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# An Experimental Study of Growth and Reproduction in the Hawaiian Tree Snails *Achatinella mustelina* and *Partulina redfieldii* (Achatinellinae)[1]

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ABSTRACT: Hawaiian tree snails of the subfamily Achatinellinae are unique to the Hawaiian Islands and highly endangered in the wild. Achatinellines are arboreal pulmonate gastropods characterized by slow growth and late age at first reproduction. Objectives of the laboratory studies described here were to add to the understanding of growth and reproduction of achatinelline snails. Juvenile *Partulina redfieldii* (Newcomb) and *Achatinella mustelina* Mighels were kept in laboratory environmental chambers with conditions set to emulate those in the native habitat of *P. redfieldii*. The snails were provided with fresh leaves and branches of *Metrosideros polymorpha* Gaud., a natural substratum for the snails. Laboratory comparisons of *P. redfieldii* and *A. mustelina* maintained with a natural diet augmented or not with cultures of native fungi grown on potato dextrose agar revealed that snails of both species grew significantly faster on the augmented diet and that *P. redfieldii* attained sexual maturity at an earlier age. Comparison of growth of *P. redfieldii* in the laboratory with similarly sized snails in the field revealed significantly faster growth in the laboratory animals. There was no significant difference between growth rates of *A. mustelina* provided with an augmented food supply in the laboratory and similarly sized animals in the field. It is likely that food availability limits growth rate in the field for *P. redfieldii*, but there is no evidence that growth in the field for *A. mustelina* is food-limited. However, the natural diet or temperature-humidity requirements of *A. mustelina* may not have been adequately met in the laboratory, obscuring laboratory-field comparisons. *Partulina redfieldii*, collected from the field as adults and maintained in isolation in the laboratory, produced offspring for at least 4 yr without the opportunity to outcross. Fecundity of isolated individuals was comparable with that reported for animals in the field, and there was no indication of fecundity decreasing over time in isolation. In addition, four of five *P. redfieldii* isolated as juveniles attained apparent sexual maturity at ages of 3.2 to ca. 5 yr. A single offspring was produced by one of these snails, suggesting self-fertilization as one mechanism allowing the species to reproduce for prolonged periods of time in the absence of mates.

BECAUSE GEOGRAPHIC ISOLATION often leads to evolutionary divergence, the flora and fauna of isolated archipelagos are frequently useful in the study of processes of speciation. Tropical islands are especially interesting, because many bear a greater variety of habitats than are typically found on temperate islands (Clarke and Murray 1969). Geographically isolated, the Hawaiian Islands exhibit a great diversity of climates and habitats ranging from deserts and tundras to rain forests and bogs. This combination of geographic isolation and a diverse array of habitat types has resulted in an un-

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paralleled degree of endemism. It has been estimated that 95% of the terrestrial native Hawaiian flora and fauna are endemic (Carlquist 1980). Over 250 species of fruit flies (Carlquist 1980) and ca. 60 species of passerine birds (Freed et al. 1987) have been described for the Hawaiian Islands. Among land molluscs, ca. 800 species have been described (Zimmerman 1948), over 99% of which are endemic (Carlquist 1980).

Tree snails of the subfamily Achatinellinae, family Achatinellidae, are unique to the Hawaiian Islands. Achatinelline snails are arboreal, feeding on epiphytic fungi that grow on native plants. Students of animal evolution have long been attracted to these snails because of their striking radiations of shell color, banding patterns, and shapes (Gulick 1905), but only five modern papers have addressed major life-history characteristics of achatinelline snails (Hadfield and Mountain 1980, Severns 1981, Hadfield 1986, Hadfield and Miller 1989, Hadfield et al. 1993). A common suite of life-history traits is reported for all achatinelline species thus far studied: they are born live and relatively large (4–5 mm), grow slowly, become reproductively mature at a relatively late age, and have low fecundity compared with most other terrestrial snails (e.g., *Achatina fulica* [Kekauoha 1966], *Partula* spp. [Murray and Clarke 1966], *Liguus fasciatus* [Voss 1976], *Caracolus* and *Polydontes* spp. [Heatwole and Heatwole 1978]). This achatinelline life-history pattern renders these endemic snails extremely vulnerable to introduced predators and environmental disturbances.

It was estimated more than 20 yr ago that at least 50% of the Hawaiian terrestrial snail species had become extinct since Western colonization of the Islands (Y. Kondo, unpubl. ms.). Causes of this massive decline range from habitat loss (e.g., agriculture) to shell collectors, and most important in rcent times, to predation (Hadfield 1986). Introduced rats (*Rattus* spp.) and a carnivorous snail, *Euglandina rosea*, are quickly decimating many remaining achatinelline populations, especially the *Achatinella* spp. of O'ahu. *Euglandina rosea*, introduced into many Pacific Islands in an ill-conceived attempt to control the giant African snail, *Achatina fulica*, has proven to be minimally efficient in its intended role but is proving to be the primary agent of extinction of several native snail faunas (Van der Schalie 1969, Hadfield and Mountain 1980, Clarke et al. 1984, Murray et al. 1988). On 13 January 1981, the entire genus *Achatinella* (comprising some 41 species), endemic to the island of O'ahu, was placed on the U.S. Fish and Wildlife Service Endangered Species List, the first taxon above the level of species to be so listed. The recovery plan for the O'ahu tree snails of the genus *Achatinella* signaled the necessity of captive propagation as an integral part of the recovery process (U.S. Fish and Wildlife Service 1992).

A captive-rearing program for achatinelline snails was started in 1986 at the University of Hawai'i. The first goal of this program is to preserve in the laboratory a representative sampling of the genetic diversity of remaining populations of achatinelline snails. A second purpose of the captive-rearing program is to generate sufficient numbers of laboratory-born snails to enable their introduction to the wild when existing hazards to the species are reduced or eliminated (i.e., when predators are controlled). To create laboratory conditions conducive to optimal growth, fecundity, and survivorship, understanding the basic biology of the target animal is essential. To this end, data gleaned from field and laboratory studies enhance our ability to meet the objectives of a captive propagation program; for instance, environmental parameters (temperature, humidity, rainfall) are monitored in the field and emulated in the laboratory. Laboratory studies, on the other hand, provide an opportunity to isolate and investigate environmental parameters that cannot be controlled in the field. Although results of ex situ studies may not duplicate what is happening in nature, the data obtained from such studies provide useful insights into the biological needs and capabilities of the animal.

The research questions addressed in this study arose from preliminary observations of laboratory populations of an achatinelline species from the island of Moloka'i, *Partu-*

*lina redfieldii* (Newcomb). Those studies suggested that *P. redfieldii* grew faster in the laboratory than in the field, leading us to investigate the basis for the difference. Assuming that the increased growth rate observed earlier was not an artifact of a small or somehow biased sample, we tested the hypothesis that growth rate is food-limited in the field for two species of achatinelline snails, *P. redfieldii*, and a species from O'ahu, *Achatinella mustelina* Mighels. Using a strictly controlled laboratory environment, we sought to determine if increased food availability enabled juveniles of these species to grow at an accelerated rate, and then we compared snail growth rates between the laboratory and field. We also considered the alternative hypothesis that optimized environmental conditions created in the laboratory, perhaps by providing greater feeding time, promote increased growth rates.

The second preliminary laboratory observation that stimulated this study was that individuals of *Partulina redfieldii*, isolated in the laboratory as adults, continued to produce offspring for 2 yr in the absence of a mate. The question addressed here is whether there is a cost to reproduction in isolation, such as lowered fecundity or lowered survivorship of offspring. We also hoped to learn whether reproduction in the absence of mating partners results from sperm storage, which would require at least one mating experience, or, alternatively, from self-fertilization or parthenogenesis.

Successful captive propagation of endangered species such as the achatinelline snails relies on in-depth understanding of the animals' life histories, and at the same time, in-depth understanding of life histories may be applicable to management of field populations. Thus, the ultimate objectives of the laboratory studies presented here were to elucidate factors limiting growth and reproduction in achatinelline snails and thereby to gain insight into how environmental parameters influence growth, age at sexual maturity, and, by inference, generation time. Discoveries made in the laboratory, such as the ability of achatinelline snails to continue reproducing for years without mating, provide insight into the evolution of the snails, provide a basis for further investigation, and enhance the prospect that populations can recover from extreme environmental catastrophes, even when the likelihood of a snail encountering a mating partner is severely reduced.

## MATERIALS AND METHODS

### *General Laboratory Setup*

All animals used in this study were kept in screened containers within environmental chambers set to emulate field conditions. Temperatures fluctuated between 16°C at night and 20°C during the day. The chambers ran on a 12-hr dark cycle, and a sprinkler system delivered a fine water spray every 8 hr for 2-min intervals, 5 days per week. Watering was suspended 2 days of the week (Friday and Sunday) to produce a cycle of wet and dry periods approximating the natural situation. All containers (replicate groups) were provided each week with freshly collected, leafy branches of *Metrosideros polymorpha* Gaud., a tree native to Hawai'i, on which the snails typically live. The sources of food were (1) the light film of natural fungi that grow epiphytically on leaves and branches of *M. polymorpha* and (2) two strains of fungi, cultured in the laboratory on Difco brand potato-dextrose agar (PDA). The original laboratory-cultured fungal stocks were isolated from leaf surfaces of *M. polymorpha*.

### *Effects of Enhanced Food Supply on Growth and Survivorship*

All juvenile snails used in this study were born in the laboratory to snails collected as adults from the field. The 26 mothers of the juvenile *Partulina redfieldii* were collected from The Nature Conservancy's Kamakou Preserve on the island of Moloka'i at an elevation of 1300 m, four between November 1986 and July 1987, 12 in June 1989, and a final 10 in May 1991. The 22 adult snails

TABLE 1

SOURCES OF SNAILS USED IN GROWTH AND ISOLATION STUDIES

| SPECIES | COLLECTION INFORMATION | | | NO. COLLECTED | ASSIGNED TREATMENT | OFFSPRING TREATMENT |
|---|---|---|---|---|---|---|
| | DATE | LOCATION | AGE | | | |
| *P. redfieldii* | January 1986–July 1987 | Kamakou Preserve | Adults | 4 | None | Growth study |
| *P. redfieldii* | June 1989 | Kamakou Preserve | Adults | 12 | 6 snails isolated June 1989 | Growth study, isolation study |
| *P. redfieldii* | May 1991 | Kamakou Preserve | Adults | 10 | 5 snails isolated February 1992 | Growth study |
| *P. redfieldii* | June 1989 | Below Kamakou Preserve | Juvenile | 1 | Isolated May 1991 | None |
| *A. mustelina* | May 1990 | Honouliuli Preserve | Adults | 12 | None | Growth study |

collected in June 1989 and May 1991 and kept in individual containers (detailed in "Effects of Isolation," below) were mothers of the juveniles utilized in the growth study. The 12 mothers of the juvenile *Achatinella mustelina* were collected from The Nature Conservancy's Honouliuli Preserve, O'ahu, at an elevation of 600 m on 12 May 1990. A summary of the sources of snails used in both studies is provided in Table 1.

The juvenile snails were separated into two treatment groups. The "food-enhancement group" was provided with laboratory cultures of fungi, in addition to branches and leaves of *M. polymorpha*. The control group received nutrition strictly from the natural film of epiphytic fungi on leaves and branches of *M. polymorpha*. Juvenile snails were assigned randomly to a treatment group and to a container (replicate) within each treatment group by first marking each snail with a unique code and then pulling tags with the same set of codes out of a bag. A cursory check of the resultant assignment was made to ensure that no containers were overly represented by the offspring of any one mother. There were three replicates for each treatment group of *P. redfieldii*, each replicate initially containing six or seven individuals with initial shell lengths ranging from 4.31 to 20.99 mm. Two replicates were established for each treatment group of *A. mustelina*; each replicate initially contained six or seven individuals, ranging from 5.00 to 14.59 mm in initial shell length. The location of each replicate container within the environmental chambers was changed weekly, based on a random schedule using the same technique described for the treatment container assignments. Length and weight of each snail were recorded on a bimonthly basis.

The data for juvenile growth rates from field populations, used for comparisons with laboratory animals of similar size, were taken from long-term field studies conducted by Hadfield et al. (1993 and unpubl. data). The study populations of *A. mustelina* are located in Honouliuli Preserve, O'ahu, and the *P. redfieldii* populations are located in Kamakou Preserve, Moloka'i. The populations studied within these preserves also served as source populations for the snails observed in the laboratory. The methods used in the mark-recapture studies of field populations were described by Hadfield and Mountain (1980).

### *Effects of Isolation on Fecundity and Size at Birth*

Juvenile and adult *P. redfieldii* were kept in isolation to measure fecundity in the absence of breeding; apparent age at sexual maturity, as indicated by the addition of a shell lip (callus at the shell aperture), was also recorded. Six adult snails were collected from the field in June 1989 and maintained in individual terraria. Ten additional adults were collected in May 1991 and put into two containers, each housing five snails. Beginning

2 February 1992, five of the snails collected in May 1991 were transferred to individual containers, but were placed together in a single container overnight once a week to provide an opportunity for mating, to serve as a control group. For the purposes of this study, birth data for offspring of isolated adults were recorded up to 30 November 1992. Dates of births, sizes, and weights of all offspring from each adult were recorded. Five juvenile *P. redfieldii* were isolated in May 1991. Four of these juveniles were born between 19 June 1989 and 1 February 1990 to snails collected as adults in June 1989 from Kamakou Preserve. The fifth snail was collected by accident as a juvenile of unknown age and unrecorded size in June 1989 near the Waikolu Lookout, just below the Kamakou Preserve boundary; the size of this snail when first measured in June 1990 suggests an age of 1.5–2.0 yr when collected. Until the latter snail was placed in isolation, it was kept in a container with two juveniles of *A. mustelina*.

### *Data Analyses*

GROWTH STUDY: A nested analysis of variance was employed to test for differences in growth rates between snails in laboratory treatments: growth rates of individual snails were nested within containers within treatment groups (enhanced food supply versus control). A growth rate for each snail was calculated by dividing the change in length by the duration of the growth period in days. The length of the growth study was 6.5 months for *A. mustelina* and 9.5 months for *P. redfieldii*. An analysis of variance was also used to determine whether there was snail-size bias introduced as a result of the initial container assignment.

Comparisons between a subset of laboratory and field animals were made using Wilcoxon's signed-rank test. To minimize growth-curve effects, the animals used in this analysis were selected in a pairwise manner (one from a laboratory population, one from the field population) on the basis of similarity in shell lengths at the start of the growth study. Changes in shell length over the study period for 10 pairs of *P. redfieldii* were used in this comparison; individuals in each pair differed by less than 5% in initial shell length. Seven pairs of *A. mustelina* were compared; individuals in each pair differed by less than 10% in initial shell length. The time period between initial and final measurements varied between 3 and 4 months among pairs, but was approximately equal within pairs (less than 2 weeks difference).

ISOLATION STUDY: The survival of offspring born to isolated *P. redfieldii* was analyzed as a function of birth size and mother using a logistic regression model. This model is a special case of a general linear model for binary response variables. The analysis was based on whether offspring lived 120 days or more, and the response variable was either positive or negative. Logistic regression was also used to test whether there were significant container (maternal) effects.

Linear regression was used to determine whether there was a relationship between (1) increasing time in isolation of adult *P. redfieldii* and birth size of their offspring and (2) increasing time in isolation and the time interval between successive births.

Polynomial regression (to the fourth order) was employed as a preliminary test, to pursue circumstantial evidence of a trend between the time interval between successive births and birth size of subsequent offspring for isolated adult *P. redfieldii*.

The average birth size for each isolated and nonisolated (control) adult *P. redfieldii* was calculated, and an unpaired *t*-test was used to determine whether there was a difference between birth sizes.

## RESULTS

### *Growth Study*

The results of the analysis of variance suggest that the random assignments made for the natural food versus enhanced food groups did not unduly bias any one container toward larger or smaller snails. For initial

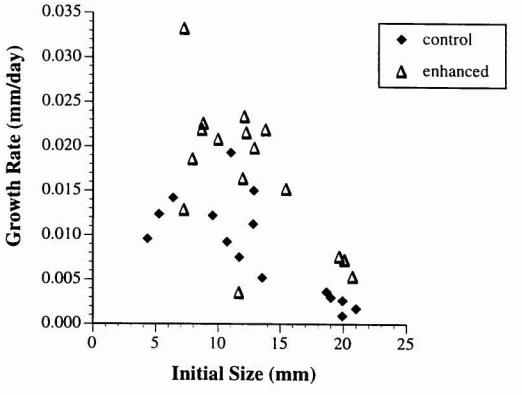


FIGURE 1. Comparison of laboratory-reared *Partulina redfieldii* provided with only the naturally occurring food source (control group) and laboratory snails provided with enhanced food supply. Each symbol represents one snail.

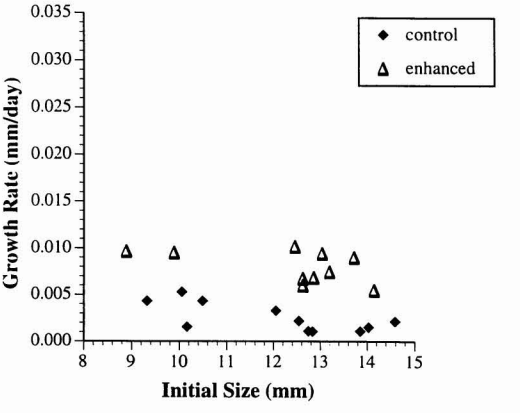


FIGURE 2. Comparison of laboratory-reared *Achatinella mustelina* provided with only the naturally occurring food source (control group) and laboratory snails provided with enhanced food supply. Each symbol represents one snail.

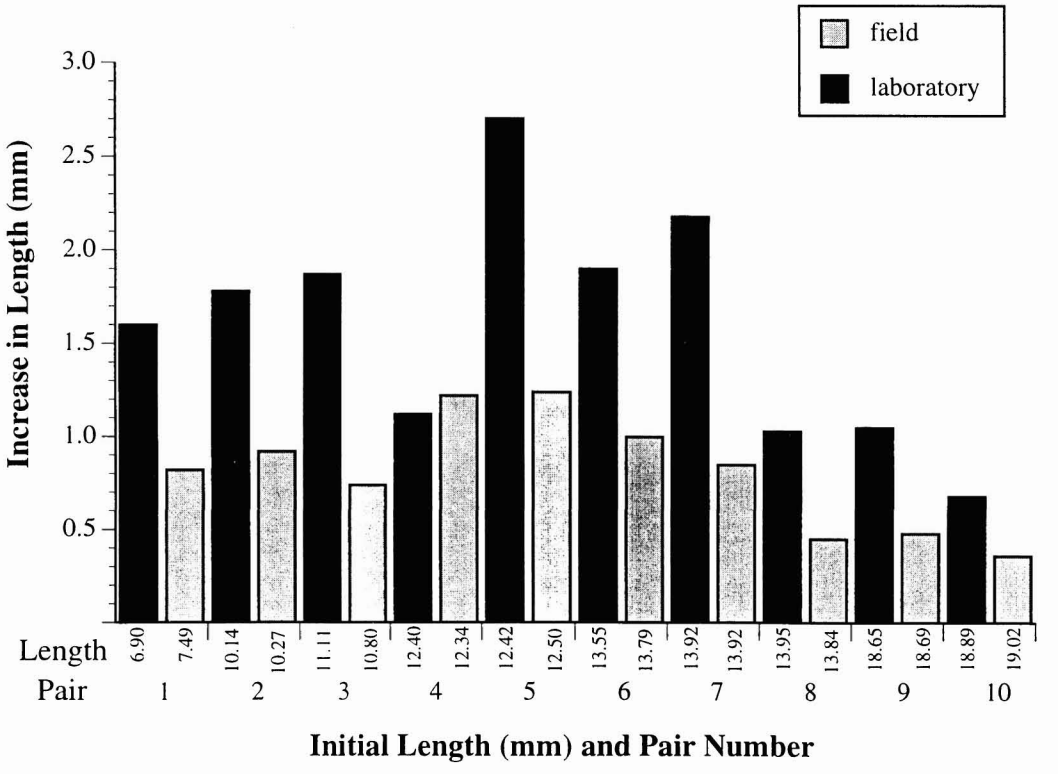


FIGURE 3. Paired comparison of growth of *Partulina redfieldii* raised in the laboratory with enhanced food availability and similarly sized animals in the field. Pairs are arranged by increasing initial shell lengths. Data from 10 pairs were analyzed by Wilcoxon's signed-rank test ($P = 0.0069$).

shell length, there were no significant differences between treatments or containers within treatments for either *P. redfieldii* or *A. mustelina*.

Growth rates of *P. redfieldii* and *A. mustelina* maintained in the laboratory with an enhanced food supply were significantly faster than those of snails maintained with only the naturally occurring food (Figures 1 and 2). The amount of variation attributable to container effects for both species was negligible.

Growth rates of juvenile *P. redfieldii* raised in the laboratory and provided with only the naturally occurring food were significantly faster than those of similarly sized snails in the field ($z = -2.701$) (Figure 3). Growth rates of juvenile *A. mustelina* reared in the laboratory with an enhanced food supply were not significantly different from those of similarly sized snails in the field ($z = -1.859$). However, in four out of seven pairs of *A. mustelina*, field snails actually grew faster than laboratory-reared snails and the results are, in fact, only marginally non-significant (Figure 4).

Six *P. redfieldii* born in the laboratory and raised with an enhanced food supply achieved maximum size and developed a shell lip at the shell aperture. A seventh snail (isolation study), collected from the field as a juvenile, also developed a shell lip. The mean age at sexual maturity for the six snails was 3.35 yr ($\pm 0.52$) and ranged from 2.40 to 3.81 yr. The mean size at sexual maturity was 23.82 mm ($\pm 0.53$) (Table 2).

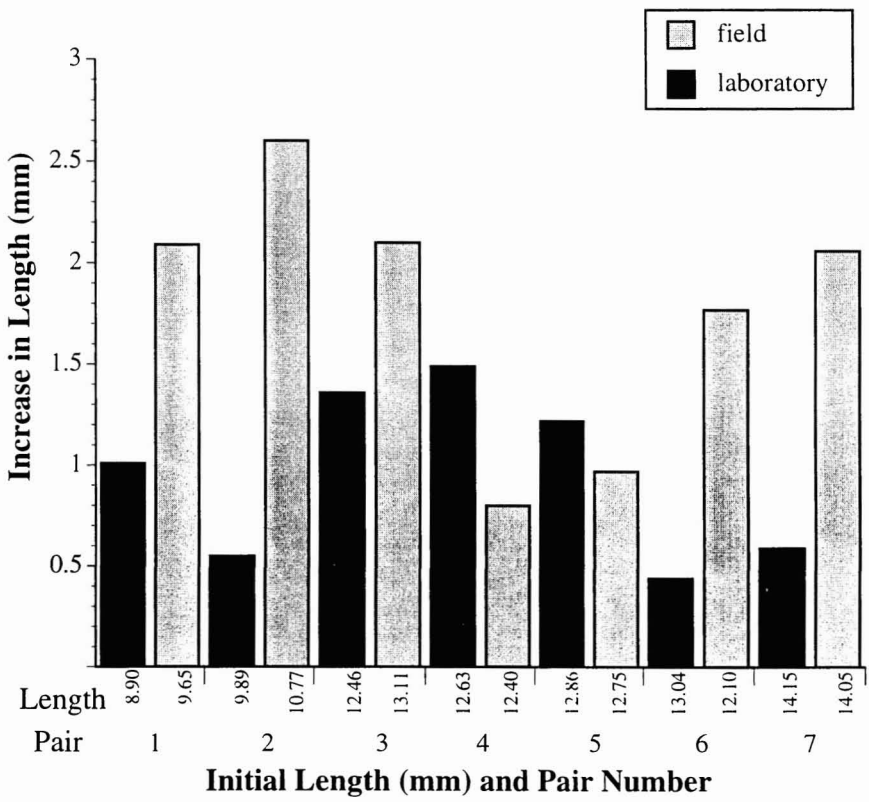


FIGURE 4. Paired comparison of growth of *Achatinella mustelina* raised in the laboratory with enhanced food availability and similarly sized animals in the field. Pairs are arranged by increasing initial shell lengths. Data from seven pairs were analyzed by Wilcoxon's signed-rank test ($P = 0.063$).

TABLE 2

MAXIMUM SIZE AND AGE AT WHICH *Partulina redfieldii* DEVELOPED A SHELL LIP IN THE LABORATORY

| TREATMENT/ CONTAINER | SNAIL (CODE) | BIRTH DATE | SHELL LIP FORMATION | | MAXIMUM SIZE (mm) |
|---|---|---|---|---|---|
| | | | DATE | AGE (yr) | |
| Enhanced 1 | PA | 23 June 1989 | 4 March 1993 | 3.7 | 22.42 |
| Enhanced 2 | BD | 16 November 1990 | 10 April 1993 | 2.4 | 22.70 |
| Enhanced 2 | OD | 21 July 1989 | 4 March 1993 | 3.6 | 23.16 |
| Isolated | YA | 19 June 1989 | 10 April 1993 | 3.8 | 23.82 |
| Isolated | GD | 19 June 1989 | 11 November 1992 | 3.4 | 23.60 |
| Isolated | MA | 1 February 1990 | 27 March 1993 | 3.2 | 23.25 |
| Isolated | OH | ? | 5 June 1992 | ? | 22.55 |

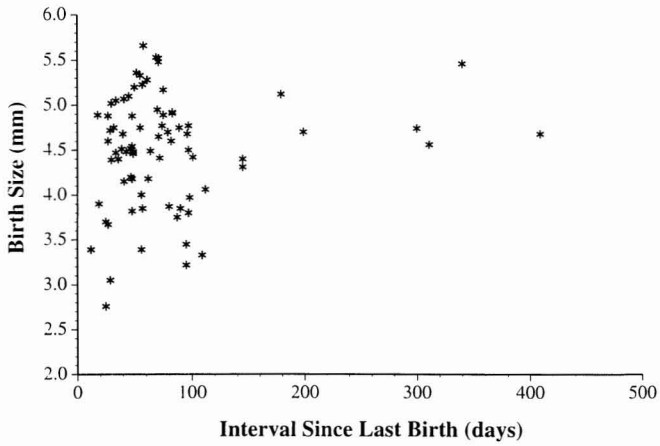


FIGURE 5. Effects of the duration of the interval since the last birth on subsequent birth size of *Partulina redfieldii* born to isolated mothers.

## *Isolation Study*

The average number of offspring per snail per year for isolated *P. redfieldii* was four, and ranged between three and five. A scattergram of birth size versus interval since prior birth suggested that larger than average birth sizes occurred when the interbirth duration was ca. 150 days or longer (Figure 5): there is no statistical evidence of a trend, however. Based on a polynomial regression analysis, birth size cannot be described as a function of interval since prior birth ($r^2 < 0.091$).

Within the 3.5 yr of this study, 36 (42%) of the 85 offspring born to the six isolated *P. redfieldii* died. The frequency distribution

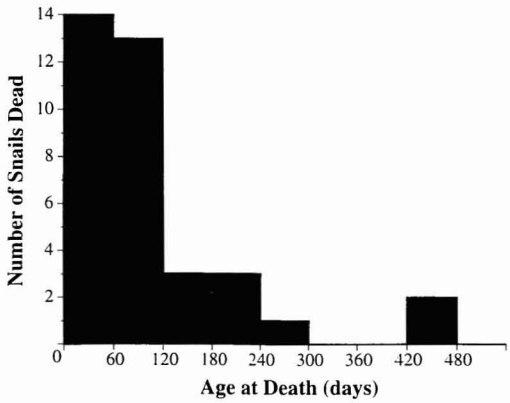


FIGURE 6. Frequency distribution of age at death for *Partulina redfieldii* born to isolated mothers in the laboratory.

of offspring mortality as a function of age (Figure 6) showed that most (74%) died within 120 days of birth. Fitting the data to a logistic regression model revealed that the probability of living longer than 120 days of age increased significantly with increasing birth size (Figure 7).

Birth sizes ranged from 3.05 to 5.66 mm, with a mean of 4.53 mm (±0.62) for offspring of isolated *P. redfieldii* (Figure 8); birth sizes ranged from 3.61 to 4.38 mm with a mean of 4.16 mm (±0.46) for offspring of control snails. Average birth sizes were not significantly different between isolated and control adult snails, although it should be noted that control snails were monitored for a shorter length of time and, as a result, had fewer offspring. There were no significant maternal effects on birth size, and survival of offspring born to isolated snails did not vary significantly among isolated adult snails.

An examination of birth size as a function

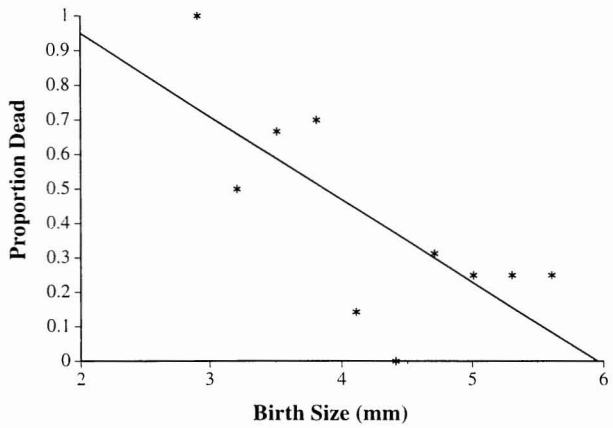


FIGURE 7. Survival to 120 days as a function of size at birth for offspring born to isolated *Partulina redfieldii*. Offspring were grouped into 10 size classes by birth size. Data were analyzed by logistic regression ($P = 0.0082$). Survival of offspring did not vary significantly among mothers ($P > 0.4$), and birth size did not vary significantly among mothers ($P > 0.5$).

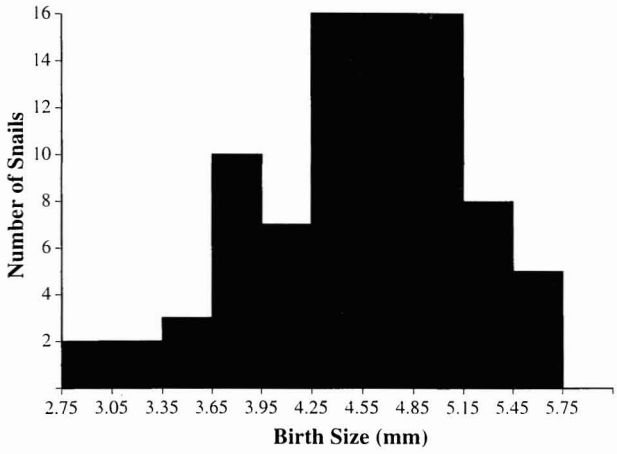


FIGURE 8. Size-frequency distribution of offspring born to isolated *Partulina redfieldii*.

of the duration a parent snail was held in isolation yielded inconsistent trends (Figure 9). For only one of six isolated snails did regression data indicate a significant relationship between these variables, with birth size appearing to increase over time in isolation. The slopes of the regression data display a positive, albeit nonsignificant, relationship between birth size and duration of isolation for four of the remaining five snails.

The average time interval between births was 80 days, and the time intervals between births did not appear to change with time in isolation (Figure 10). Although regression data indicated positive relationships between interbirth duration and time in isolation for three of six isolated snails, the relationships between the variables were not significant for any of the snails.

Since the five juvenile *P. redfieldii* reported on here were isolated in May 1991, four developed a shell lip and are presumed to have reached sexual maturity. One year and 3 months after the first of these isolated snails formed a shell lip, it produced an offspring, on 1 October 1993. The recorded birth size was 4.65 mm, a size comparable with that reported above for offspring born to the isolated snails.

## DISCUSSION

Because age at sexual maturity is an important factor in the rate of increase of a population (Bell 1980), the question of whether faster growth will lead to a lower age at sexual maturity is an important one. An enhanced food supply in the laboratory results in faster growth rates for both *P. redfieldii* and *A. mustelina* and a younger age at sexual maturity for *P. redfieldii*. The mean size at sexual maturity for *P. redfieldii* in the laboratory was within the range observed for wild populations, but the mean age at sexual maturity in the laboratory was 3.35 yr compared with an estimated 4 yr in the field (Hadfield 1986). Sexual maturity thus appears to be more size dependent than age dependent in this species, and faster growth, from whatever the cause, should lead to reproduction at an earlier age. Consequently, faster generation time is predicted where and when conditions are optimal for growth. It is important to verify this finding for other species.

The observation that snails provided with only a natural diet in the laboratory still grew faster than similarly sized snails in the field indicates that the physical environment (other than food quantity or quality) influences growth in *P. redfieldii*. The mild and constant climatic conditions created in the laboratory may allow the animals to feed undisturbed for longer periods of time, whereas in the field extreme weather conditions like storms and drought may force long periods of inactivity. In addition, 12-hr nights only occur during the winter months in Hawai'i, and the nocturnally active animals may have grown faster because they were able to feed for longer periods in a year-round 12-hr light : 12-hr dark regime.

*Partulina redfieldii* kept in the laboratory and provided with an enhanced food supply grew faster than both the laboratory control group and animals in the field, strongly suggesting that food is a limiting factor in the field. It has been demonstrated that intraspecific competition for food can affect juvenile growth rate (Baur 1990*a*) as well as age at first reproduction and fecundity (Baur 1990*b*) in other land snails. Rapid population growth currently observed in study populations of *P. redfieldii* in the field (Hadfield, unpubl. pers. observ.) may result in growth of individuals in these populations being constrained by competition for a limited food resource. We will have the opportunity to verify this prediction.

Growth in *A. mustelina* did not increase in the laboratory environment; in fact, snails provided with only a natural diet in the laboratory grew slower than animals in the field. The reason for the different responses of *A. mustelina* and *P. redfieldii* may lie in their dietary requirements (discussed below). Perhaps the physical environment in the laboratory (other than food quality or quantity) may not have replicated sufficiently that of the native environment of *A. mustelina*. The climate (temperature and "rainfall") in the

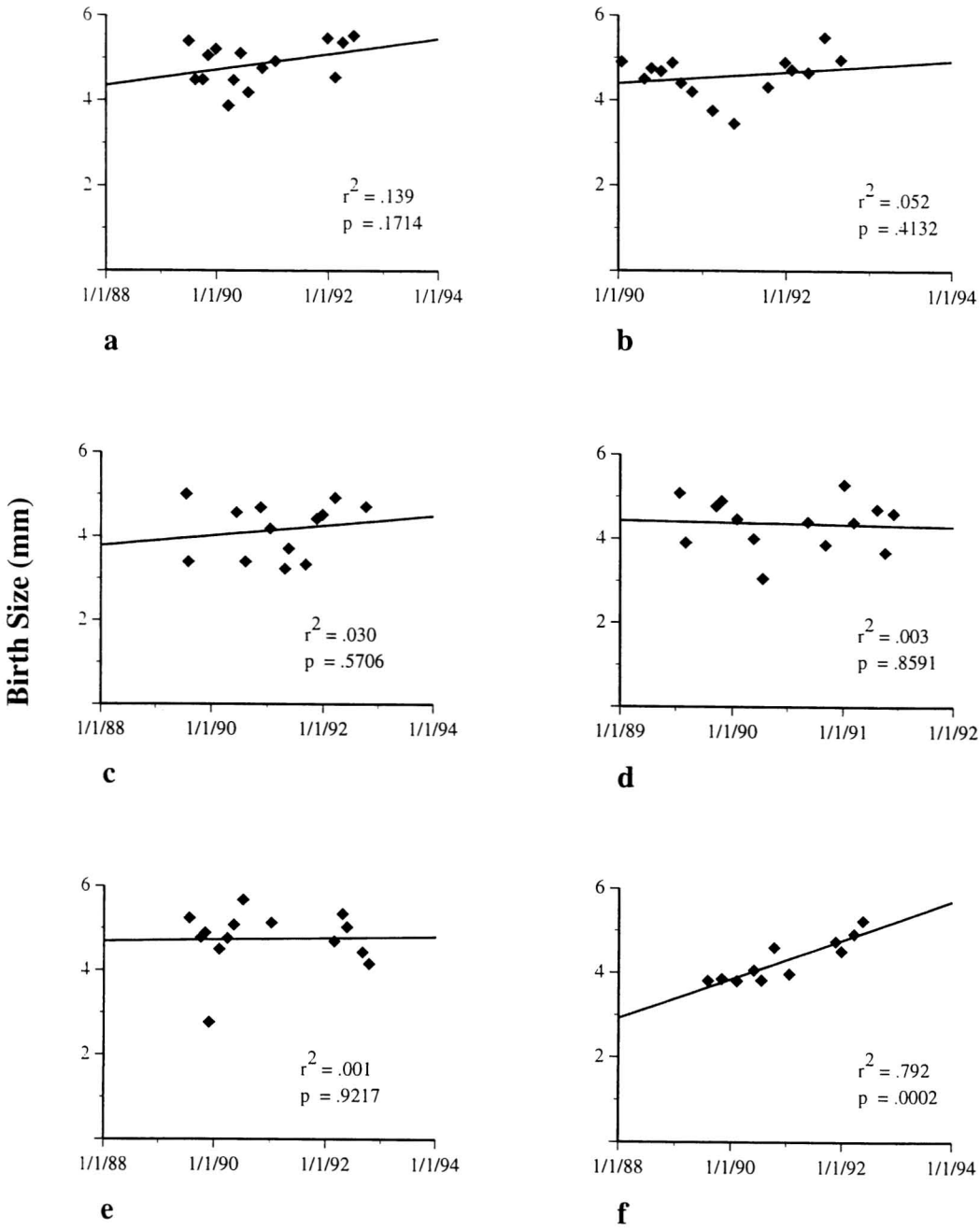


FIGURE 9. Size of offspring as a function of time in isolation for six isolated *Partulina redfieldii*. Each graph represents one mother; each symbol represents one birth.

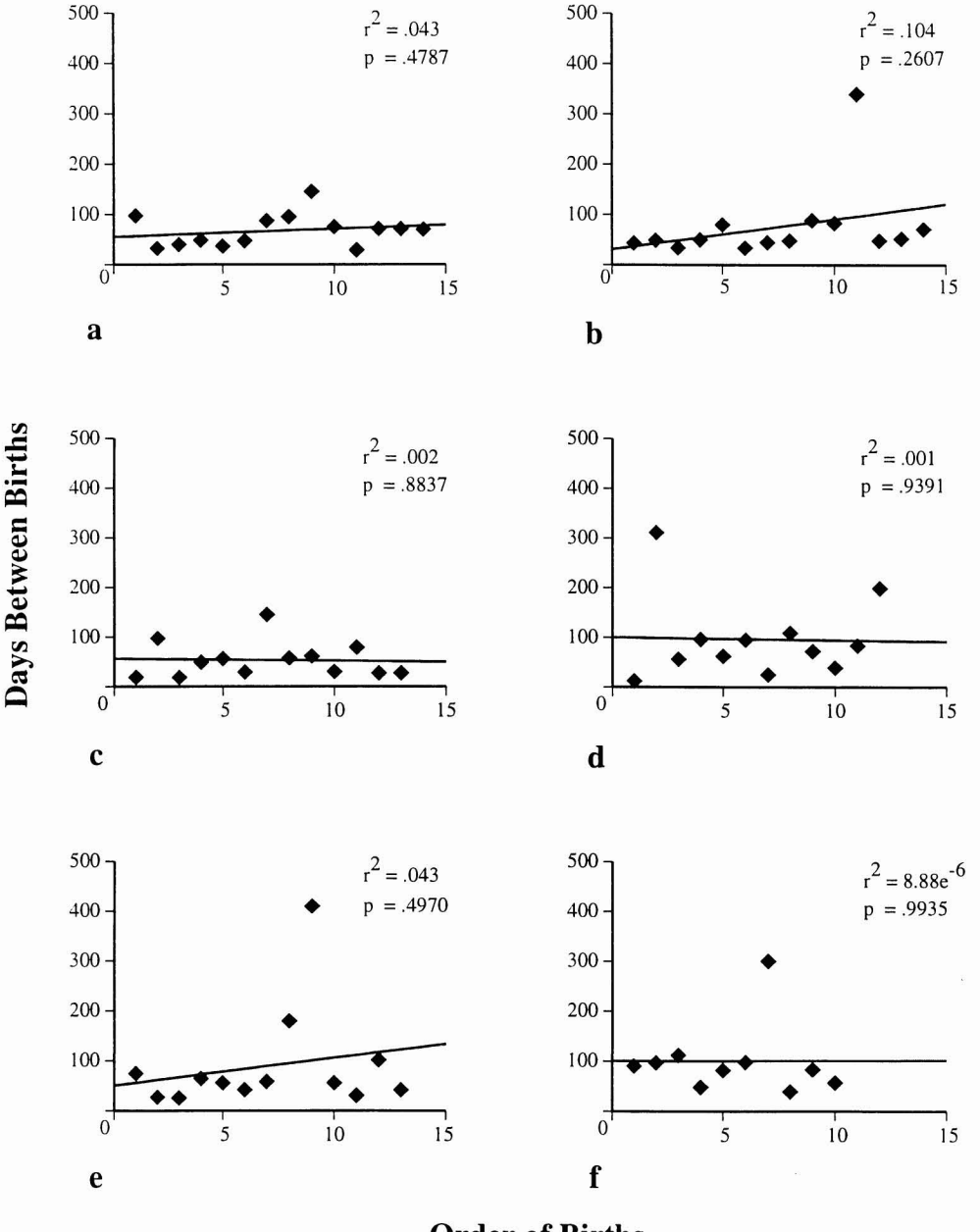


FIGURE 10. Interval (in days) between parturitions for six individual *Partulina redfieldii* in isolation. Each graph represents one mother; each symbol represents one birth.

laboratory more closely resembled that of Kamakou Preserve at 1300 m than that of Honouliuli Preserve at 600 m, which is generally warmer and drier.

It is possible that the quality or quantity of food provided to *A. mustelina* in the laboratory was not the equivalent of that available in the field and thus resulted in slower growth rates in the laboratory. It has been demonstrated that variation in lipid, carbohydrate, protein, and fiber can affect growth in terrestrial gastropods [summarized by Ireland (1991)], and when providing natural and living food, it is difficult to quantify the food resources available to the animals.

Although sexual maturity may be attained at an earlier age in the laboratory when conditions are optimal for growth, there are undoubtedly genetic constraints on both growth rate and earliest age at which sexual maturity can be attained for achatinelline snails. Even under optimal conditions, growth (and, consequently, age at sexual maturity) is much slower in *P. redfieldii* than has been recorded for most other terrestrial snails. For example, in Greece, *Bradybaena fruticum* (Müller) hatches at 2 mm and becomes sexually mature within 1–2 yr at 19 mm (Staikou and Lazaridou-Dimitriadou 1990). *Polydontes acutangula* (Burrows) from Puerto Rico hatches at 22 mm and becomes sexually mature in a year at 130 mm (Heatwole and Heatwole 1978). Ovoviviparous *Partula* spp. from Mo'orea are 3–3.35 mm at birth and within a year attain a shell length of 15–16 mm and sexual maturity (Murray and Clarke 1966). In Hawai'i, eggs of the introduced species *Achatina fulica* are 5 mm in diameter and snails were reported to be sexually mature (exceeding 60 mm in length) within a year (Kekauoha 1966), and *Liguus fasciatus* (Müller) from Florida hatches at 7 mm and is sexually mature in 4 yr at 48 mm (Voss 1976). In an effort to explain the unusual life-history characteristics of achatinelline snails, Hadfield and Mountain (1980) speculated that growth rate is constrained by the poor nutrient quality of epiphytic fungi; they also hypothesized that large birth size in achatinellids is driven by interspecific competition for food and/or space. If growth rate is constrained by poor food quality and minimum adult size is limited by the large birth size of offspring, it follows that age at sexual maturity will be protracted.

The adult *P. redfieldii* isolated at the beginning of these studies continued to produce offspring nearly 4 yr later, and there was no indication that they will cease to do so in the near future. Birth rate and birth size remain constant and comparable with these characters estimated for field populations of this species (Hadfield 1986). Although average size at birth in the laboratory is smaller than that estimated for field populations (Hadfield 1986), survivorship of snails in the first year class is comparable with that estimated for field populations (Hadfield, unpubl. pers. observ.).

The mechanism that allows *P. redfieldii* to reproduce for prolonged periods in the absence of mates is poorly understood. The birth of offspring to a virgin *P. redfieldii* produced in the laboratory proves that these snails must be capable of either self-fertilization or parthenogenesis. Self-fertilization is more likely, because it has been documented in a number of gastropod groups. Freshwater *Helisoma* spp. are capable of self-fertilization, but with fecundity significantly depressed (Lobato Paraense and Correa 1988). Fecundity of virgin *Arianta arbustorum* (L.), a terrestrial gastropod, was lower compared with nonisolated individuals (Baur 1988). However, fecundity measurements for reproductively isolated *Punctum pygmaeum* (Draparnaud) (Baur 1989) and *Rumina decollata* (L.) (Selander and Kaufman 1973) were not significantly different from those of outcrossing individuals. The prevalent mode of reproduction among some species of terrestrial slugs may be either obligate-outcrossing or self-fertilizing, varying from population to population. In other species of terrestrial slugs, all individuals are facultatively self-fertilizing, depending on the availability of mates (McKraken and Selander 1980).

Long-term sperm storage has been documented in a number of terrestrial gastropods and cannot be ruled out as an explanation for continued reproduction by *P. redfieldii*

maintained in isolation for 4 yr. *Arianta arbustorum* is capable of storing sperm for 2 yr; *Cepaea nemoralis* (L.) stores sperm for as long as 3 yr; and *Helix aspersa* (Müller) has been reported to store sperm up to 4 yr (summarized in Baur 1988). Parthenogenesis is a less likely explanation for solitary reproduction by *P. redfieldii* simply because it is a very rare mode of reproduction among pulmonates (Duncan 1975, Fretter and Graham 1964).

If the self-fertilization hypothesis holds true, the consequences of this mode of reproduction on heterozygosity and the inbreeding coefficient of both laboratory and wild populations may be substantial (Hillis 1989). Greater understanding of the prevalent mode(s) of reproduction and how it affects the genetic composition of populations is essential for accurately determining parameters such as minimum viable population size that are used in conservation management.

A thorough understanding of demographic characters affecting growth and reproduction is important to efforts aimed at promoting recovery of endangered species. An enhanced food supply led to faster laboratory growth in both *P. redfieldii* and *A. mustelina* and also enabled *P. redfieldii* to attain sexual maturity at a younger age, therefore reducing generation time. It follows that, if the longevity of early maturing snails is comparable with that of snails that mature later, a younger age at first reproduction will translate to a longer reproductive life and higher lifetime fecundity (thereby reducing the possibility of bottleneck effects [Lovejoy 1977], a particular concern for small populations). In the field, it is not uncommon for a few trees to be densely populated by achatinelline tree snails, while most of the surrounding native vegetation seems acceptable but uninhabited. Thus, practical application of the results presented here might include translocating small numbers of snails from densely populated trees to adjacent uninhabited trees, potentially lowering intraspecific competition and maximizing the rate of increase of populations. Using computer simulations, Lacy (1987) found that subdivided populations (with occasional migration) maintain greater genetic variation than that of panmictic populations, possibly due to directional selection within each microhabitat. Genetic analyses of snail populations in the field would verify this prediction and serve to guide translocation efforts. In addition, the propensity of achatinelline snails to self-fertilize may indicate that fewer individuals are necessary to establish a viable population than would be possible if these snails were obligate outcrossers. The fewer snails required to start a viable population means greater availability of food resources per snail. It is conceivable, then, to create conditions conducive to rapid growth of populations in selected areas, enhancing the chances of species survival.

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