

The Potential for Seed Dispersal by the Banana Slug (*Ariolimax columbianus*)

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ABSTRACT.—We observed wild banana slugs (*Ariolimax columbianus*) eating fruits of several Pacific Northwest plant species. Slime trails and direct observations indicated that slugs are capable of reaching the fruits of many wild plants. This motivated us to test the hypothesis that slugs may act as seed dispersers, provided that they defecate viable seeds. We fed captive slugs the fruits of *Rubus spectabilis*, *R. discolor*, *Vaccinium ovatum*, *V. parvifolium*, *Gaultheria shallon* and *Disporum smithii* to determine the effects of slug ingestion on seed germination. At least some seeds of each species germinated after the fruits were consumed by the slugs, but the effects on germination were species-specific. Seeds of *Rubus spectabilis* were less likely to germinate after passage through the guts of slugs, and we found significant evidence that the two fruit color morphs reacted differently over time. *Disporum smithii* seeds did not statistically differ in germination behavior between treatments, although the trend suggested possible germination enhancement following rasping of the seeds by slugs. All other species of seeds tested germinated following consumption by slugs, but results could not be tested statistically. Gut passage times of *R. discolor* seeds were determined ($\bar{x} = 25.4$ h, $SE = 3.6$ h). We conclude that despite the short distances slugs are likely to disperse seeds, their generalist habits and ubiquity suggest that they may have complex and ecologically significant effects on seed dispersal in Pacific Northwest forests.

INTRODUCTION

Slugs are frequent and unwelcome visitors to gardens, and gardeners have long recognized their willingness to consume cultivated fruits such as raspberries and strawberries. Ecologists have extensively studied vertebrate frugivory (Herrera, 1992; Fleming and Estrada, 1993; Jordano, 1995). The ecological role of invertebrate frugivores in the seed dispersal of wild fleshy-fruited plants is not nearly as well-known, although seed dispersal by ants and earthworms has been studied to some extent (McRill and Sagar, 1973; Levey and Byrne, 1993; Horvitz and Schemske, 1994). We observed the banana slug, *Ariolimax columbianus* Gould (Pulmonata: Stylommatophora), feeding on wild fruits in the Pacific Northwest, and investigated the potential for wild slugs to act as seed dispersers.

Banana slugs are among the largest of terrestrial mollusks, reaching lengths of over 20 cm (Gordon, 1994) and weights of 20–30 g (Richter, 1979; Rollo, 1983). They are native to the Pacific Northwest region of North America, with a range extending from the central

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coast of California N through SE Alaska (Harper, 1988). Although they are primarily generalized herbivores (Cates and Orians, 1975; Richter, 1976; South, 1992), slugs also eat wild fruits, including those of salal (*Gaultheria shallon*), huckleberry (*Vaccinium parvifolium*) and Oregon grape (*Berberis nervosa*, Richter, 1976). In addition, we observed slugs feeding on Himalaya berry (*Rubus discolor*) and salmonberry (*R. spectabilis*), as well as red elderberry (*Sambucus racemosa*). Slime trails and fecal matter also occurred on *G. shallon*, *V. parvifolium*, *V. ovatum*, and *Disporum smithii*, and we observed *Rubus* seeds within fecal matter deposited away from the parent plants.

These observations led us to several questions: (1) Do slugs indeed defecate viable seeds, and how does gut passage affect seed germination? (2) Do gut passage times suggest that slugs are effective dispersal agents? (3) Does slug ingestion differentially affect germination in the two fruit morphs of *Rubus spectabilis*, as bird ingestion has been shown to do in another fruit-polymorphic plant species (Willson and O'Dowd, 1989)? Accordingly, we examined the effect of banana slug ingestion of fruits on the germination of seeds of *R. spectabilis* Pursh (Rosaceae), *Disporum smithii* Hook (Liliaceae), *Vaccinium ovatum* Pursh (Ericaceae), *V. parvifolium* Smith (Ericaceae), *Gaultheria shallon* Pursh (Ericaceae) and *Rubus discolor* Weihe & Nees (Rosaceae). We also obtained gut passage times for seeds of *R. discolor*.

MATERIALS AND METHODS

We captured and maintained wild slugs individually in plastic dishpans covered with fine mesh; the animals ranged in size from 8 to 15 cm in length when resting. Larger individuals were selected since these animals would presumably eat more, and the seed-collection process would be shorter than if we used small animals. We observed slugs of all sizes eating wild fruits in the field. Slugs were maintained on a diet of potato, carrot, lettuce and water ad lib. We supplemented their diet with leaves of wild local plants. We kept all slugs for a minimum of 2 days before using them in experiments to allow any seeds eaten in the wild to be voided, and we did not find any seeds within their feces after 1 day in captivity. Fruits were placed on the floor of the cages and were changed daily. The defecated seeds were wiped clean with paper towels and stored in petri dishes or plastic bags in a dark cabinet at room temperature before planting.

We conducted three sets of experiments: (1) We tested the effects of ingestion on seed germination of the two fruit-color morphs of *Rubus spectabilis* (*R. spectabilis* color morph germination). (2) We examined the effects of ingestion on seed germination of five forest plant species (*Disporum smithii*, *Vaccinium ovatum*, *V. parvifolium*, *Gaultheria shallon* and *R. discolor*; multiple species seed germination). (3) We determined the gut passage times of the seeds of *R. discolor* (gut passage).

Rubus spectabilis color morph germination.—We carried out germination experiments to assess the effects of banana slug gut passage on the red and orange color morphs of *R. spectabilis* in Juneau, Alaska, in July 1994. We collected six slugs from a forest near Juneau and randomly assigned them to two groups, one of which was fed red fruits initially, the other orange fruits. Color morphs were reversed 7 days later, after a 2-day period during which the slugs did not receive fruit. In this way all slugs were exposed to both color morphs until we had collected a total of 250 slug-treated seeds of each morph. The slugs were then released where they had been collected.

We planted the seeds in 10-cm² pots in commercial potting soil, 50 seeds per pot, five pots per morph, for a total of 10 pots. Replication at the level of pot decreases the likelihood that microhabitat of a pot and its impact on seed germination unduly influences the results. Seeds from each slug were planted in each pot in the proportion they represented of the

total. For example, slug 3 contributed 29% of the total number of recovered orange-morph seeds, so 14 seeds from slug 3 were planted in each of the orange morph pots. In this way, the effects of each individual slug were accounted for in all pots, but we did not attempt to keep track of which seeds had originated from each slug. Control seeds were collected from ripe fruits and planted in a similar manner, but these were planted 100 seeds per pot as they were also being used for a separate experiment. We planted 10 pots of control seeds. We placed all the pots outdoors in a screen box, systematically mixing them with pots containing *Rubus spectabilis* seeds for another germination experiment (Traveset and Willson, 1997). The screen box was placed in partial shade, near naturally occurring *R. spectabilis*, and watered only by rainfall. We checked all pots for germination weekly beginning in early May through August, and recorded the number of seedlings present. After counting, we removed the seedlings.

These data were analyzed using multivariate repeated-measures ANOVA on the cumulative proportion of germinating seeds per pot through time. The data were angular transformed before analysis. Following transformation, the residuals were still not normally distributed, but this test is considered robust to departures from the normal distribution. We considered the effects of both slug treatment and fruit color morph to be fixed in this ANOVA model (Zar, 1984; Bennington and Thayne, 1994).

We also compared final percent germination between the two morphs and their controls using t-tests. An adjusted degree of freedom was used for comparing the orange morph groups because of unequal variances (Dowdy and Wearden, 1991), but this was not necessary for the red morph comparisons. The red morph control pots met the assumption of normality only after an outlier value was removed. The analysis was performed both with and without this value.

Multiple species seed germination.—We collected 15 banana slugs in Arcata, California, in the autumn of 1994, and used them to test the effects of slug ingestion on seed germination in *Vaccinium ovatum*, *V. parvifolium*, *Disporum smithii*, *Gaultheria shallon* and *Rubus discolor*, all locally occurring forest plants. Slugs were randomly assigned to three groups of five individuals each; we fed the first group fruits of *V. ovatum*, the second group fruits of *G. shallon* and *R. discolor*, and the third group fruits of *V. parvifolium* and *D. smithii*. We presented fruit species simultaneously in the second and third groups as the seeds were easily distinguished from each other. Slugs did not ingest the seeds of *D. smithii*, but rasped the fruit pulp from the seeds. We considered these to be "treated" by the slugs. We presented the slugs with fruit until we had collected at least 50 *G. shallon* seeds, 150 seeds each of *V. ovatum* and *V. parvifolium*, and 100 seeds of *R. discolor* per animal, and 150 seeds of *D. smithii* from all five slugs combined. Slugs were then released at their point of capture. Control seeds were gathered from fresh fruit.

We planted the seeds in 10-cm² pots half-filled with commercial potting soil. Fifty seeds from a single slug were planted per pot for all plant species except for *Disporum smithii*; seeds for this species were not separated by slug, and were planted 25 seeds per pot. Control pots contained the same number of seeds as did the treatment pots. We placed all pots randomly within a screen box with 1-cm² mesh in late October. The box was placed in partial shade and natural rainfall provided water. We checked for germinating seeds bi-weekly from January 1995 until mid-March; at that time, we noted that insect larvae were attacking many of the seeds of all species except *D. smithii*, and we discontinued our observations. All germinating seeds were removed as they were counted.

We analyzed the data for *Disporum smithii* using multivariate repeated measures ANOVA on the cumulative number of germinating seeds per pot through time. We compared the three controls to the six pots of slug-rasped seeds. No transformations were necessary, and

the treatment effect was considered fixed in the ANOVA model. We also compared the final percent germination between the groups using a t-test. All other treatment-pot data were simply examined for the presence of germinating seeds, since the destruction of an unknown number of the seeds by the insect larvae prevented quantitative analysis.

Gut passage.—We collected an additional nine banana slugs in Arcata, California, in the autumn of 1995, and fed them *Rubus discolor* fruits to obtain gut-passage times for the seeds. Each slug was presented with fresh fruit, and when it had eaten at least one drupelet, we noted the time and removed the remaining fruit. We checked the animals every 2–3 h throughout the day and at least once per night, recording the time at which seeds were defecated to keep the error of time measurements to within 3 h. Only data for slugs that defecated during the day were used; this excluded only one individual. One trial was performed per slug.

RESULTS

Rubus spectabilis color morph germination.—Seed passage through slug guts had a strong negative effect on *R. spectabilis* germination rates ($F_{1,26} = 23.7$, $P < 0.01$). Although we did not find statistical evidence of a difference in germination behavior between the two color morphs (COLOR: $F_{1,26} = 2.19$, $P = 0.16$, COLOR * TREATMENT: $F_{1,26} = 2.07$, $P = 0.27$), this may be a result of our small sample sizes, as it appears that there may be a considerably greater negative effect on red-morph seed germination (Fig. 1). Time effects and time-by-treatment effects were both significant (Wilks' Lambda, $W = 0.0480$, $F_{9,18} = 39.70$, $P < 0.01$ and $W = 0.2745$, $F_{9,18} = 5.29$, $P < 0.01$, respectively), as were time-by-morph-by-treatment effects ($W = 0.4474$, $F_{9,18} = 2.47$, $P = 0.05$). There also was evidence of a time-by-morph effect ($W = 0.4660$, $F_{9,18} = 2.29$, $P = 0.06$).

Final percent germination for each group differed considerably. The final percent germination for the orange morph did not differ between the slug-ingested and control groups ($\bar{x} = 32.0\%$, $SE = 6.6$, $n = 5$ and $\bar{x} = 40.7\%$, $SE = 1.29$, $n = 10$, respectively; $t = -1.29$, adjusted $df = 4.46$, $P = 0.27$). Significantly fewer slug-treated red morph seeds germinated than the control seeds, however ($\bar{x} = 17.2\%$, $SE = 3.0$, $n = 5$ and $\bar{x} = 40.0\%$, $SE = 3.1$, $n = 10$, respectively; $t = -4.65$, $df = 13$, $P < 0.001$). This result did not change when the outlier value was removed to meet the assumption of normality.

Multiple species seed germination.—Treatment by slugs may slightly enhance germination of *Disporum smithii* ($F_{0.05,1,7} = 4.10$, $P = 0.08$, Fig. 2). There was a slight time effect ($W = 0.0739$, $F_{0.05,5,3} = 7.51$, $P = 0.06$) but no time-by-treatment interaction ($W = 0.5268$, $F_{0.05,5,3} = 0.5389$, $P = 0.08$). Final germination percentages did not differ between treated seeds and controls ($\bar{x} = 75.3\%$, $SE = 2.8$, $n = 6$ and $\bar{x} = 64.0\%$, $SE = 10.6$, $n = 3$, respectively; $t = -1.29$, $df = 7$, $P = 0.27$).

Seeds of *Vaccinium ovatum*, *V. parvifolium*, *Gaultheria shallon* and *Rubus discolor* germinated after ingestion by slugs. Due to the confounding effects of insect larvae preying on the seeds, no comparisons were made between control and experimental treatments.

Gut passage.—The average gut passage time of *Rubus discolor* seeds was 25.4 h ($SE = 1.28$, $n = 8$).

DISCUSSION

Banana slugs have been overlooked as frugivores in Pacific Northwest forests, but they are almost certain to play at least a minor role in forest plant regeneration. Seeds of all species we tested were capable of germination after slug ingestion and gut passage, although effects on each species were variable. Field observations of slugs, their slime trails, and fecal deposits on parent plants indicate that wild, free-ranging slugs are quite capable of reaching

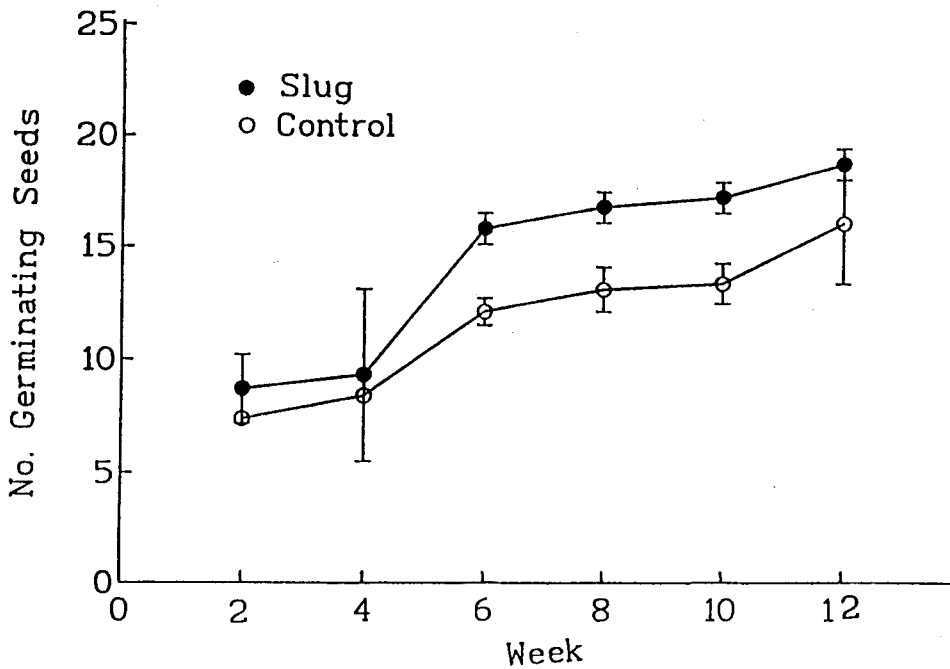


FIG. 2.—Cumulative mean number of germinating seeds per pot of *Disporum smithii*. Error bars are ± 1 SE. $N = 6$ pots for the slug treatment, and $n = 3$ pots for the control; all pots contained 25 seeds

the fact that most slugs do not cover great distances in their usual movements, or in the time it takes seeds to pass through their digestive tracts. Banana slugs traveled over 12 m in the course of a nightly foraging bout in captivity, but they rarely strayed far from shelters and frequently returned to them (Rollo, 1978; Rollo and Wellington, 1981). Much of their defecation also occurred within these cool damp refuges. Wild slugs in western Washington traveled between 5 and 15 m in 24 h, but the area covered was only a few square meters (Richter, 1976). It seems likely that most seeds consumed are deposited close to the parent plant, and often in underground sites with many other seeds.

Seeds deposited by slugs may benefit from dispersal to underground sites, as has been shown by ant dispersal. Seeds moved to refuse piles by ants show enhanced seedling germination and seedling emergence (Levy and Byrne, 1993; Horvitz and Schemske, 1994). This may be true for seeds deposited by banana slugs and offset the disadvantage of remaining within the vicinity of the parent plant.

Although slugs often consume both the fruit and the seeds, their frugivory may prevent effective seed dispersal for some forest plants when slugs damage the fruit but do not remove the seed. Insect-damaged *Vaccinium ovalifolium* fruits were less attractive to birds (Traveset *et al.*, 1995). Slugs removed the elaiosomes from *Trillium ovatum* seeds, leaving the seeds behind (Mesler and Lu, 1983). This last example, however, has an interesting twist: slugs left visible striation marks on the seed coats of *Trillium ovatum*, and such treatment may actually enhance germination by seed-coat scarification (Willson and O'Dowd, 1989; Barnea *et al.*, 1990; Izhaki and Safriel, 1990). Seeds of *Disporum smithii* in this study

germinated readily after such treatment, although we did not observe any obvious marks on the seed coat.

We found evidence that germination rates of the two color morphs of *Rubus spectabilis* reacted differently to slug-gut treatment. This is worth testing further, as in at least one other fruit-color polymorphic species, *Rhagodia parabolica* (Chenopodiaceae) of Australia, the various color morphs exhibited very different responses in germination behavior to ingestion by birds (Willson and O'Dowd, 1989). Interestingly, *R. spectabilis* did not show these effects after ingestion by bears and several bird species, although species differed in their effects on overall germination rates (Traveset and Willson, 1997). Particularly for short-distance dispersal, germination rate differences may allow seeds to differentially disperse in time.

We also observed slugs feeding on the droppings of vertebrate animals such as black bear (*Ursus americanus*), elk (*Cervus canadensis*) and gray fox (*Urocyon cinereoargenteus*). Since seeds are sometimes present in these droppings, slugs may act as secondary dispersers in these cases. This may be important in removing seeds from the sometimes intense competition found in seedlings germinating from fecal deposits of birds or mammals (Loiselle, 1990). Slime in slug fecal deposits might also protect seeds from predation by insects or small rodents; to the best of our knowledge, this is another question that has not yet been explored.

Slugs are generalist feeders, but they do show decided food preferences (Cates and Orians, 1975). These preferences, in addition to the effects slugs are likely to have on seed survival, deposition, and germination, could have ecologically significant consequences in seedling establishment and survival. This could ultimately impact forest plant succession, even though slugs are minor frugivores compared to birds or bears in Pacific Northwest forests.

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LITERATURE CITED

- BARNEA, A., Y. YOM-TOV AND J. FRIEDMAN. 1990. Differential germination of two closely related species of *Solanum* in response to bird ingestion. *Oikos*, 57:222–228.
- BENNINGTON, C. C. AND W. V. THAYNE. 1994. Use and misuse of mixed model analysis of variance in ecological studies. *Ecology*, 74:717–722.
- CATES, R. G. AND G. H. ORIAN. 1975. Successional status and the palatability of plants to generalized herbivores. *Ecology*, 56:410–418.
- DOWDY, S. AND S. WEARDEN. 1991. Statistics for research. John Wiley and Sons, New York, New York. 629 p.
- FLEMING, T. H. AND A. ESTRADA (EDS.). 1993. Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic Publishers, Belgium. 392 p.
- GORDON, D. G. 1994. Field guide to the slug. Sasquatch Books, Seattle, Washington. 48 p.
- HARPER, A. B. 1988. The banana slug. Bay Leaves Press, Aptos, California. 32 p.
- HERRERA, C. M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *Am. Nat.*, 140:421–446.
- HORVITZ, C. C. AND D. W. SCHEMSKE. 1994. Effects of dispersers, gaps, and predators on dormancy and seedling emergence in a tropical herb. *Ecology*, 75:1949–1958.

- IZHAKI, I. AND U. N. SAFRIEL. 1990. The effect of some Mediterranean scrubland frugivores upon germination patterns. *J. Ecol.*, 78:56-65.
- JORDANO, P. 1995. Spatial and temporal variation in the avian frugivore assemblage of *Prunus mahaleb*. patterns and consequences. *Oikos*, 71:479-491.
- LEVEY, D. J. AND M. M. BYRNE. 1993. Complex ant-plant interactions: rainforest ants as secondary dispersers and post-dispersal seed predators. *Ecology*, 74:1802-1812.
- LOISELLE, B. A. 1990. Seeds in droppings of tropical fruit eating birds: the importance of considering seed composition. *Oecologia*, 82:494-500.
- MASON, C. F. 1974. Mollusca, p. 551-591. In: C. H. Dickenson and G. J. F. Pugh (eds.). *Biology of plant litter decomposition*. Academic Press, Inc. New York, New York.
- MCRILL, M. AND G. R. SAGAR. 1973. Earthworms and seeds. *Nature*, 243:482.
- MESLER, M. R. AND K. L. LU. 1983. Seed dispersal of *Trillium ovatum* (Liliaceae) in second-growth redwood forests. *Am. J. Bot.*, 70:1460-1467.
- RICHTER, K. O. 1976. The foraging ecology of the banana slug *Ariolimax columbianus*, Gould (Arionidae). Ph.D. Dissertation, University of Washington, Seattle.
- . 1979. Aspects of nutrient cycling by *Ariolimax columbianus* (Mollusca: Arionidae) in Pacific Northwest forests. *Pedobiologia*, 19:60-79.
- ROLLO, C. D. 1978. The behavioral ecology of terrestrial slugs. Ph.D. Dissertation, University of British Columbia, Vancouver.
- . 1983. Consequences of competition on the reproduction and mortality of three species of terrestrial slugs. *Res. Population Ecol.*, 25:20-43.
- AND W. G. WELLINGTON. 1977. Why slugs squabble. *Nat. Hist.*, 86:46-51.
- AND ———. 1981. Environmental orientation by terrestrial Mollusca with particular reference to homing behavior. *Can. J. Zool.*, 59:225-239.
- SOUTH, A. 1992. *Terrestrial slugs: biology, ecology and control*. Chapman and Hall, London. 428 p.
- TRAVESET, A. AND M. F. WILLSON. 1997. Effects of birds and bears on seed germination of fleshy-fruited plants in temperate rainforests of southeast Alaska. *Oikos*, 80:89-95.
- AND ———. 1998. Ecology of the fruit-colour polymorphism in *Rubus spectabilis*. *Evol. Ecol.*, in press.
- , ——— AND J. C. GAITHER, JR. 1995. Avoidance by birds of insect-infested fruits of *Vaccinium ovalifolium*. *Oikos*, 73:381-386.
- WILLSON, M. F. AND D. J. O'DOWD. 1989. Fruit color polymorphism in a bird-dispersed shrub (*Rhagodia parabolica*) in Australia. *Evol. Ecol.*, 3:40-50.
- ZAR, J. H. 1984. *Biostatistical analysis*, 2nd ed. Prentice Hall, Englewood Cliffs, New Jersey, 718 p.

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