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The sticky fruit of manzanita: potential functions beyond epizoochory

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In the coast range of California, the fruit of several manzanita (*Arctostaphylos*) species, including *A. viscida*, *A. glandulosa*, and *A. hooveri*, are covered in glandular-sticky hairs. The blueberry-sized fruit remain viscid after ripening, and if you walk through dense manzanita patches during the late spring and summer you are bound to end up with globs of fruit hanging loosely from your shirt and pants. While picking the fruit off your clothes, you may also notice that many of the fruit have dead insects firmly stuck in the glue-like exudates secreted by their dense glandular trichomes (Figure 1).

Sticky fruit, either caused by viscid secretions or hooked spines, are a common trait of many different plant species (Ridley 1930). A well-supported explanation for this phenomenon is that this stickiness allows fruit to adhere to animals for dispersal, a phenomenon known as epizoochory, and, in the cases of parasites and epiphytes, to other plants while they are dispersed (Sorensen 1986; Reid 1991; Aukema 2003). While most naturalists assume that viscid-sticky fruit, such as those of manzanita, is exclusively an epizoochorous dispersal strategy, this trait may also change interactions with other organisms. In this brief piece we will highlight several lesser-studied hypotheses of the functional significance of sticky fruit, based on our observations and an array of literature (Appendix S1: Table S1). None of these hypotheses have been rigorously tested in this or other sticky-fruit systems, and we hope that providing some preliminary data and natural history background in California manzanitas, this article will inspire others to examine the potentially diverse functions of sticky fruits.

While most viscid-sticky fruit are likely epizoochorous and this may have been the sole driver of their evolution, we propose six other hypotheses related to the role of this trait in mediating biotic interactions, and which may contribute to the selective environment

experienced by the plant or post-dispersal fruit (Figure 2, Appendix S1: Table S1). The first two hypotheses are related to plant defense: (1) stickiness may directly defend fruits against insect herbivores by ensnaring their legs or bodies or (2) insects caught in the trichomes attract and retain predatory insects and spiders, which reduces the loss of fruit to herbivores. The next three hypotheses are nutritional: (3) insect carrion entrapped by sticky fruit may decompose near the plant or its progeny and act as fertilizer, (4) entrapped insects could be digested by the plant, or (5) the feces of insects scavenging on the entrapped insects would be useable by the plant. The final hypothesis is of dispersal, (6) the presence of a nitrogenous addition to the fruits would make those specific fruits more appealing to birds and mammals which consume the fruit and lead to increased dispersal of these sticky fruit.

Direct defense (Hypothesis 1) in sticky plants is a matter of debate; while many studies have demonstrated that stickiness negatively impacts herbivores, it has been more difficult to link this to plant performance. For example, Van Dam and Hare (1998) demonstrated a convincing case that stickiness negatively impacted herbivores of *Datura wrightii*, yet a reduction in herbivory did not increase fitness of sticky genotypes (Hare et al. 2003). Eisner et al. (1998) observed ladybugs incapacitated on sticky *Mentzelia* (Loasaceae) and inferred that a common aphid had a refuge from predation. Recently, it has been demonstrated that stickiness may mediate an indirect defense in sticky plants (Hypothesis 2). Several studies have experimentally manipulated insect carrion abundance on sticky plants and showed that carrion is associated with increased predator abundance, and increased plant performance (Krimmel and Pearse 2013; LoPresti et al. 2015).

Our own observations and limited experimentation occurred on *A. viscida* at UC-Davis's McLaughlin Reserve, located in the Northern Coast Range of California. Manzanita fruit are commonly consumed by a three species of caterpillars in the genus *Eupithecia* (Geometridae), which move over on these sticky surfaces without trouble from their earliest stages of growth, suggesting adaptation to these fruit (e.g. Voigt and Gorb 2008). At our site, the most common species are *E. scabrogata* and *E. gilvipennata*, with *E. cf. mystiata* less commonly collected (Figure 2: Robinson & Strauss *in revision*). Interestingly, co-occurring *A. manzanita* plants, which lack sticky trichomes on their fruits, support dramatically lower abundances of *Eupithecia*: of 48 *Eupithecia* caterpillars collected in 2014 and 2015, 47 were collected from *A. viscida* (despite equal sampling across both manzanita species). It is possible that stickiness creates enemy-free space, or may trade off with other defenses, such as secondary compounds within fruit tissue, making sticky fruits more palatable to frugivores able to cope with a sticky environment.

A great variety of predators that may serve as plant bodyguards are present in the vicinity of these shrubs; several of the studies demonstrating this defense have occurred at this same site (LoPresti et al 2015; LoPresti and Toll 2017; LoPresti et al 2018), and certain of the same predators, including the assassin bug *Pselliopus spinicollis*, the crab spider *Misumenoides schlingeri*, and the stilt bug *Jalysus wickhami*, do occur on clumps of manzanita berries. Densities of these predators in the landscape build up throughout the season and early-fruiting manzanitas never host many of these predators; furthermore, the early-laying moths and early spring caterpillars almost certainly escape the highest predator densities. For these reasons we believe that the benefit to the plant of having these scavenging predators (Hypothesis 2) is probably less than in other systems.

Eisner and Aneshansley (1983) suggested (Hypothesis 3) that the sticky petals and fruit of *Befaria racemosa*, another ericaceous shrub, may serve as a fertilization method for the shrub or its progeny; shed petals with entrapped insects would decompose near the shrub and increase available nitrogen in the nutrient-poor sandy soils where it grows. Burger (2005) suggested the same for the extremely sticky infructescences of *Pisonia grandis* (Nyctaginaceae), which are known to catch and kill birds. We are unable to test for and unwilling to speculate on any benefit of this sort for *A. viscida*; however, the gravelly serpentine soils it grows on are quite nitrogen-poor. Eisner and Aneshansley (1983) also suggested (Hypothesis 4) that *Befaria* may absorb nitrogen directly from the dead insects. We did a simple test of this possibility in *A. glandulosa* at the UC-Santa Cruz's Big Creek Reserve. We either added 2-3 dead fruit flies (n=109) or removed any insects already caught by the fruit (n=90), to developing fruit on 11 bushes, randomizing these two treatments within each plant. Roughly a month later we collected all the developed fruit, dried them, and examined seed mass, fruit mass, and seed number. We found no significant differences in any of these metrics between fruit that had received supplementary carrion and those that had not. This experiment was cheap and easy to run, but it has serious limitations to pick up a small effect and a more rigorous experiment might examine enzymatic activity or track nitrogen isotopes. Therefore, while we found no evidence for carnivory by *A. glandulosa*, we do not conclude that it could not occur in this or other systems. A tantalizing possibility also exists that the nitrogenous feces from the scavenging predator community may be absorbed (Hypothesis 5); the spectacular African *Roridula* species (Roridulaceae) absorb nitrogen from the feces of an assassin bug (Reduviidae) which feeds on insects entrapped by the plant's sticky hairs (Anderson and Midgeley 2003). However, we again do not believe the predators are in abundant enough for this benefit to accrue to any measurable degree and our small experiment provided no suggestion of this pathway.

Hypothesis 6, our personal favorite, concerns the interaction between entrapped insects and fruit dispersal. These sticky manzanitas have both epizoochorous and endozoochorous (digestion and excretion) dispersal; the sticky, slightly sweet berries are consumed by a great variety of birds and mammals, including jays, foxes, coyotes, and even bears. In many places, manzanitas dominate the chaparral community, and, in a good fruiting year, each plant has thousands of fruit. Of the millions of fruit in a patch of manzanita, many will not get consumed and will dry and eventually fall off. While a bear probably just grabs “pawfuls” of fruit without inspecting them too closely, do fruit-eating birds or smaller mammals choose particularly nitrogen-rich berries? Would the presence of an extra bit of nitrogen on the surface, in the form of entrapped insects, increase the reward value of that food – at limited cost to the plant – and result in an increased removal rate? We tested this hypothesis on *A. viscida* at McLaughlin Reserve experimentally by adding carrion to 69 infructescences on 17 shrubs (n=543 total fruit) and leaving 68 infructescences on the same plants as controls (n=555). Over two months (26-June to 18-Aug-2015) we monitored the removal rates of fruit from these infructescences, adding insect carrion at each check. As removal rates did not differ between the two treatments (Figure 3), we found no support for this fascinating hypothesis in this system, however, we feel strongly that this possibility – and all the other proposed hypotheses – deserve consideration in other systems (27 genera listed in Appendix S1: Table S2), as assuming epizoochory is the sole function of viscid sticky fruit limits our view of this interesting and repeatedly evolved trait.

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Figure 1: *Eupithecia gilvipennata* in typical resting pose on *Arctostaphylos viscida*. Note the entrapped flies on the fruit and pedicel. Photo: Moria Robinson

Figure 2: An illustrated guide to the hypotheses presented here, numbers correspond to those in the manuscript and Table 1. Illustration by Moria Robinson.

Figure 3: Results of a carrion addition experiment. Control infructescences received no supplementary carrion; carrion addition received one dead fruit fly per fruit present per check. Standard errors are plotted. No significant differences in removal rate between treatments were found with a repeated measures mixed-effect binomial regression with shrub ID and data as random effects; a null model fit better than any including treatment.



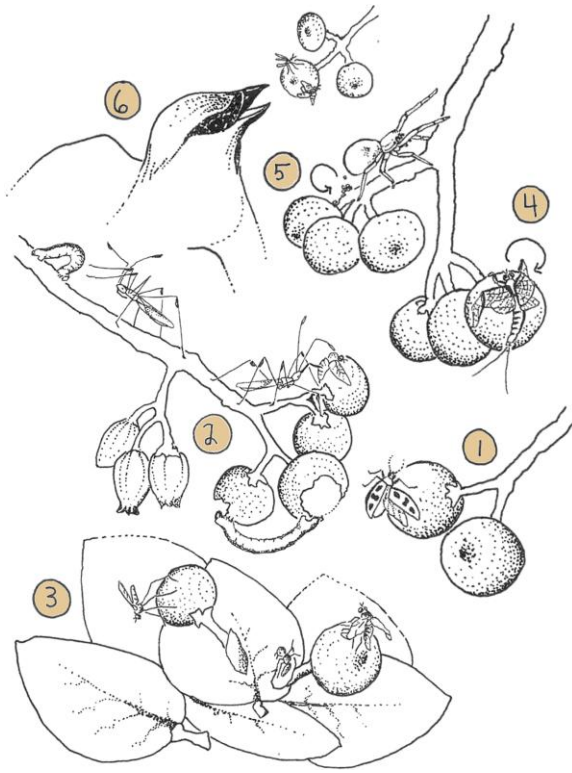


Figure 3:

