How and Why Horses Open *Crescentia alata* Fruits

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ABSTRACT

Costa Rican range horses break the hard, ripe fruits of *Crescentia alata* with their incisors and swallow the small seeds imbedded in the sugar-rich fruit pulp. The seeds survive the trip through the horse and germinate in large numbers where horses have defecated. The ripe fruits required about 200 kg pressure to break, and fruits that were too hard for the horses to break required 272 to 553 kg to break. Unbreakable fruits had thicker hulls, and their presence provides an example of how a fruit trait may serve to spread seeds among more than one kind of large dispersal agent.

Crescentia alata (Bignoniaceae, 'jicaro') is a common and widespread shrubby tree in the lowland, grassy habitats of the Pacific side of Central America. It is native to this area, yet in many places the large, cauliflorous, hard, and indehiscent fruits (fig. 1a) fall to the ground below the tree, ripen over the next three-five weeks, and rot without ever being touched by a potential dispersal agent. The many small, soft seeds imbedded in the sugar-rich pulp die without germinating in the unopened fruits. This fate is typical even in National Parks containing an apparently normal fauna of large mammals. These observations bring to mind the question of what animal is the normal dispersal agent of *C. alata* and how does this agent eat such a large fruit? The answer is found in habitats where horses have access to *C. alata* trees. The brittle, ripe fruits are bitten open by range horses and the black, moist, sweet, and seed-rich contents are swallowed after only slight chewing. Many of the seeds survive the trip through the horse and shortly thereafter germinate in the remains of the dung (fig. 1e). The modern, introduced horse (*Equus caballus*) is a dispersal agent of *C. alata*, so, presumably, the Pleistocene horse that undoubtedly occupied *C. alata* habitats until 10,000 years ago was also (Janzen and Martin 1982). In Santa Rosa National Park, as elsewhere in the semi-forested pastures in the lowlands of Pacific coastal Costa Rica, range horses are avid consumers of the contents of ripe fruits of *C. alata*. Here I describe in detail how they do it, ask how much effort it requires, and consider the significance of the fruits that are so hard that horses cannot break them.

If the fruit is small enough to get into the mouth, it is broken with the incisors (fig. 1b), not the molars. It is then dropped to the ground and the pulp scooped out with the lower incisors (fig. 1c). The act may require as little as one minute from encounter until the fruit pulp has been swallowed, but more commonly requires two to five minutes. If the fruit is too large for the horse to get into its mouth (the upper limit is 12-15 cm diameter for most Santa Rosa range horses), the horse bites the curved surface of the fruit with its incisors until surface irregularities are caught by the teeth (usually the lower ones). At this point it bites a hole in the fruit wall (fig. 1d), or cracks the fruit wall and later forces the fruit open at the crack with its incisors. A normal meal is seven to 20 fruits.

To ascertain how much force was required to break jicaro fruits, I blindly removed 40 fruits from a sack of 200 that I had collected from beneath a single large *C. alata*; when the remaining 160 fruits were given to a herd of 17 horses, they broke and ate the contents of all of them in an afternoon (10 March 1980). The 40 remaining fruits were stored in plastic bags to avoid water loss and in early May broken in an Instron machine at the University of Pennsylvania. This device crushes the spherical fruit between two flat, steel surfaces and records the amount of force required for the fruit to crack. Since different fruits have different curvatures at the point of contact with the flat, steel surfaces, part of the variability in crushing resistance may be due to the force being distributed over different amounts of surface area. All fruits were broken with the force being applied at the equator, since the horse usually rotates the fruit until it is applying pressure in this general area. The flat, steel surfaces of the Instron reasonably approximate the surfaces with which the horse contacts the fruit because the incisors are about 5 mm wide and 10 mm broad at this point, the incisors as a group constitute two flat surfaces pushing against the curved surfaces of the fruit, and the fruit wall usually ruptures not through puncture but through linear cracks when being bitten by a horse.

The fruits required an average of 199 kg to break (s.d. = 55, range 113 to 340 kg). They had an av-

FIGURE 1. Characteristics of *Crescentia alata* fruits. a. Full-sized 8-12 cm diameter green fruits shortly before dropping from the tree. b. An adult-sized range horse several seconds after breaking fruit with its incisors (under the horse's neck is visible another horse holding a fruit in its mouth). c. An adult-sized range horse licking and biting the fruit pulp out of a fruit that it bit open a few seconds earlier. d. Scrape marks and a partial puncture on the ripe fruit wall made by the horse in c. above. e. Seedlings (117) growing in the remains of a single defecation from a range horse that had been eating *C. alata* fruit. Defecation occurred in the last week of April and the photograph was taken in the first week of June (ruler is 15 cm long). All photographs Santa Rosa National Park, Guanacaste Province, Costa Rica.

erage pole-to-pole diameter of 8.4 cm (s.d. = 1.1, range 6.3 to 10.2 cm) and average equatorial diameter of 7.9 cm (s.d. = 0.8, range 6.2 to 9.6 cm). They weighed an average of 113 g fresh weight (s.d. = 39, range 43 to 188 g). By inspection, there was no conspicuous relationship among the fruit weight, the fruit diameters, or the force required to break the fruit. For example, the 10 fruits with the largest pole-to-pole diameter ($\overline{X} = 9.8$ cm, s.d. = 0.5) had an average force to break of 210 kg (s.d. = 57.2) while the 10 fruits with the smallest pole-to-pole diameter ($\overline{X} = 7.2$ cm, s.d. = 0.4) had an average force to break of 187 kg (s.d. = 53.5) (means not significantly different by inspection).

When horses have free access to a jicaro grove, some fruits are left unbroken. To examine the basis for this rejection, native assistants were instructed to collect a large sample of jicaro fruits from below several large trees not generally accessible to Park horses. They collected all fruits encountered except those with visible cracks, holes, or other apparently weakening defects, or those that appeared to have remained from the previous year's fruit crop (such very old fruits are conspicuously gray in color and very light in weight). The 755 fruits were then dumped in a 5 x 5 m area in the corner of a 4 ha pasture containing 17 moderately well-fed Park horses (22 May 1980). After 24 hours, 89 intact fruits remained, and the horses appeared to have lost interest in trying to break the remaining fruits.

The 89 remaining fruits were easily divided into two conspicuously different groups. Thirty-four fruits were normal in size but gray in color, light in weight, rough-textured, and obviously old fruits from the previous year. They were very light in weight ($\bar{X} = 77$ g, s.d. $= 24.8$), had a pole-to-pole diameter of 8.1 cm (s.d. $= 1.0$), and had an average equatorial diameter of 7.7 cm (s.d. $= 0.9$). By inspection, these linear dimensions are not significantly different from those of the sample of 40 described earlier. These old, gray fruits had no incisor scars on them, and the horses were observed to ignore them in choosing fruits to break. The other 55 remaining fruits were brown, shiny smooth, and conspicuously small for jicaro fruits. These fruits weighed less ($\bar{X} = 88$ g, s.d. $= 27.7$) than did the normal-sized fruits in the sample of 40 but still more than the 34 old, gray (and dry) fruits rejected by the horses. All the small, brown fruit were scarred on the surface by numerous scrape marks made by horse incisors (fig. 1d). The horses had obviously tried repeatedly to break them, but failed. A set of 18 of these fruits, blindly selected from the larger bag of 55, was again smashed in the Instron. They required 427 kg to break on average (s.d. $= 89.2$, range 272 to 553 kg). This value is very highly significantly larger than that for the 40 fruits representative of those normally broken by the horses ($t_{56 d.f.} = 10.02$). The unbreakable fruits were all of the size easily taken into the front of the mouth by the horses (average pole-to-pole diameter of 7.5 cm, s.d. $= 0.5$, average equatorial diameter of 7.2 cm, s.d. $= 0.8$).

The set of unbreakable fruits is not merely a set of small fruits, as shown by the force required to break the 10 smallest fruits of the sample of 40; these small fruits required only 43 percent as much force to break as did the unbreakable fruits, yet have an average pole-to-pole diameter indistinguishable from that of the sample of fruits that were unbreakable by the horses. However, the unbreakable fruits visibly differed on one trait. While the small, breakable fruits looked like smaller editions of the larger fruits, the unbreakable fruits were often somewhat distorted from the shape of a nearly perfect, flattened sphere. That is to say, the reduction in size was not symmetrical. Their surfaces were often gently bumpy, and they were often irregularly distorted spheres. In addition, they appeared to have thicker hulls than did the breakable fruits. The unbreakable fruits gave the impression of being fruits developmentally destined for larger size but arrested somewhat irregularly in expansion through mild internal damage or nutrient starvation. The cause of this deformation is under investigation, and it was associated with the trait of containing relatively few viable seeds.

Hull thickness is both quantifiable and relevant to fruit strength. An average of four measurements, made along radii separated by 90°, was taken as representative of hull thickness for a given fruit. While there was no conspicuous relationship between average hull thickness and the force required to crush a fruit within each of the samples of breakable or unbreakable fruits, the hull thicknesses of the sample of breakable fruits and the sample of unbreakable fruits were highly significantly different. The former had an average thickness of 2.3 mm (s.d. $= 0.36$, n $= 56$) while the latter had an average thickness of 3.2 mm (s.d. $= 0.40$, n $= 19$) ($t_{73 d.f.} = 8.92$). The measurements were made with calipers to the nearest 0.01 mm.

Hardness of mature *Crescentia alata* fruits is a trait that is a compromise between several opposing selective forces. On the one hand, the harder the fruit wall, the more difficult it will be for seed-predator rodents to open the fruit. Likewise, a hard fruit will prevent termites, ants, and fungi from entering and either destroying seeds or lowering the fruit's attractiveness to a seed-dispersal agent. Also, the harder a fruit, the less likely it is to crack when falling from the tree on hard ground during the dry season. On the other hand, the harder the fruit, the more difficult it may be for dispersal agents to get to the seeds and the edible pulp surrounding them. *Crescentia alata* clearly can produce a fruit wall that is too hard for horses to break. However, other large Pleistocene mammalian dispersal agents such as gomphotheres or ground sloths probably had a more forceful bite than does a contemporary horse. Trees with a wide range of fruit hardness might well have had seed shadows generated by a wider variety of animals and therefore spread over a wider variety of habitat types. The actual strength of a ripe *C. alata* fruit is the result of the compromise between keeping out the seed predators and fruit degraders, and letting in a variety of seed dispersers, some of which are no longer present.

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