of the original population.

If the family populations are randomly produced from the original population, variance is expected to be the same as that of the original population. Inbreeding gives rise to the possibility of lower variance. Allendorf and Utter (5) concluded that inbreeding was the cause of reduction in variation at a number of polymorphic loci in a cultured stock. Decrease of the egg number per lump may

TABLE 1. *Summary of quantitative parameters in the original population of the apple snail*

	Traits	No. of egg lumps	Average ± S.D	CV (%)
(1)	Weight of egg (mg)	47	12.8 ± 3.0	23.4
(2)	Egg number per lump	47	197.3 ± 106.8	54.1
(3)	Hatchability (%)	47	51.7 ± 18.0	34.8
(4)	Body weight at hatch (mg)	47	3.3 ± 0.9	27.3
(5)	Survival rate at day 15 (%)	47	78.6 ± 22.1	28.1
(6)	Body weight at day 15 (mg)	28	48.0 ± 18.6	38.8
(7)	Body weight at day 30 (mg)	28	168.8 ± 59.3	35.1

TABLE 2. *Summary of quantitative parameters in family populations (brothers and sisters) of the apple snail*

	Traits	No. of family populations	Average±S.D	CV (%)
(1)	Weight of egg (mg)	8 (367)	12.7± 1.2	9.4
(2)	Egg number per lump	8 (367)	99.9±31.5	31.5
(3)	Hatchability (%)	8 (367)	32.2± 5.2	16.1
(4)	Body weight at hatch (mg)	8 (258)	2.0± 0.3	15.0
(5)	Survival rate at day 15 (%)	6 (26)	78.4±24.2	30.9
(6)	Body weight at day 15 (mg)	5 (5)	72.9±28.5	39.1
(7)	Body weight at day 30 (mg)	5 (5)	209.0±57.0	27.3

Number of egg lumps was represented in parentheses.

be related to size differences among females. On the other hand, decrease in hatchability and body weight at hatch might be caused by inbreeding depression. Fujio *et al.* (2) revealed that hatchability per egg lump was lower when the probability of heterozygotic pairs of chromosomal combination in the apple snail was reduced from 75% to 50%, and they suggested a correlation of fitness with chromosomal combination, indicating the superiority of heterozygotic pairs of chromosome for high hatchability. Such a phenomenon indicates the existence of inbreeding depression as a result from homozygosity of deleterious recessive alleles. Fujio *et al.* (2) also found a correlation between the weight of egg and the weight of newly hatched snails. The same correlation was observed in the original population but not observed in family populations. This latter result suggests the possibility that decrease of body weight at hatch is caused by inbreeding depression. The high correlation between hatchability and survival rate was observed in both the original and family populations. This latter result suggests that selection for reproductive-traits could be relaxed for detrimental effects on so-called fitness traits. Such circumstance gives one of possible interpretation for the increase in body weight of family populations.

2. *Estimation of heritability*

Estimates of heritability for reproductive- and growth-related traits were made in the family populations shown in Table 2 on the basis of full-sib families. All estimations are derived from full-sib family components of variance. The result is shown in Table 3. Weight of egg, egg number per lump, and hatchability were measured for 9 family populations. One of the 9 family populations laid all unhatched egg lumps. The star in Table 3 represents estimates for egg lumps which included unhatched egg lumps. A large difference in hatchability between excluded (0.022) and included (0.141) unhatched egg lumps was observed, suggest-

TABLE 3. *Heritability of quantitative parameters in family populations of the apple snail*

	Traits	No. of family populations	Heritability
(1)	Weight of egg (mg)	8 (367)	0.075
	Weight of egg (mg)*	9 (703)	0.024
(2)	Egg number per lump	8 (367)	0.136
	Egg number per lump*	9 (703)	0.167
(3)	Hatchability (%)	8 (367)	0.022
	Hatchability (%)*	9 (703)	0.141
(4)	Body weight at hatch (mg)	8 (258)	0.076
(5)	Survival rate at day 15 (%)	6 (26)	0.476
(6)	Body weight at day 15 (mg)	5 (5)	0.770
(7)	Body weight at day 30 (mg)	5 (5)	0.580

* indicates average which are included with unhatched egg lumps and number of egg lumps was represented in parentheses.

ing the existence of a deleterious recessive gene. Estimates of heritability of reproductive-related traits (1)-(4) ranged from 0.022 to 0.167, while heritability for growth-related traits (5)-(7) varied from 0.476 to 0.770, indicating higher heritability in growth-related traits than for reproductive-related traits.

Estimations of heritability are available for the family populations, however, the values of such estimates depend on the following factors. (1) The genetic models employed assumed a simple additive relationship between genetic and environmental effects. Epistatic and dominance effects are involved in the estimation. (2) Component of variance within-family is biased due to existence of genetic variance within a family population. (3) Sampling error effects are involved both in parent and in offspring measurements, and in selection of breeding snails.

Most sources of bias cause overestimation of heritability values. But using the same populations, relative values for heritability indicate differences in genetic influence among traits. Furthermore, information from family populations is arguably of more relevance when making predictions of selection response. The results suggest that individual selection is effective for growth-related traits which showed high heritability and family selection is useful for heterotic effects in reproductive-related traits which showed low heritability.

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