

Effects of food availability and age on the reproductive effort of the apple snail, *Pomacea canaliculata* (Lamarck) (Gastropoda: Ampullariidae)

Gerardo F. Estoy, Jr.,^{*,1} Yoichi Yusa,² Takashi Wada,² Hironori Sakurai and Koji Tsuchida

Laboratory of Entomology, Faculty of Agriculture, Gifu University, Gifu 501–1193, Japan

² National Agricultural Research Center for Kyushu Okinawa Region, Nishigoshi, Kumamoto 861–1192, Japan

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Abstract

The effects of food availability and age on the reproductive traits of *Pomacea canaliculata* were determined in snails fed at three food levels under laboratory conditions (14L:10D; 25°C). In males, copulation frequency tended to increase with age, while food availability did not affect copulation frequency. In females, spawn production was lower in food-limited conditions, but current or weight-specific reproductive effort (RE) did not differ among food levels. The weight-specific RE and spawn frequency of the well-fed females decreased with age, but their current RE increased with age.

Key words: *Pomacea canaliculata*, food, age, reproductive effort

INTRODUCTION

Organisms should optimize reproductive allocation for maximization of fitness in a given environment (Roff, 1992). The two main determinants of reproductive allocation are when to start allocation to reproduction (age at maturity) and after maturation, what proportion of assimilated energy to allocate to reproduction (reproductive effort, abbreviated as RE). Current and weight-specific RE are probably the most widely used indices (see reviews by Carefoot (1987) and Roff (1992)). Current RE is defined as proportion of resources allocated to reproduction instead of growth, and weight-specific RE is the amount of resources allocated to reproduction (reproductive output) per unit time in a given body weight (Hughes and Roberts, 1980; Carefoot, 1987).

Among various factors possibly affecting RE, the effects of age on RE have received considerable attention both theoretically (Roff, 1992) and empirically in gastropods (Browne and Russell-Hunter, 1978; Hughes and Roberts, 1980; Perron, 1982). On the other hand, effects of food availability on RE have been less well investigated (Calow and Woollhead, 1977). In particular, very little is known about how direct manipulation of food

availability affects RE in gastropods.

The apple snail, *Pomacea canaliculata* (Lamarck) is indigenous to South America. The snail has invaded into many tropical and temperate Asian countries (Halwart, 1994; Wada, 1999). Their distribution expanded and the snails became a major pest on rice there, not only because of voracious feeding on rice seedlings (Halwart, 1994; Wada, 1999) but also because of high reproductive activities (Tanaka et al., 1999). Therefore, studies on the reproduction of the snail and factors affecting it are needed. Although no information on current RE has been available in *P. canaliculata*, weight-specific RE has been studied in the Argentinean snails by Estebenet and Cazzaniga (1993) and Albrecht et al. (1999). However, these studies are based on relatively short observation periods of 28–41 d, hence the effects of age on RE remain unknown for this snail.

A series of laboratory experiments was undertaken to ascertain how the snails respond to food availability and age with reference to reproduction. The effects of food availability on age and size at maturity were reported in a previous paper (Estoy et al., 2002). In that paper, we found that food availability did not affect age at first copulation in males, while females at a high food level started

* To whom correspondence should be addressed at: E-mail: gfestoy@philrice.gov.ph

¹ Present address: Crop Protection Division, Philippine Rice Research Institute (PhilRice), Maligaya, Science City of Munoz, Nueva Ecija 3119, Philippines

both copulation and spawning earlier than those at lower food levels. Since growth rates were higher at a high food level, body sizes at the first copulation and spawning of well-fed snails were larger in both sexes. The present paper deals with the effects of food availability and age on traits relevant to the other determinants of reproductive allocation, RE, after the snails reached sexual maturity.

MATERIALS AND METHODS

General methods. The details of the experimental procedures have been reported in Estoy et al. (2002). To summarize, *P. canaliculata* were collected from rice fields in Shichijo, Kumamoto, Southwest Japan. Test male and female snails (initial shell height=15.0–18.0 mm) were paired with mature snails of the opposite sex (27.5–30.0 mm). Each pair was reared in a 2.3 l plastic pot under laboratory conditions (14L:10D; 25°C). The pot was covered with fine netting to prevent snail escape, and a plastic bag (260 mm×380 mm) was placed inside the pot before addition of water to facilitate spawn collection. The pairs were randomized in terms of body size and assigned to one of the following food treatments: high food level (sufficient quantity of cabbage leaves was available daily), medium food level (fed 4 d/wk) and low food level (fed 2 d/wk). The pairs were supplemented with carp pellets (32% protein content; “Hikari,” Kyorin Co., Ltd., Himeji, Japan) at 1 pellet (0.2 g)/wk in all the food treatments. Water (approximately 1.7 l) was changed twice a week, and a small amount of powdered oyster shell was added as a calcium supply.

At each food level, 40 test males and 60 test females with their partners were used. Their weight (blotted dry) was measured at almost biweekly intervals from the start until the end of the experiment (182 d). Copulation and spawning were checked twice daily (8:30–9:30 am and 8:30–9:30 pm). Spawns were collected as soon as possible by cutting off the spawned area of the plastic bag. They were individually placed in petri dishes, weighed without the cut plastic pieces after 3–5 d, and incubated at 25°C. Hatched and unhatched eggs were counted after 14–21 d.

Effects of food availability on reproductive traits. Various reproductive traits of male and female snails were compared among the three food

levels. For each sex, the duration from the first copulation or spawning up to the end of the experiment varied among individuals. Thus, a compromise had to be made between the length of the observation periods and the number of individuals available for the analyses. Based on the collected data, we decided to use the data for 38 d after the first copulation (for both sexes) and 37 d after the first spawning (for females) as bases of comparison. Individuals with shorter observed reproductive periods (including dissected samples; Estoy et al., 2002) or those showing only one or no spawning or copulation throughout the observation period were excluded from the analysis.

Since body weight was measured at almost biweekly intervals, body weight at the first copulation or spawning was estimated assuming a linear growth between the two measurements.

Effects of age on reproductive traits. In males, the effects of age on reproduction were analyzed at all food levels. Based on the collected data, males with a minimum observed reproductive period of 83 d were used for analyses at all food levels, since food availability did not affect age at maturity (Estoy et al., 2002). Only males that copulated at least twice throughout the observation period were used for the analysis.

Since females fed at the high food level matured earlier than those at lower food levels (Estoy et al., 2002), longer records of reproduction were available for these females. Thus, the effects of age on reproductive traits were analyzed mainly in the well-fed females. Females with a minimum observed reproductive period of 83 d, and showing at least two spawning events throughout the observation period, were used for the analysis. Additionally, females fed at the medium food level were also analyzed. In this case, those with a minimum observed reproductive period of 65 d were used for the analysis. No analysis was made on females at the low food level, as their observed reproductive periods were in most cases too short to analyze age effects.

For both sexes, the observed reproductive period of each individual was divided into three phases (early, middle and late). The early or middle phase had the duration of 30 d, while the late phase continued to the end of the experiment, resulting in various durations among individuals. However, this method should cause a systematic skew of overesti-

Table 1. Effects of food availability on the reproductive traits (mean \pm SD) of male *Pomacea canaliculata* within 38 d after first copulation

Food level	N	No. of copulations/d	Body weight at first copulation ^a (g)	Daily weight change (mg)
High	29	0.18 \pm 0.09	6.43 \pm 2.02 a	45.1 \pm 41.1
Medium	28	0.17 \pm 0.09	5.22 \pm 1.43 b	44.9 \pm 21.9
Low	28	0.19 \pm 0.10	3.66 \pm 1.20 c	37.5 \pm 20.0
p (ANOVA)		>0.7	<0.001	>0.5

^a Values followed by the same letter within a column are not significantly different by Tukey-Kramer test ($p > 0.05$).

mating copulation or spawning frequency in the early phase, since it always starts with a copulation (in the case of males) or spawning (females), whereas the other phases need not. To avoid this problem, the interval between the first and second copulations or spawning events was calculated for each individual, and the start of the early phase was set at half that interval in advance of the first reproduction.

Estimation of reproductive effort. The reproductive effort was estimated in two ways using the formulae by Perron (1982) with some modifications. They are: (1) Current reproductive effort = $R(R + CW)^{-1}$, where R represents the reproductive output (spawn weight (g)) over the fixed duration and CW is the estimated change in the female's body weight (g) over the same duration; (2) Weight-specific reproductive effort = $R(W)^{-1}$, where R is also the reproductive output and W is the estimated female's body weight at the beginning of the observation period.

Statistical analyses. Data on the reproductive traits of snails fed at different food levels were subjected to ANOVA, and multiple comparisons of the means between food levels were evaluated by Tukey-Kramer tests. Data for age-specific observation were analyzed in a repeated measures ANOVA without multiple comparisons, and a Greenhouse-Geisser correction (StatSoft Inc., 1995) was made to reduce the probability of type I error. No transformation was done on most of the data since they were regarded as normally distributed. However, current RE data were right-skewed and hence were log-transformed before being subjected to proper statistical tests. Statistical analyses were done using the statistical software programs StatView Version 5.0.1 (SAS Institute Inc., 1998) and Statistica Pro 98J (StatSoft Inc., 1995).

RESULTS

Effects of food availability on male reproductive traits

Food availability had no effects on the frequency of copulation in male *P. canaliculata* (Table 1). However, food availability did affect the estimated body weight at the first copulation (Table 1; see also Estoy et al., 2002). It also affected body weight at 38 d after the first copulation (mean \pm SD (g) at the high food level = 8.14 ± 2.21 ; medium = 6.93 ± 1.50 ; low = 5.08 ± 1.46 ; $p < 0.001$; ANOVA). There was no difference in daily weight change among food levels (Table 1).

Effects of age on male reproductive traits

The effects of age on male reproductive and growth traits were generally similar among the different food levels (Table 2). The frequency of copulation tended to increase with age at all three food levels. The difference among reproductive phases of ca. 30 d was significant at the medium and low food levels, but not at the high food level (Table 2). The estimated body weight at the start of each reproductive phase increased significantly with age at all food levels, but the daily weight change decreased significantly, indicating the growth rate decreased with age.

Effects of food availability on female reproductive traits

No significant differences among food level treatments were found in the frequencies of copulation and spawning in females (Table 3). On the other hand, significant differences were observed in the daily spawn production (i.e., total spawn weight/d) of females fed at different food levels. Multiple comparisons between food level treatments revealed a significant difference in spawn

Table 2. Effects of reproductive phase (ca. 30 d) on the reproductive traits (mean \pm SD) of male *Pomacea canaliculata* fed at three food levels

Food level	Reproductive phase ^a	N ^b	No. of copulations/d	Body weight at start (g)	Daily weight change (mg)
High	Early	29	0.14 \pm 0.10	5.77 \pm 2.22	57.0 \pm 61.6
	Middle	29	0.16 \pm 0.11	7.47 \pm 2.12	35.9 \pm 36.7
	Late	29	0.19 \pm 0.10	8.55 \pm 2.05	24.3 \pm 17.3
	<i>p</i> (repeated measures ANOVA)		0.10	<0.001	<0.05
Medium	Early	26	0.13 \pm 0.08	4.49 \pm 1.58	61.3 \pm 35.7
	Middle	26	0.14 \pm 0.13	6.33 \pm 1.52	41.4 \pm 15.9
	Late	26	0.23 \pm 0.13	7.57 \pm 1.49	22.3 \pm 17.0
	<i>p</i> (repeated measures ANOVA)		<0.001	<0.001	<0.001
Low	Early	28	0.14 \pm 0.09	3.46 \pm 1.22	41.6 \pm 23.4
	Middle	28	0.20 \pm 0.11	4.71 \pm 1.35	25.2 \pm 13.5
	Late	28	0.22 \pm 0.10	5.47 \pm 1.58	20.6 \pm 15.6
	<i>p</i> (repeated measures ANOVA)		<0.01	<0.001	<0.001

^a Starts at half of the interval between first two copulations in advance of first copulation.

^b Snails that copulated for at least 83 d.

production between snails fed at the high food level and those fed at the low food level (Table 3). The difference in daily spawn production is due to the variation in the number of eggs per spawn, rather than in spawning frequency or egg weight, since only egg number was significantly different among the food levels. Most of these reproductive traits showed large variance among individuals, as indicated by large standard deviations.

Food availability affected estimated body weight at the first spawning (Table 3; see also Estoy et al., 2002). Food availability also affected body weight at 37 d after the first spawning (mean \pm SD (g) at the high food level=12.19 \pm 3.05; medium=10.00 \pm 2.47; low=8.49 \pm 1.16; p <0.01; ANOVA). However, there was no difference in the daily weight change of females among the food level treatments (Table 3). Current RE was 0.87–0.90, and it did not show a significant difference among the food levels. Also, weight-specific RE ranged from 0.015 to 0.022 at different food levels, but the difference was not significant.

Effects of age on female reproductive traits

At the high food level, the frequency of copulation or spawning decreased as the female's age increased (Table 4). Also, daily spawn production (weight) decreased with increasing age. On the other hand, hatchability tended to increase as the

animals got older (p =0.06). Number of eggs per spawn or egg weight did not show significant changes with age.

Estimated body weight at the start of each reproductive phase increased significantly with advancing age (Table 4). However, the daily change in body weight decreased greatly, indicating that the growth rate decreased with age and almost stopped at the late phase of reproduction.

Current RE increased significantly with age (Table 4). In the middle or late phase, current RE increased up to 0.96, indicating that 96% of the total weight increment was allocated to reproduction and only 4% to growth. On the other hand, weight-specific RE decreased significantly with age.

At the medium food level, significant differences are less likely to be detected because of the smaller number of individuals (N =7) with shorter observed reproductive periods (65 d or more). However, in general, females at the medium food level responded to age similarly to the well-fed females: their spawning frequency decreased with age, although the differences in copulation frequency or in daily spawn production were not significant (Table 4). Body weight at the start of each reproductive phase increased significantly, but daily weight change tended to decrease with age (p =0.08). Like well-fed females, current RE of fe-

Table 3. Effects of food availability on the reproductive traits (mean ± SD) of female *Pomacea canaliculata* within 37 d after first spawning

Food level	N	No. of copulations /d ^a	No. of spawnings /d	Total spawn weight/d ^b (g)	No. of eggs /spawn ^b	Egg weight (mg)	Hatchability (%)	Body weight at first spawning ^b (g)	Daily weight change (mg)	Reproductive effort	
										Current	Weight-specific
High	17	0.28±0.14	0.14±0.04	0.23±0.10 a	167.8±37.7 a	9.2±1.4	65.0±11.3	11.48±3.32 a	22.9±29.7	0.90±0.13	0.022±0.008
Medium	11	0.24±0.11	0.12±0.03	0.17±0.06 ab	158.8±45.1 ab	8.8±1.4	70.0±14.2	9.13±2.48 ab	24.5±20.9	0.87±0.08	0.018±0.006
Low	9	0.22±0.15	0.11±0.05	0.12±0.04 b	126.9±24.0 b	9.2±1.1	62.0±15.8	8.16±1.20 b	13.6±35.3	0.90±0.18	0.015±0.007
p (ANOVA)		>0.4	>0.1	<0.01	<0.05	>0.7	>0.4	<0.05	>0.6	>0.9	>0.1

^aData within 38 d after first copulation.
^bValues followed by the same letter within a column are not significantly different by Tukey-Kramer test ($p>0.05$).

Table 4. Effects of reproductive phase (ca. 30 d) on the reproductive traits (mean ± SD) of female *Pomacea canaliculata* fed at two food levels

Food level	Reproductive phase ^a	N ^b	No. of copulations /d ^c	No. of spawnings /d	Total spawn weight/d (g)	No. of eggs/spawn	Egg weight (mg)	Hatchability (%)	Body weight at start (g)	Daily weight change (mg)	Reproductive effort	
											Current	Weight-specific
High	Early	10	0.36±0.11	0.13±0.04	0.21±0.09	174.3±31.8	9.2±1.4	57.5±11.2	11.17±3.05	40.3±41.3	0.85±0.15	0.019±0.006
	Middle	10	0.33±0.11	0.13±0.04	0.21±0.12	151.6±39.0	10.2±1.9	70.3±10.0	12.37±2.52	6.3±12.0	0.96±0.07	0.016±0.007
	Late	10	0.22±0.12	0.08±0.04	0.12±0.09	149.6±46.6	10.2±1.8	71.5±17.8	12.56±2.51	1.8±8.6	0.96±0.07	0.010±0.006
p (repeated measures ANOVA)												
			<0.01	<0.05	<0.05	>0.2	>0.2	0.06	<0.01	<0.05	<0.05	<0.05
Medium	Early	7	0.24±0.15	0.12±0.05	0.14±0.08	144.9±45.9	7.9±1.3	63.0±13.0	8.44±2.80	28.7±25.4	0.83±0.12	0.016±0.007
	Middle	7	0.21±0.06	0.10±0.04	0.10±0.04	119.0±31.2	9.5±2.1	68.6±19.9	9.30±2.87	9.2±14.9	0.90±0.10	0.011±0.003
	Late	7	0.30±0.12	0.09±0.05	0.09±0.06	110.3±45.8	9.1±1.4	69.3±24.3	9.57±2.89	0.9±2.4	0.99±0.02	0.009±0.005
p (repeated measures ANOVA)												
			>0.3	<0.05	>0.1	>0.1	0.09	>0.6	<0.01	0.08	0.07	0.05

^aStarts at half of the interval between first two spawnings in advance of first spawning.
^bSnails that spawned for at least 83 d (high food level) or 65 d (medium).

males at the medium food level tended to increase with age, while weight-specific RE tended to decrease with age, although neither reached a statistically significant level (Table 4).

DISCUSSION

Male RE

In *P. canaliculata*, copulation frequency did not differ among males at different food levels. Unfortunately, male reproductive output is very difficult to quantify, because not only sperm used in a copulation but also energy needed for the act of copulation and male-male competition should be quantified. Thus, current or weight-specific RE cannot be compared among males at different food levels. Similarly, the effect of age on weight-specific RE in males cannot be specified: copulation frequency generally increased with age in males, but body weight also increased with age. Thus, weight-specific RE might increase, decrease, or remain constant, depending on the reproductive output per copulation in males of different ages.

However, the effect of age on male current RE can be inferred. As already stated, male copulation frequency generally increased with age. This suggests that male reproductive output per unit time also increased with age, if reproductive output per copulation in older, larger males is similar or larger than that of young, smaller ones. On the other hand, growth (daily weight change) in male *P. canaliculata* decreased with age at all food levels. The decreasing growths, together with the likely increase in reproductive output, suggest that current RE increases with age in males. The adaptive significance of the increase in current RE will be discussed later, as a similar increase was found in females.

Male growth after reaching sexual maturity (37.5–45.1 mg/d depending on the food level; Table 1) was larger than that of females (13.6–24.5 mg/d; Table 3). This suggests that more energy is allocated to growth in males than females, and hence current RE is probably lower in males. The lower current RE in males appears to be related to the earlier maturation of males than females (initiation of copulation 21–42 d earlier in males; Estoy et al., 2002), but the adaptive significance remains unclear.

Effects of food availability on female RE

Well-fed females grew larger and were more fecund than poorly-fed ones. As growth and fecundity responded similarly with respect to food availability, neither current nor weight-specific RE differed among food levels. Since mortality is a major ultimate factor determining RE (Calow and Woollhead, 1977; Hughes and Roberts, 1980; Roff, 1992), the lack of a difference in RE is expected when mortality is independent of food availability. Actually, snail mortality did not differ among food levels in the laboratory (Estoy et al., 2002). In the paddy field, mortality of snails over 15 mm in shell height is very low during the rice-growing season and is irrespective of snail density or size (Tanaka et al., 1999). Thus, food availability is unlikely to affect snail mortality in the field as well.

In females fed at different food levels, current RE was 0.87–0.90. Also, current RE increased up to 0.96 (high food level) or 0.99 (medium) with increasing age. These values suggest that 90% or so of resources (weight basis) were allocated to reproduction. This value appears to be constantly high compared with other gastropods (0.40–0.53 in *Aplysia punctata*, 0.2–1.0 depending on age and species in *Littorina* spp., 0.35–0.85 in *Conus pennaceus*; Carefoot, 1987), although care must be taken for the units (weight, volume or calories) on which calculations of RE are based. Higher RE is expected in semelparous (reproduce only once throughout life) organisms than iteroparous ones (reproduce more than once), since semelparous organisms should use all their resources for reproduction if death will definitely occur just after reproduction (Roff, 1992; in snails, Browne and Russell-Hunter, 1978; Calow, 1978). Apple snails in Japanese paddy fields are probably semelparous because adult snails over 30 mm generally do not survive during winter (Kiyota and Okuhara, 1987; Oya et al., 1987). Interestingly, weight-specific RE in this study (0.015–0.022) appears to be higher than that of Argentinean conspecifics (0.007 in Estebenet and Cazzaniga, 1993; 0.007–0.017 in Albrecht et al., 1999; after converting into a daily basis). *P. canaliculata* show both semelparity and iteroparity depending on the environment (Estebenet and Cazzaniga, 1993), and the Argentinean snails experimented on were apparently iteroparous (Estebenet and Cazzaniga, 1993; Albrecht et al., 1999).

Effects of age on female RE

Daily spawn production decreased with age in females at the high food level. Their body weight increased with age, but the growth rate slowed down drastically. Consequently, current RE increased with age, while weight-specific RE decreased with age. Although less clear, similar trends were observed in females at the medium food level. The observed reproductive periods of well-fed females (83 d or more) are long enough to cover most of the reproductive periods of the snails in the paddy field (end of June to early October; Tanaka et al., 1999). The changes in RE observed in this study therefore appear to reflect their life history strategies.

The decrease in weight-specific RE may simply reflect an allometric law that, in general, assimilated energy increases with body weight of an organism, but with a rate less than 1 (Roff, 1992). In fact, such a decrease in weight-specific RE has been reported in several other gastropods (Browne and Russell-Hunter, 1978; Hughes and Roberts, 1980). On the other hand, the increase in current RE may represent a trade-off between current and future reproduction. In theory organisms should generally increase current RE with age, since future reproductive value is reduced as mortality increases with age (Browne and Russell-Hunter, 1978; Roff, 1992). Increase in current RE has also been reported in other gastropods (Browne and Russell-Hunter, 1978; Hughes and Roberts, 1980; Perron, 1982; Carefoot, 1987).

Implications for snail ecology in the field

The high RE of *P. canaliculata* suggests high energy allocation to reproduction. Together with its voracious feeding behavior, this trait appears to make the snail an important biological invader and agricultural pest (Halwart, 1994; Wada, 1999). Plasticity in the life history showing both semelparity and iteroparity (Estebenet and Cazzaniga, 1993), which accompanies changes in RE, also enables this snail to adapt to various environments.

As a result of inhabiting various environments, snail populations might have adapted to the local environments. Recently, Martin and Estebenet (2002) reported a local variation in the reproductive output in Argentinean *P. canaliculata* and showed that the variation is partly genetic. After introduction to Asia some 20 years ago, snails in temperate Japan

and those in tropical areas like the Philippines have been faced different selection pressures from each other, and probably also from Argentinean conspecifics. Thus, it is interesting to compare life history traits including RE between different localities.

Comparable RE among food levels means that when food availability is high, snails attain higher reproductive output. This characteristic is probably the main cause of the density dependent reproduction in this snail (Tanaka et al., 1999). Under a low density of snails food availability for each snail is likely to be high, resulting in more offspring per female. Thus, reducing snail density to some extent will have only a minor effect on the snail density in the next generation (Tanaka et al., 1999). Instead, reducing food availability for snails is effective, as it delays sexual maturity of prospective female parents (Estoy et al., 2002). This study has clarified another merit of reducing food availability: food limitation will reduce the number of offspring a female produces per unit time even after maturity. For successful snail control, practical techniques to reduce food availability for snails should be developed (Estoy et al., 2002).

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