Cyanide two-step: fruits lead and seeds follow in the chemical phenology of a subtropical cherry

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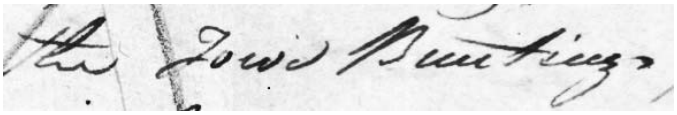

Fig. 1—Audubon's original handwritten "Towe Buntings" which Corning (1929) transcribed as "Iowa Buntings." From the collections of the Ernst Mayr Library, Museum of Comparative Zoology, Harvard University.

Wilson (1808) called it the towhee bunting and later Audubon (1831) himself called it towhe bunting, but in this journal he consistently called it towe bunting. The mistakenly transcribed Iowa bunting was corrected in another transcription of Audubon's journal by Irmscher (1999).

In his Introduction, Corning (1929) thanked Ruthven Deane, Francis H. Herrick, and Glover M. Allen for help with the transcription. Apparently none of these leading ornithologists and Audubon scholars caught the reference to the "Iowa Buntings."

I thank R. Young and D. Fisher, Special Collections Librarians at the Ernst Mayr Library in the Museum of Comparative Zoology at Harvard University, for confirming that towe bunting was in the original manuscript. Two anonymous reviewers made several editorial suggestions. J. Butler originally suggested that "Iowa Buntings" might be a typographical error.

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CYANIDE TWO-STEP: FRUITS LEAD AND SEEDS FOLLOW IN THE CHEMICAL PHENOLOGY OF A SUBTROPICAL CHERRY

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Abstract—We described the chemical transition that takes place in the fruits and seeds of laurel cherry (*Prunus caroliniana*), an evergreen tree native to the subtropical United States with bird-dispersed seeds. The unripe fruits contain cyanide and release it when the fruit tissue is damaged, whereas ripe fruits are cyanide free. The reverse was true for seeds: immature seeds were free of cyanide whereas mature seeds were cyanogenic. We also described the reproductive phenology of laurel cherry and suggest that the chemical trait we described protects the fruits during their unusually long maturation period.

Resumen—Describimos la transición química que ocurre en los frutos y las semillas de laurel cherry (*Prunus caroliniana*), un árbol perennifolio nativo de los Estados Unidos subtropical cuyas semillas son dispersas por aves. Los frutos inmaduros contienen cianuro y lo liberan cuando el tejido del fruto está dañado. El fruto maduro no contiene cianuro. Para las semillas es al revés: las semillas inmaduras no

contienen cianuro mientras que las semillas maduras son cianogénicas. Describimos también la fenología de reproducción de *P. caroliniana* y sugerimos que la característica química descrita aquí sirve para proteger al fruto durante su maduración excepcionalmente larga.

Plant reproductive structures are often defended morphologically, chemically, or biotically (Levin, 1976; Whitehead et al., 2013; Pringle, 2014). The nature of these defenses can change across developmental stages of the tissues. For instance, in plants with animal-dispersed seeds, removal of unripe fruit bearing immature seeds is often discouraged by deposition of distasteful or toxic chemicals in fruit tissue (Cipollini and Levey, 1997). When seeds are mature, removal and consumption of fruit becomes advantageous to the plant, and these chemicals can be degraded or removed from fruit tissue (Goldstein and Swain, 1963; Cipollini and Levey, 1997; Whitehead et al., 2013).

Cyanide, in the form of cyanogenic glycosides (cyanide bound to a sugar molecule), is typically present in the vegetative tissues, fruits, and seeds of species in the genus *Prunus* (family Rosaceae), and might defend seeds against predation (Levin, 1976; Swain et al., 1992; Haque and Bradbury, 2002). Cyanide is thus a likely candidate for defense of the unripe fruit in this genus. Cyanogenic glycosides liberate cyanide when the cyanide molecule is enzymatically cleaved from the sugar molecule (Swain et al., 1992). In *Prunus,* enzymes associated with this activity include amygdalin hydrolase, prunasin hydrolase, and mandelonitrile lyase (Swain et al., 1992). Functionally cyanogenic tissues liberate cyanide when the tissue is disrupted, allowing cyanogenic glycosides to interact with cyanide-cleaving enzymes. Thus, a tissue that contains cyanogenic glycosides, but lacks cyanide-cleaving enzymes, is functionally acyanogenic. Cyanogenic glycosides are typically present in fruit tissue of *Prunus* species. Though the unripe fruit of some *Prunus* species is cyanogenic, many lack the necessary enzymes to release cyanide from tissues of their unripe fruits, rendering them acyanogenic and precluding any defensive function in fruit tissue (Machel and Dorsett, 1970; Nahrstedt, 1970; Swain et al. 1992; Sanchez-Perez et al., 2012).

Fruits of many *Prunus* species ripen quickly, with those fruits initiated in spring being fully ripe by midsummer. The reproductive phenology of the laurel cherry (*Prunus caroliniana*) stands in sharp contrast to its north-temperate congeners. In this species flowering occurs in the early spring, and fruit ripening does not occur until new flowers are produced the following year. Thus, laurel cherry presents year-old ripe fruit along with new flowers each spring. This extended fruit maturation period amplifies the risk of premature fruit removal or seed predation relative to its fast-developing congeners. Given this extended period of vulnerability, we suspected that unripe laurel cherry fruit might be chemically defended from damage or premature removal by way of cyanogenicity of the unripe fruit. Our goal was to determine whether laurel cherry was divergent from the majority of its congeners or conformed to the pattern of fruit and seed chemistry typical for the genus.

We collected unripe (firm and green) and ripe (soft and black) fruits and seeds from laurel cherry growing in riparian forest along the Colorado River at University of Texas Brackenridge Field Laboratory in Austin, Texas, in spring of 2013 and 2014; and we assayed fruit and seed tissues for cyanide. We macerated the entirety of each tissue for each sample in 5-mL distilled water, strained and collected the resulting liquid, and used a Quantofix® cyanide test kit (Reference number: 91318; Macherey-Nagel GmbH & Co, Düren, Germany) to measure cyanide concentrations. This kit worked through addition of chloramine T, pyridine, and phosphate buffers to a liquid sample. We then applied this solution to a test strip containing a barbituric acid derivative (H. Medollo, CTL Scientific, pers. comm.), which changed color in response to presence of cyanide. We compared the color on the strip with a color scale provided with the kit (similar to pH test strips) categorizing tissues into 0-, 1-, 3-, 10-, or 30-mg cyanide per L concentrations.

Unripe fruits liberated cyanide after damage, whereas seeds in these fruits did not (Fig. 1). We found an inverse

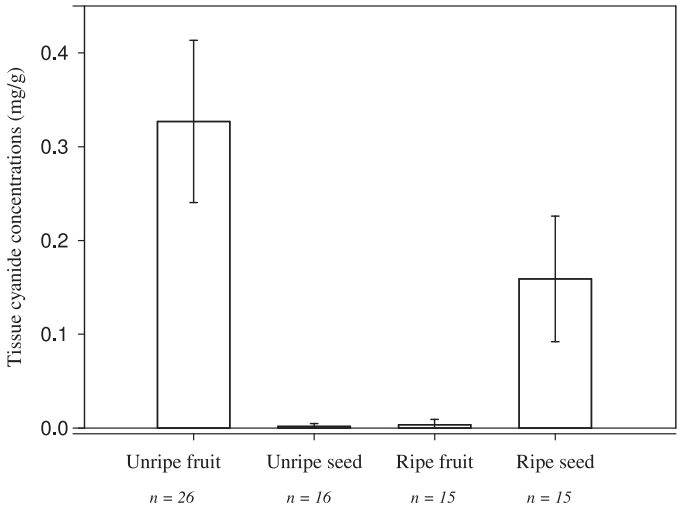

Fig. 1—Cyanide concentrations in ripe and unripe seed and fruit tissue of laurel cherry (*Prunus caroliniana*). Unripe fruits liberated cyanide upon tissue disruption, whereas unripe seeds did not. Upon ripening, this pattern reversed—seeds became cyanogenic and the fruit became functionally acyanogenic. Fruit and seed samples came from single propagules; unripe and ripe samples came from common trees. Each tree was sampled only once for each measurement. Error bars represent two *SE*s above and below the mean for each group.

pattern in ripe fruits and seeds, with ripe fruit failing to liberate cyanide, whereas ripe seeds were approximately half as cyanogenic as unripe fruit (Fig. 1).

Laurel cherry's exceptionally long fruit-maturation period likely necessitates long-term protection of its fruits, which might be provided via the observed cyanogenicity. Though more detailed study of the chemical and seed dispersal ecology of laurel cherry is necessary to discern whether fruit cyanogenicity holds any functional significance for the species, we pose the hypothesis that cyanogenicity in developing laurel cherry fruits serves as a defense against premature removal and insect or bird damage, facilitating exceptionally long fruit-maturation period of the laurel cherry.

We began this study after observing that flocks of American robins (*Turdus migratorius*) and cedar waxwings (*Bombycilla cedrorum*) left behind seemingly ripe fruit after visiting patches of laurel cherry for days. It was unclear why the fruit was left behind by flocks capable of fully stripping large fruit crops in other species such as the Ashe juniper (*Juniperus ashei*). We suggest that there may be a lag between color transition and loss of cyanogenicity, and that this may influence fruit removal rates.

Though slower fruit removal may at first appear disadvantageous because of the potential opportunity cost via reduced quantity of dispersal in a given period of time, it may in fact result in a higher quality dispersal pattern overall. The broader the area over which an individual's seeds are dispersed (the seed shadow), the higher the success rate for that seed crop (Janzen, 1970, 1971; Connell, 1971; Howe and Miriti, 2000). However, seed rain tends to follow a leptokurtic distribution, with the majority of seeds deposited near the parent plant (Janzen, 1971; Ward and Paton, 2007). When a large flock of birds strips the entire fruit crop from a stand in a short time period, the seed shadow for those plants is limited to the area that the flock covers within a given gut-retention-time window. Though this may be a large area, the seed shadow that would be created by visitation of multiple flocks, separated in time, is likely to be much larger because of stochastic variation in flock movements. Thus, mechanisms that effectively slow the release of seeds from a parent plant may improve the overall quality of seed dispersal.

The balance of potential opportunity cost to the benefit of a potentially larger seed shadow would thus be context-dependent—if visitation by frugivores is high, then a slow-release mechanism might be more beneficial; whereas if visitation is low, then simultaneous release might be favored. The study of pollen dispersal has produced similar predictions. In many zoochorous pollination systems, the benefit of broader pollen dispersal via visitation by more individual pollinators must be weighed against the potential opportunity cost of incomplete pollen removal. Ecological modeling of such systems suggests that high visitation should favor gradual release of pollen (Harder and Thomson, 1989; Harder, 1990). Indeed, pollen release timing is facultative in some plant species with respect to visitation frequency (Harder, 1990). Though the mechanisms would not be comparable, it is conceivable that some plants exhibit analogous facultative control over fruit ripening in response to removal frequency by frugivores. Investigation of such phenomena would require controlled fruit-removal experiments with careful tracking of the onset of transition to mature fruit color and the loss of cyanogenic properties.

Our observations suggest that a closer look at other plants with comparable patterns of lag between flowering and fruiting seasons, as described by Croat (1978), could uncover similar metabolic dances between fruits, seeds, dispersers, and seed predators. Seasonal patterns of seed disperser and seed predator abundance and behavior are likely to underlie such chemo-phenology patterns.

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RAZORBACK SUCKER TRANSBASIN MOVEMENT THROUGH LAKE POWELL, UTAH

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Abstract—We documented four razorback sucker (*Xyrauchen texanus*) individuals originally stocked in the San Juan River, New Mexico, subsequently recaptured in the Colorado and Green rivers, Utah. Each fish moved >550 km between stocking and recapture locations. The time between detections was 171–1,519 days. These movements included ≥210 km through Lake Powell. Lake Powell was previously thought to be a barrier between razorback sucker populations in the San Juan River and the Colorado and Green rivers.

Resumen—Documentamos cuatro individuos de matalote jorobado (*Xyrauchen texanus*) que originalmente fueron sembrados in el río San Juan, Nuevo México, que después fueron recapturados en los ríos Colorado y Green, Utah. Cada pez se desplazó >550 km entre el lugar de la siembra y el lugar de la recaptura. El tiempo entre las detecciones fue 171–1519 días. Estos movimientos incluyeron ≥210 km a través de lago Powell. Anteriormente se pensó que lago Powell era una barrera entre las poblaciones del matalote jorobado en el río San Juan y los ríos Colorado y Green.

Razorback sucker (*Xyrauchen texanus*) is an endemic catostomid of the Colorado River Basin. Although formerly abundant across the basin (Minckley, 1983; Platania et al., 1991; Modde et al., 1996; Marsh et al., 2003), populations have declined due to the combined effects of habitat fragmentation, loss, and modification caused by the construction of large main-stem dams; and predation on and competition with nonnative fish species (Holden, 1979; Tyus and Saunders, 2000; USFWS, 2002; Clarkson et al., 2005). Razorback sucker are federally protected (USFWS, 1991) and the San Juan River Basin Recovery Implementation Program and Upper Colorado River Endangered Fish Recovery Program carry out management actions in the Upper Colorado River Basin, including augmentation with hatchery-reared fish and nonnative fish removal to recover and restore populations of razorback sucker (Campbell et al., in litt.). Hatchery-reared razorback sucker were implanted with 134-KHz full duplex passive integrated transponder (PIT) tags (BIOMARK, Boise, Idaho) prior to stocking to provide a unique identifier for recaptures that occur during management and monitoring activities.

Long-distance movements by razorback sucker have been associated with spawning aggregations and migra-