NATURAL HISTORY OF SEED PREDATION BY *ROSELLA SICKINGIAE* WHITEHEAD (CURCULIONIDAE) ON *SICKINGIA MAXONII* (RUBIACEAE) IN COSTA RICAN RAINFOREST

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ABSTRACT

Natural histories of the neotropical rainforest tree *Sickingia maxonii* and its weevil seed predator *Rosella sickingiae* are briefly discussed. Attack rate is highest on the first fruits produced, gradually declining for fruits becoming susceptible later in the season. Up to 6 weevil larvae may attack each fruit; a single weevil per fruit destroys about 25% of the seeds, whereas 4 or more per fruit destroy 100%. However, under the normal, poorly insolated, humid forest conditions, fruits with exit holes are invaded by moth larvae, fungi, rain water, and various fruit scavengers, resulting in loss of remaining viable seeds.

In the rainforest in the vicinity of the town of Puerto Viejo, Sarapiquí District, Heredia Province, Costa Rica, *Sickingia maxonii* (Rubiaceae) is a moderately abundant subcanopy tree. Adult trees are found most frequently on stable and well-forested banks of small streams and rivers. The seeds in *S. maxonii* fruits are eaten by the larvae of the large weevil *Rosella sickingiae* Whitehead. We briefly discuss the natural histories of the tree and of the weevil as background for describing the interaction between them.

SICKINGIA MAXONII

In an intact forest, the crown of an adult *S. maxonii* (guaytil colorado) is normally under moderately intense shade from canopy-member crowns directly above. When a break in the overstory canopy occurs such that a small fraction of the *S. maxonii* crown is directly insolated, that crown segment bears a moderate number of yellow flowers sometime between July and September. These flowers produce a small number of large fruits which require 8 months or more to mature. Mature fruits may persist on the tree for several more months. The winged seeds inside are separate and somewhat dry. Eventually the husk dries and splits, and the heavy seeds fall to the ground. Laboratory feeding tests with *Heteromys desmarestianus,* a common rainforest rodent, indicate the seeds are highly desirable as food items (T. H. Fleming, personal communication).

The spheroidal, smooth gray-green fruits of *S. maxonii* are 5-7 cm in diameter with a 4-6 mm thick rind or husk. The seeds are layered neatly inside. Most seeds are viable (filled) before the weevil larva gets to them. A sample of 103 fruits from one tree contained an average of 27.08 seeds (S.D. = 7.64); if this value varies significantly among individual trees, the variation is too slight to be conspicuous in our examination of fruit collections. The low percentage of aborted seeds in the fruits suggests that the tree either can self pollinate (unlikely), that the pollen arriving at a flower is sufficient to fertilize all of its ovules, and/or the plant aborts all flowers except those with a full complement of fertilized ovules. Perhaps even some fully-fertilized fruits are aborted in order to match the fruit crop size to the energy reserves then available.

The adult *S. maxonii* in the forest have extremely small fruit crops. For example, in September-October 1970, we surveyed 20 adult trees in the forest at Finca La Selva near Puerto Viejo, and the numbers of mature and nearly mature fruits were (number of fruits in parenthesis): 10(0), 4(1), 2(2), 1(3), 1(15), and 2(20). It is possible that this was a "low" seeding year for *S. maxonii,* but crops in other years appear to be of the same small size. However, 3 trees (not included above) that were fully exposed to the sun bore several thousand fruits in the same sample period. It appears that the usual fruit crop size for *S. maxonii* is less than 20, usually borne on 1 or 2 insolated branches.

That the size of *S. maxonii* fruit crops is determined by the fairly immediate amount of insolation received by the individual trees is suggested by their behavior when shading trees are removed. For example, in the arboretum at Finca La Selva, there are 2 large adult *S. maxonii* whose crowns were partly freed of vertical and lateral shading by the removal of neighboring trees. In 1970-71, at the time of clearing, these trees were producing the usual small fruit crops. At present (1974, 1975, 1976) however, these lightly insolated trees are producing crops of as many as 500 fruits.

The most extreme example was provided by 4 adult *S. maxonii* growing in the forest along the west bank of the Rio Sarapiquí. Sometime between 1966 and 1970, all the forest to the southwest of these trees was cut and converted to pasture, thereby exposing the top and southwest half of their crowns to direct insolation. The eastern sides of the crowns were heavily shaded by the dense taller crowns of evergreen rainforest tree species. Tree number 128 had an estimated 1,625 fruits on its insolated side and 225 on its shaded side. Tree number 257 had an estimated 1,050 fruits on its insolated side and none on its shaded side.

The details of sexual phenology have never been worked out for *S. maxonii.* However, censuses of tree numbers 128 and 257 on 3 September 1970 revealed that all fruits were old enough to have full-sized milk seeds or mature seeds, and the oldest fruits had just begun to split (less than 1% had actually dehisced). We estimated that it would have taken at least 3 months before the least mature fruits would have begun to dehisce on these fully insolated trees. It is probable that the analogous period would be even longer in the heavily shaded forest sub-canopy habitat occupied by the crowns of most *S. maxonii.*

ROSELLA SICKINGIAE

Adult *R. sickingiae* arrive at the fruits when they are full-sized but contain milk seeds not yet full-sized. Adults (sex unknown) puncture the fruit wall with their mandibles to a depth of 1-2 mm, apparently feeding on this tissue. An egg is laid in one of these apparent feeding pits, and the newly hatched larva mines down the core of the fruit and then out into the full-sized but not yet mature seeds. As many as 5 or 6 larvae may mine into one fruit, but each appears to represent a separate oviposition. As the larva grows, it mines from seed to adjacent seed, eating most or all of the content of each seed in the process. The larva pupates in the fruit, and the newly emerged adult chews a circular exit hole through the fruit wall and departs. Adults fly readily upon emergence from the fruit. Some adults fail to burrow out and die in the fruits.

Based on the stages of larvae in the fruit crop of trees number 128 and 257, we hypothesize that by the time the first adults emerge from a fruit crop, the most immature fruits are usually too old for further oviposition, and thus there is only one generation of weevils per fruit crop.

We also hypothesize that these beetles have no other hosts until the following year's *S. maxonii* fruit crop appears at the appropriate state of ripeness. To date, fruits or seeds from no other plant species in this area have produced *R. sickingiae,* nor has damage resembling that made by this weevil been observed. The newly emerged adults can live at least 4 months in dry clean bottles but die in the fifth month (n = 16). Perhaps they feed on vegetative parts of *S. maxonii,* as they do on the green fruits, until the next crop appears.

INTERACTION OF *S. maxonii* AND *R. sickingiae*

A more detailed analysis of the pattern of seed predation by *R. sickingiae* in the crops of the 4 heavily insolated trees (128, 257, 258, 259) near Puerto Viejo summarizes the overall interaction (Table 1).

At the time of fruit collection, the fruits in tree 128 could be categorized as oldest (dry and ready to dehisce), middle-aged (mature but still soft with moist "pulp" around the seed), and young (green full-sized fruits with milk seeds nearly all full-sized). About 52% of the old and middle-aged fruits had been attacked by *R. sickingiae,* while only 28% of the young fruits had been attacked. None of the fruits had young larvae in them, implying that entry by weevils had been terminated for some time. We interpret these observations to mean that the attack rate is highest on the first fruits produced in the crop and gradually declines for fruits that reach a susceptible stage progressively later in the season. The decline in attack rate could be due to exhaustion of the oviposition ability of the weevils, removal of the weevils by mortality, or both, as the season progresses.

This hypothesis is indirectly supported by the number of weevils per fruit in this crop. We found a maximum of 6 larvae in a fruit. For any number of larvae greater than 3, however, virtually all seeds were destroyed and we assume that the larvae exhausted the food. We further suspect that to avoid predation on her larvae by other larvae, a female weevil lays only one egg per fruit and prefers fruit lacking larvae. However, when the fruits first become susceptible to oviposition, there should be a maximum number of weevils and a minimum number of fruits. This should lead to multiple ovipositions because of repeated encountering of fruits by the same and different weevils, and the shortage of vacant fruits. As can be seen from Table 1, the oldest fruits in tree 128 have the greatest number of weevils per attacked fruit (1.77), the middle-aged fruits an intermediate number (1.36), and the youngest the least (1.19).

The 4 trees described in Table 1 were all within 40 m of each other and had nearly contiguous crowns. Thus the pattern of weevil attacks may be viewed as a product of differential ripening in different parts of one huge crown. With this interpretation in mind, the synchronized crops of trees 128, 257, and 258 would represent only one crop and thus the similarity of percentage attacked is not unexpected. However, tree 259 may be viewed as a large branch within this crown with fruit development at least 2 months behind the others. It is paradoxical that its young to early middle-aged fruit have a much higher percent attack and a higher number of weevils per fruit than the fruits of the same age on tree 128. We interpret this to mean that as the crops on trees 128, 257, and 258 passed through their susceptible stages and susceptible fruits became rare, the few remaining weevils from each of trees 128, 257, and 258 could add up to a large number for a single tree. If this event actually occurred, it could have resulted in even a more precipitous decline in seed attack for trees 128, 257, and 258 than would have occurred had 259 not been present with its large number of younger fruits late in the season.

TABLE 1. Distribution of weevils among fruits of *Sickingia maxonii* in the Puerto Viejo region.

Tree (Date)	n	% of fruits with 1 or more weevils	average number of larvae per attacked fruit
128 (3 Sept. 1970)			
Mature dry fruits	214	51.9	1.77
Mature moist fruits	73	53.4	1.36
Immature to full-sized milk seeds	247	27.5	1.19
Aborted	0		
TOTAL	534	48.8	1.44
257 (26 Oct. 1970)			
Mature dry fruits	59	55.9	1.70
Mature moist fruits	6	16.6	1.00
Aborted	37	0	not applicable
258 (26 Oct. 1970)			
Mature dry fruits	75	66.6	1.60
259 (26 Oct. 1970)			
Immature to full-sized milk seeds	75	56.0	2.14

What difference does it make to the parent plant whether one or more weevils attack a given fruit? Probably little or none, depending on the degree of insolation. In the sample from tree 128, a single weevil per fruit destroyed 24.4% of the seeds (n = 32), 2 per fruit destroyed 47.24% (n = 18), 3 per fruit destroyed 86.1% (n = 15), and if there were 4 or more weevils per fruit all seeds were always destroyed. However, an attack with subsequent exit by even one weevil can lead to the subsequent entry by moth larvae (*Synanthedon* sp.), fungi, rain water, and various fruit scavengers long before the fruit is ready to dehisce. At the time we sampled tree 128, 9% of the fruits with exit holes had already been invaded by something, resulting in loss of the remaining seeds. In fruits collected in the less insolated and more humid forest subcanopy, virtually all with exit holes were wet inside and/or had animals in them.

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