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Growth and Activity Patterns in a Backyard Population of the Banana Slug, *Ariolimax columbianus*

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Abstract. The study was carried out on and around a redwood deck in a suburban area of central California, using bait-plates to attract nearby banana slugs. Over a period of two years 150 individual *Ariolimax columbianus* weighing between 0.4 and 75.4 g were identified using photographs of the patterns on their maculated bodies. In many subsequent sightings of these slugs, we recorded their weight, their appearance, the time and location, and their activity.

In both 1999 and 2000, slugs weighing less than a gram appeared in January and, feeding both day and night, gained weight at an average rate of 0.11 g/day. The weight of individual slugs fluctuates widely, and only below 20 g does weight correlate with the age of a slug. Maximal weights are reached in summer. In the following autumn months, slugs may lose up to 50% of their maximal weight. Within one day, feeding slugs showed an average weight increase of 10.12%.

Slugs over 20 grams appeared at the bait-plates during early morning hours and towards dusk; they did not feed during the night. Slugs frequented specific sites, usually appearing at the same or nearby bait-plates, or repeatedly selecting the same night roosting site, and little long distance movement was seen. Slugs recorded on the deck did not cross the grass to bait-plates 4.8 m away. They displayed a cyclic behavior, appearing at a bait-plate for one or two days followed by an absence of an equal or longer period before reappearing. Adult slugs did not feed at bait-trays with many young slugs. On a July day, 46 individual slugs weighing a total of 750 g were recorded in an area of approximately 60 square meters. Our evidence indicates that these slugs do not live much longer than two years.

The number of slugs on the deck was highest with temperatures between 8° and 16°C and a relative humidity near 75%. On warm September days, slug numbers on the deck declined as temperatures rose and humidity fell. On cool, wet March days, their numbers increased with the temperature.

INTRODUCTION

The term banana slug is applied to several large terrestrial gastropods of the genus *Ariolimax* occurring in western North America. The taxonomy within the genus has been complicated by the many color variations encountered: individuals within a population were found to vary from white, to yellow to brown, to almost black, and many may be monochromatic or maculated. In a revision of the genus, Mead (1943) identified species on the basis of genital morphology. *Ariolimax columbianus* (Gould), a large slug well known in forested areas of coastal California from the Salinas Valley northward to Alaska, was recognized as the only species of banana slug with both monochromatic and maculated individuals.

The literature on slugs is greatly biased towards those that are agricultural pests, and there is little information about benign native slugs such as *Ariolimax columbianus*. Of the few existing studies, some have been concerned primarily with the reactions of these slugs in artificially controlled situations (i.e., Hamilton & Wellington, 1981a, b; Rollo, 1983a, b; Rollo & Wellington, 1981); others have described their role in forest dynamics (Richter, 1979; Gervais et al., 1998). Few publications are concerned with the behavior of unconfined banana slugs, however, and the most extensive study of this kind, in a dissertation, remains largely unpublished (Richter, 1976).

In the small area of our study, most *A. columbianus* have melanistic areas on their dark, mustard-colored bodies. The pattern of these areas is distinct in young animals and remains as the slugs grow, thus providing a non-invasive means of identifying individuals. We have taken advantage of this fact to record the growth and activity of slugs in our local population, and to learn more of their biology.

METHODS

The study site, in Orinda, Contra Costa County, California, is located on the eastern side of the inner coast range. The climate is Mediterranean, with mild temperatures and with moderate rainfall between October and March. Although we have watched slugs on our property for many years, the observations presented here were made be-

* Deceased March 4, 2003.

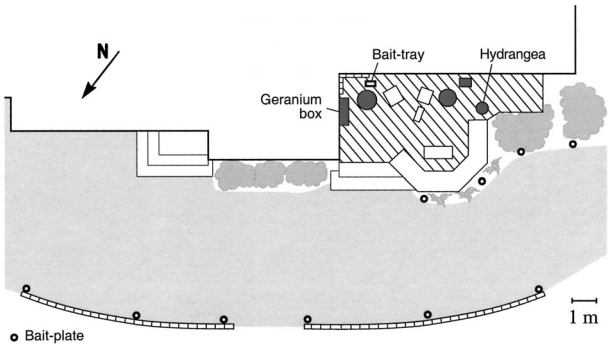

Figure 1. Diagram of the site where the study took place. The boards of the redwood deck are indicated. Containers with plants are shaded dark; grass and shrubbery are lightly shaded; deck furniture is unshaded. A brick wall lines the grassy area.

tween May 1998 and May 2000, on and around a deck composed of 14 × 14 cm redwood planks separated by 6.5 mm spaces. The deck, 27 square meters in size, is at 37.9035°N;122.17508°W (datum WGS 85), and is a meter above the earth on the west side on the house (Figure 1). Observations were continuous over these two years, except for a period in 1998 from mid-October to the end of December. The house is on several uncultivated acres with California bay and coast live oak trees, shrubby areas including coyote brush, blackberry, and poison oak. A few redwood trees planted 60 years ago are 6 meters from the western edge of the deck where our observations were made. In summer, plant containers on the deck are watered by a drip system, and the lawn between the deck and a brick retaining wall also is regularly watered.

Over the two years of our study we placed on the deck a 27 × 35 cm aluminum tray, which, when we were in residence, was continuously supplied with lettuce, melon rind, cucumber, zucchini, apples, and occasional other food items. After the first three months, four 20 cm, round aluminum pie plates with similar food items as bait were added at 1.5 m intervals under the ferns and camellias which border the deck but are a meter below the level of the deck. For short periods (one month in 1998; one week in 1999), baited pie plates also were placed along the brick wall, a distance of 4.8 m from the deck.

At each observation we recorded and identified slugs at bait-plates and at any other site on the deck, such as on a potted plant or on adjacent walls of the house. Observations were made at irregular time intervals, both day and night, up to 27 observations in a 24-hour period.

To identify individual slugs, we focused on the pigmented pattern of the body just posterior to the mantle on the slug's left side. Originally we sketched the pattern of dark spots in this area; later we photographed each slug facing left on a ruler (Figure 2). The photographs were valuable in identifying individuals, as slug appearance changes dramatically with posture, but patterns remained distinct and discernable. The slugs were transported inside the house on an index card to be photographed, assigned an identifying number, and weighed on an electronic balance (Acculab Pocket Pro 150B, Newton, PA). Within five minutes they were returned to the site where they had been found. Date, time, location, activity and weights were recorded. Slugs were reweighed and rephotographed at irregular intervals thereafter; other data were recorded each time a slug was seen, without disturbance to the slug.

Figure 2. Photographs of slugs (#98-32, 3.2 g & #98-90, 31.1 g) showing areas posterior to the mantle that were used for identification.

We identified and assigned numbers to 150 *A. columbianus* that weighed between 0.4 and 75.4 grams. We refer to those under 2 g as juveniles, from 2–20 g as subadult, from 21–50 g as adult, and above 50 g as large adult. Our handling methods apparently did not distress the slugs, for usually they continued their observed behavior when returned to the site where they were found. We did not identify individually the numerous small slugs (i.e., <5 g), but ascertained their numbers in 1999 at approximately two-week intervals by retaining for a day all small slugs that appeared on the bait-plates. They were then returned to the plates from which they had come.

Over the two years of this study, the temperature and relative humidity were recorded with a Weather Monitor II and accompanying software (Davis Instruments, Hayward, CA). The Monitor was situated nine feet above the deck, under the eaves on the side of the house.

Data were processed using R (www.r-project.org; produced most of the figures), SPSS 11.0 and Quattro Pro 5.0 (Borland, Inc.). Robust regression using an iteratively reweighed least squares procedure with a Tukey bisquare weighing function (Huber, 1981) produced the initial growth rate estimates. Only the first year of data was used to capture the initial growth pattern for each cohort. A

robust regression was used because of the high variability of slug weight.

RESULTS

Appearance

Ninety-five percent of the slugs in our study had a conspicuous round black spot (about 3 mm diameter) in the center of the mantle and assorted melanistic spots on the body. Those without spots on the mantle lacked spots on the body, or had only a few faint spots. A few slugs could be recognized by superficial irregularities (possibly old wounds?) on their bodies. The smallest slugs that appeared on the bait-plates (<0.1 g) had markings similar to adults, with one conspicuous spot on the mantle and others on the body.

Thirteen slugs had gouges and nicks on their bodies, including four slugs known to be over a year old. One slug was missing an eye stalk in addition to wounds on its back and mantle. A slug first identified at 3.3 g had a gash on its 38.9 g body 10 months later (May, 1999). After a further three months (August, 1999), the same slug (now 51.6 g) had a nick on the edge of its mantle. By September it had several more mantle nicks as well as more wounds on its body, and it was last seen in early October. This slug had been seen on 91 different days in the 15 months we had been recording it. We have no evidence concerning the source of the wounds, although slugs are known to have a variety of predators (Harper, 1988).

Two dead slugs were seen. One, a squashed juvenile on the deck, was being eaten by an adult. The other was a dead adult slug, covered with mucous, in leaf litter near the deck, with no clues as to the cause of death.

Reproduction

In two years of observations we failed to see a mating pair or to find a cluster of *Ariolimax* eggs. However, on January 18, 1999 and on January 15, 2000, the first juvenile *Ariolimax* appeared on bait-plates below the deck. The 1999 juvenile weighed 0.6 g; that in 2000 weighed 0.3 g, which is the average weight of an egg of this species (Rollo, 1983a). Subsequently, we recorded juvenile slugs on the bait-plates weighing as little as 0.1 g. Several slugs less than 2 g appeared on the bait-plates in February and March 1999, and a few appeared as late as July (Figure 3).

When the 1999 cohort of young first appeared on the deck during the day in March 1999, there were often as many as eight of the 1998 cohort (now adults, 21–50 g) feeding on the bait-tray together, apparently tolerating each other's presence. As time passed, the young cohort of 1999 appeared in greater numbers during the day, and such aggregations of adults were no longer seen. By May 1999 it was usual to find only one adult slug with several sub-adults on the bait-plate, and sometimes only the latter.

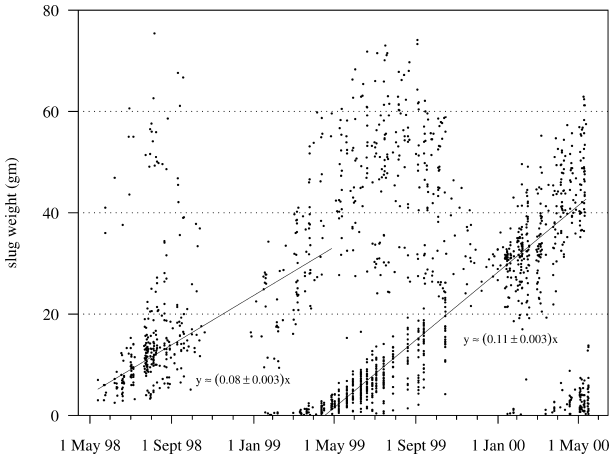

Figure 3. Weights of *Ariolimax columbianus* from May 1998 to June 2000. No observations were made from mid-October to late December, 1998. Regression lines for the 1998 and 1999 cohorts were calculated using robust regression on the first year of data for each cohort. The growth rate for 1999 (a weight gain of 0.11 ± 0.003 g/day) seems more reliable because it includes data for the youngest slugs.

Weights of Slugs

In the two years of our study, we identified and assigned numbers to over 150 *Ariolimax columbianus* initially weighing between 0.4 and 75.4 g. Subsequently, those that were seen again were reweighed at irregular intervals, some more than 80 times. These data, plus the weights of unidentified juveniles and sub-adults, also presented in Figure 3, indicate that young slugs gain an average of 0.11 ± 0.003 g per day. A monthly analysis of the composition of the slug population by weight groups also supports a rapid weight increase, as numbers of juveniles rapidly become sub-adults (Figure 4).

When initially identified, there were 12 slugs that weighed more than 50 g (i.e., large adults), and five of these were not seen again. Most large adults in the population (Figures 3, 4) were slugs initially identified as 20 to 50 g adults (11 individuals) or as 2 to 20 g sub-adults (12 individuals). Weight records of four of the longest-recorded individuals show wide weight fluctuations (Figure 5); maximal weight was recorded during the summer months and weight declined thereafter. One of these was first recorded as a sub-adult (12.8 g) in August, 1998. The regression lines of Figure 3 suggest an age of 5 months for a slug of this weight. A year later it weighed 54.0 g, and in subsequent months its weight fluctuated between 40 and 50 g in September and October, and between 30 and 40 g after that. When last seen on April 22, 2000, it weighed 39.4 g and was approximately 26 months old. Over 20 months, we had recorded this slug

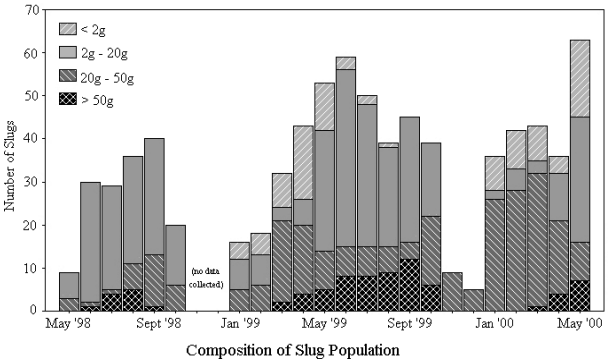

Figure 4. Age composition of the slug population in the area of our study during two years. The mean weight gain of a slug during each month was calculated to determine to which class it belonged. For the <2 g (juveniles) and 2–20 g (sub-adult) classes, in which many slugs were not individually identified, a minimal number was determined by keeping such slugs captive throughout the day they were weighed. Slugs 21–50 g are referred to as adults; over 50 g are large adults.

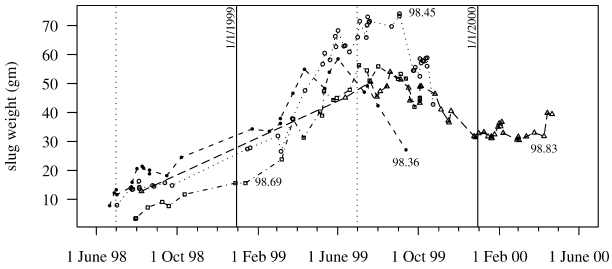

Figure 5. Weight records of four slugs tracked for more than a year. The numbers (98.69, etc.) indicate the individuals.

on 62 days. Using a similar approach with 16 slugs for which we have lengthy records, the estimated age when last seen varied from 13 to 26 months, with a mean of 18.3 months (SD ± 3.10).

Although weights of individual slugs fluctuate, some patterns are discernible. Many slugs first recorded in May and June, 1998, weighed between five and ten grams, indicating an age of two or three months (Figure 3). During the following months they gradually gained weight, but in September and October this cohort of slugs—now ranging from 35 to 74 g—started to lose weight. Some lost a great deal of weight (53%, 43%, 41% of their maximal weight), others lost a more moderate 10–25% of maximum. A slug that originally weighed 8.0 g in July 1998, increased to a maximal 74.1 g in early September of the following year. After an absence of three weeks, it weighed 54.5 g, and its weight fluctuated about this level until last seen at the end of October.

We have 67 records of slugs that were weighed twice within one day, many weighed before and after a feeding bout. Five of the 67 lost weight (0.01 to 3.6 g); the weight increases of the remaining 62 ranged from 0.1 to 9.8 g, with an average of 3.48 g (SD ± 2.35), an increase of 10.12% (SD ± 7.48). Smaller slugs generally showed larger percentage weight gains. The largest recorded gain was a slug that on a rainy February day, spent 105 minutes on the bait-tray. At the beginning of the feeding bout it weighed 26.4 g; at the end it weighed 35.7 g, an increase of 35.2%. Although uptake of moisture may have contributed to this increase, similar percentage increases in weight were also recorded in the dry month of August. There does not appear to be a correlation between the time of year and the amount of weight a slug may gain within one day.

On several days we weighed once all the slugs that appeared on the bait-tray on the deck and the four bait-plates below it throughout the day, keeping unidentified young slugs in containers to avoid duplications. As many as 27 to 52 slugs, with a combined weight approaching a kilo, were living on and around the deck (an area of less than 100 square meters) on these days (Table 1).

When feeding at night on bait-plates below the deck or at the brick wall, young *Ariolimax* were often found in the company of three species of small slugs, sometimes a snail, and occasionally, isopods.

Movements

Individual slugs showed a tendency to be found repeatedly in the same area and at the same bait-plate. One sub-adult slug, first recorded at 12.3 g on an hydrangea plant in June, 1998, was subsequently observed on the same plant on six different days in the months that followed, and five more days in May and June of the following year, when it weighed 65.4 g. Another slug, recorded in a planter box with geraniums, was transferred on four successive days to the hydrangea 1.5 m away. Each time, it appeared back in the geranium box the day following the transfer.

On several occasions we recorded the speed at which large adult slugs progressed across the boards of the deck. Values ranged from 11.7 to 19.2 cm/min. Slugs weighing 50 g were seen going through the 6.5 mm gap between the boards of the redwood deck, and a slug of similar size was seen to make its way through leaf litter and disappear into a one centimeter hole in the earth.

Slugs climbed as far as three meters up the painted redwood siding of the house, leaving a slime trail that remained visible for several months. Slugs may remain in an extended position on the wall, but often formed a loop, frequently with the head down. With their mouth near the mucous pore at the rear of their body, they could be seen consuming the mucous and anything that has stuck to it. In the morning hours of all months, a few slugs were found on the wall and on the brick chimney, and it was usually the same individuals. At night, however, wall-roosting had a different pattern. Adult slugs

Table 1

Census of slugs on the deck and on 4 bait-plates below it, on selected days in 1999.

Date	Juveniles (<2 gm)	Sub-adults (2–20 gm)	Adults (20–50 gm)	Large adults (>50 gm)	Total number	Total weight
May 20	4	28	3	3	38	368.5 gm
June 10	3	41	4	4	52	628.0 gm
July 14	2	33	8	3	46	750.2 gm
Aug. 19	1	19	4	3	27	531.3 gm
Sept. 12	0	27	4	3	34	624.5 gm

were on the wall at night only in the winter months of January to March; in August, only sub-adults (2–20 g) were found there. A slug may spend the entire night with eye stalks retracted, immobile on the wall, descending as morning approaches. Several slugs spent 12 to 19 hours in place on the wall, and one adult slug remained *in situ* over 24 hours. A coiled 10 cm string of excreta often remained behind when a large slug descended from a wall.

Of slugs that were first identified on the deck, 71% of those that were seen again were also found on bait-plates below the deck. Slugs recorded first at the bait-plates below the deck more consistently remained in their shady original sites, only 32% appearing also on the deck. Of the 114 slugs originally identified on the deck or the area below it, none was found across the grass at the brick wall 4.8 m away. Six of the 36 slugs first recorded at the brick wall subsequently appeared on bait-plates below the deck.

In September, a slug was discovered on the opposite side of the house, 28.4 meters from the site near the brick wall where it had been recorded two months earlier. This is the farthest an identified slug was found from its original location.

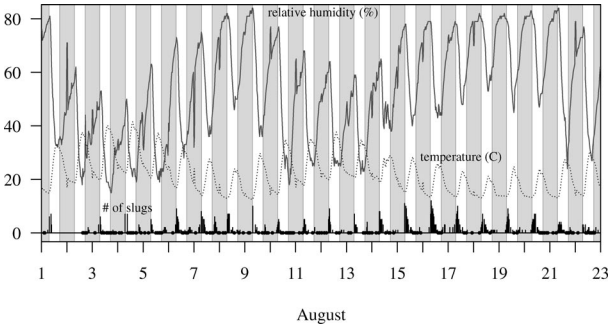

Figure 6. Records of the first three weeks of August 1998, showing the number of slugs on the deck relative to temperature and relative humidity. The vertical shaded areas represent nighttime. Numerous observations that found no slugs are shown on the zero line.

Time of Activity

No adult slugs were observed feeding during hours of darkness. When recorded on the deck at night, adult slugs were inactive, usually attached to the walls or doors of the house. They appeared at the bait-plates primarily during early morning hours; a few appeared towards dusk. In the dry summer of Orinda, when daytime temperatures may reach 30°C, slugs appeared on the deck during lows in the temperature cycle and highs in the cycle of relative humidity (Figures 6, 7): their numbers decreased as the temperature rose and humidity dropped. During the cool and humid winter conditions of March, slug numbers paralleled the rise in temperature from lows of 7°C (Figure 8). Consistently, the number of slugs on the deck was highest with temperatures between 8° and 16°C. Few slugs appeared on mornings when there was frost on the deck, and usually it was the same one or two slugs that were present.

In contrast to the diurnal feeding pattern of adults, juvenile slugs, first appearing in January, fed both day and night on bait-plates below the deck and at the brick wall, sites which offered more cover than did the bait-tray on the deck. In late March, 1999, five young slugs (0.6, 1.2, 1.9, 2.4 and 2.4 g) were the first to make their way up through the cracks of the deck and were seen feeding on the bait-tray at 9:25 PM. Although in the following month they fed on the deck both day and night, sub-adult slugs were more often observed feeding on the deck at night. By the end of May some of this cohort of slugs weighed as much as 8 g and they no longer fed at night.

Patterns of Activity

Slugs over 50 g (adults) usually appeared alone on bait-plates, or with sub-adults (2–20 g), which they appeared to ignore. Although slugs occasionally visited a bait-plate and departed immediately, most remained between one and two hours. Longer bouts were not unusual. One slug remained on the deck bait-tray for ten hours, although it is not known how much of that time it was feeding.

Analysis of the extensive records of five individuals shows a pronounced tendency for slugs to appear at the

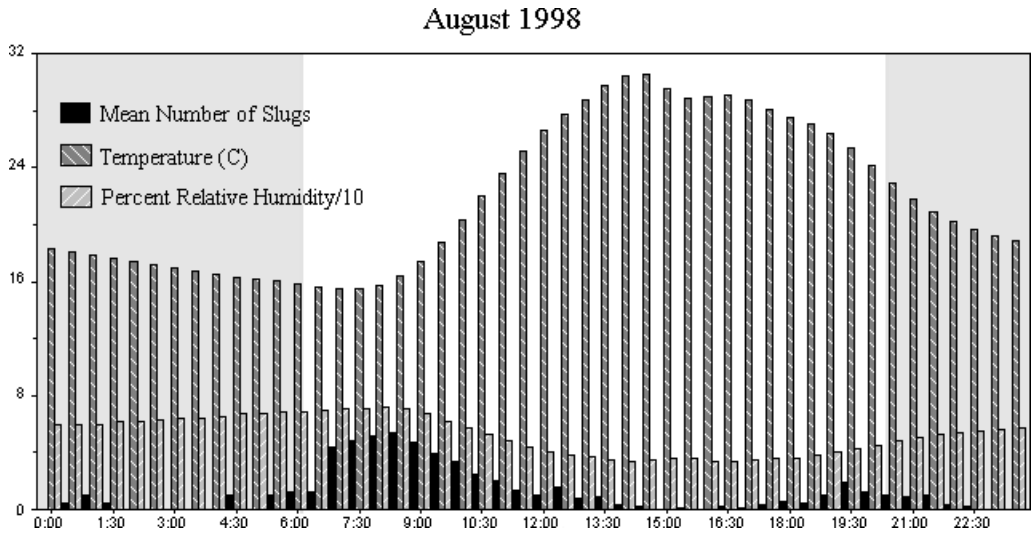

Figure 7. Average number of slugs on the deck and walls for each half-hour interval in August 1998 in relation to temperature and relative humidity. Shaded areas indicate sunrise and sunset on August 15, Pacific Standard Time.

bait-plates for one or two consecutive days, and then to be absent for longer intervals. Consecutive days recorded at a bait-plate varied from one to five, but the great majority of the 193 visits of these individuals were one day (70.5%) or two days (21.8%). Intervals between visits to the bait-plates were more spread out, ranging from one day (26.0%), two days (22.0%), to longer than 10 days (11.0%). The long absence intervals did not appear to be correlated with the seasons.

DISCUSSION

Approximately a third of the identified slugs, in all size categories, were seen only once (45 slugs), although there was no obvious reason for their disappearance. Others were seen repeatedly during the next two years. One slug was recorded numerous times on 89 different days during the two years of our observations. In 1998 we identified 86 slugs on and around the deck and within a few meters of our house. In January of the following year 25 of these slugs were still being recorded. By June 1999 we were seeing only 15 of the original slugs, and by January 2000, only one still survived. Meanwhile unidentified slugs (85% of them adults and large adults) were appearing: 33 in 1999 and 29 in the first months of 2000. When combined, these data indicate that within this 160 square meter area near our house, there was a large population of slugs with a limited life span and rapid turnover.

There are striking differences between our observations and the field observations of Richter (1976) on the same species in Washington State. In Orinda, the *Ariolimax columbianus* are remarkably larger than those noted in Richter's study, which averaged 25 to 35 g and weighed a maximum of 45 g. Many slugs in our study weighed over 50 g. Additonally, in July 2003, three years after our supplemental feeding ended, an unidentified slug weighing 107 g appeared on the deck, demonstrating that large size in the local populations was not dependent on supplied food.

The weight gain of young slugs in Richter's populations was estimated to be 0.2 to 0.3 g per month (Richter, 1976); the well-documented gain in weight of our young slugs was 10 times that. In Washington State, slugs were active and feeding both day and night from May to June, and were only seen between April and November, after which they disappeared into hibernation (Richter, 1976). In Orinda, adult slugs did not feed at night and appeared at the bait-plates throughout the year. In the Seattle area, the eggs of banana slugs hatch in late February and early March; in Orinda, recently hatched slugs appeared from January to as late as April. Climate differences may be partly responsible for these discrepancies. Average temperatures in Orinda are somewhat higher in winter, but in summer they are quite similar to those in Richter's study areas. Another possible explanation may be that the species identifications of Mead (1943), based on genital morphology, are not valid. Recent studies indicate that the systematics of ariolimacine taxa are poorly resolved (Roth, 2004; Pearse et al., 2004).

Up to 20 grams, the weight of a banana slug is a good indicator of the age group to which it belongs. Above this weight, however, slug weight fluctuates widely. Some of our monitored slugs continued to increase in weight; others remained hovering about 40 grams. Some weight fluctuations are probably due to the problems of maintaining hydration. Richter (1976) was concerned that egg production might mask normal increases in body weight. The

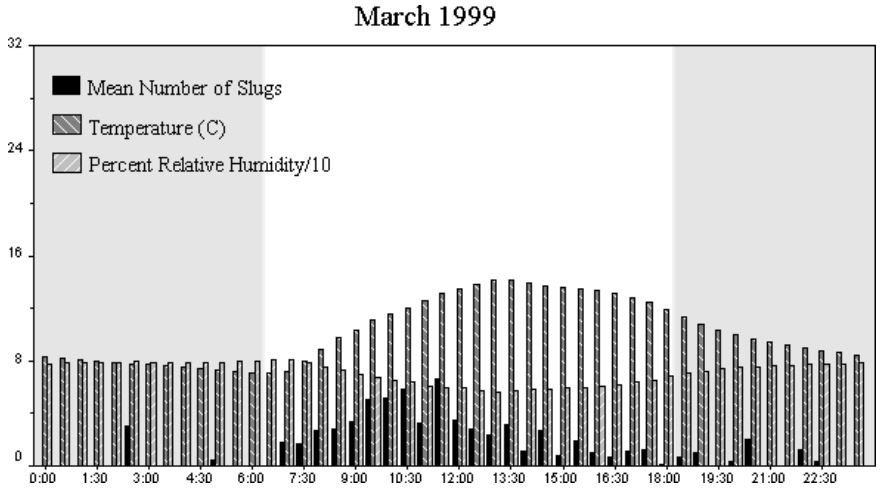

Figure 8. Average number of slugs on the deck and walls for each half-hour interval in March 1999 in relation to temperature and relative humidity. Shaded areas indicate sunrise and sunset on March 15, Pacific Standard Time.

clutches of *Ariolimax columbianus,* are relatively small for a mollusk (an average 17.7 eggs), and eggs weigh an average 0.32 gm (Rollo, 1983a). A clutch of eggs, therefore, would entail an increase in weight of approximately 6 grams, which is a modest weight change in the population we were observing. The weight fluctuations of slugs in our study probably can not be attributed to reproductive events.

The dynamics of the slug population described suggested that habituation, a constant food supply, and a high reproductive potential contributed to the large numbers of slugs that appeared on and around the deck. The surge in numbers documented in 1999 could have been produced by a few reproductive individuals. Similar surges were occurring around the deck and at the brick wall 4.8m away, however, with little intermingling of the two populations. These observations, in addition to the noted homing tendency of slugs (Rollo & Wellington, 1981), suggest that what we were recording was the potential of this slug to expand in numbers under beneficial conditions - a potential reflected in the numerous clades existing throughout its range.

It has been stated repeatedly that *Ariolimax columbianus* has a life span between 4 and 6 years (Gordon, 1995; Richter, 1976; Rollo *et al.*, 1983; and others). Our study finds no evidence that these slugs live more than a little over two years.

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