The Journal of Caribbean Ornithology

RESEARCH NOTE

Vol. 27:27–30. 2014

Questions raised by the consumption of cane sugar by a Black-throated Blue Warbler (*Setophaga caerulescens*)

Gary R. Graves


Photo: Gary Graves

BirdsCaribbean

The Journal of Caribbean Ornithology
www.birdscaribbean.org/jco ISSN 1544-4953
RESEARCH NOTE Vol. 27:27–30. 2014
BirdsCaribbean
www.birdscaribbean.org

Questions raised by the consumption of cane sugar by a Black-throated Blue Warbler (*Setophaga caerulescens*)

Gary R. Graves

Abstract I address questions raised by an observation of a Black-throated Blue Warbler (*Setophaga caerulescens*) eating unrefined granulated cane sugar in Kingston, Jamaica. Sugar consumption implies the presence of taste receptors sensitive to sucrose and digestive sucrase activity sufficient to assimilate highly concentrated sucrose solutions. The ability to efficiently digest disaccharides, such as sucrose, and more complex oligosaccharides has permitted wood warblers and other nine-primaried oscines to exploit nectars of hummingbird-pollinated flowers and homopteran honeydew that may not be easily digested by avian clades such as thrushes and mimids that appear to lack digestive sucrases. In a broader context, clade-specific differences in digestive physiology may result in resource use patterns in birds that mimic the outcome of interspecific competition.

Keywords Black-throated Blue Warbler, cane sugar, digestive enzymes, interspecific competition, Jamaica, nectarivory, saccharides, *Setophaga caerulescens*, sucrase, sucrose

Resumen Cuestiones planteadas por el consumo de azúcar de caña por *Setophaga caerulescens*—Aquí abordo preguntas surgidas por la observación de *Setophaga caerulescens* alimentándose de azúcar de caña granulada y sin refinar en Kingston, Jamaica. El consumo de azúcar implica la presencia de receptores de gusto sensibles a la sacarosa así como suficiente actividad digestiva de sacarasa para asimilar soluciones altamente concentradas de sacarosa. La habilidad para digerir eficientemente los discáridos, tales como la sacarosa, y oligosacáridos más complejos ha permitido a los parúlidos y otros oscines con nueve primarias aprovechar néctares de flores polinizadas por colibríes y la melaza producida por homópteros que pueden no ser fácilmente digeridos por clados de aves como túrdidos y mímidos que carecen de sacarasas digestivas. En un contexto más amplio, las diferencias clado-específicas en la fisiología digestiva pueden resultar en patrones de uso de recursos en aves que imiten el resultado de la competencia interespecífica.

Palabras clave azúcar de caña, competencia interespecífica, enzimas digestivas, Jamaica, nectivoría, sacarasa, sacáridos, sacarosa, *Setophaga caerulescens*

Résumé Questions soulevées par la consommation de sucre de canne par une Paruline bleue (*Setophaga caerulescens*)—Sont traitées ici les questions soulevées par l'observation d'une Paruline bleue (*Setophaga caerulescens*) se nourrissant de sucre de canne cristallisé non raffiné à Kingston, en Jamaïque. La consommation de sucre implique la présence de récepteurs du goût sensibles au saccharose, et d'une activité de digestion par la sucrase suffisante pour assimiler des solutions très concentrées en saccharose. La capacité à digérer efficacement les disaccharides tels que le saccharose, et les oligosaccharides plus complexes, a permis aux parulines et autres espèces du groupe des oscines pourvues de 9 rémiges primaires d'exploiter le nectar des fleurs pollinisées par les colibris et le miellat des homoptères, qui ne peuvent pas être facilement digérés par les clades tels que les grives et les mimidés qui semblent manquer de sucrases digestives. Dans un contexte plus large, les différences spécifiques des clades dans la physiologie digestive peuvent aboutir à des modèles d'utilisation des ressources par l'avifaune qui imitent les résultats de la compétition interspécifique.

Mots-clés compétition interspécifique, enzymes digestives, espèces nectarivores, Jamaïque, Paruline bleue, saccharides, saccharose, *Setophaga caerulescens*, sucrase, sucre de canne

Department of Vertebrate Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013, USA; and Center for Macroecology, Evolution and Climate, University of Copenhagen, 2100 Copenhagen Ø, Denmark; e-mail: gravesg@si.edu.

The Black-throated Blue Warbler (*Setophaga caerulescens*) has been recorded feeding on natural sources of sucrose at birch sap wells on the breeding grounds (Kilham 1953) and at bird-pollinated flowers (Wunderle 1995) and homopteran honeydew on the wintering grounds in the Caribbean (Latta *et al.* 2001, Latta and Faaborg 2002). It has also been observed feeding at sugar-water feeders (Niemuth 1997). Here I report an observation of an individual eating unrefined granulated cane sugar in Kingston, Jamaica. Cane sugar is composed almost exclusively of the disaccharide sucrose. The consumption of dry cane sugar suggests that the warbler has sufficient digestive sucrase activity to assimilate nectars with very high concentrations of sucrose and taste receptors capable of sensing sucrose. Of broader significance, this observation raises questions about the association between digestive enzymes for sugar assimilation, resource use in wood warblers, and interspecific competition for nectar and fruit.

Observation

I observed a Black-throated Blue Warbler (*Setophaga caerulescens*) feeding on unrefined granulated cane sugar at an outdoor restaurant in Kingston on three consecutive mornings, 13–15 December 2013 (Fig. 1). The adult male (after second year) seemed to follow a well-honed daily routine. Uncovered sugar bowls were placed on a dozen outdoor tables in a landscaped courtyard each morning between 0645 and 0700 and were left on the tables until the restaurant closed at 2200. The warbler flew directly to a particular sugar bowl about 15 min after the bowl was brought out each morning. It consumed several bill tips of sugar crystals during each feeding bout and returned to the same sugar bowl about every 15 min during my observation periods (~1 hr each morning). Several other species (e.g., *Zenaida aurita*, *Mimus polyglottos*, *Tiaris bicolor*) were observed near the restaurant tables each morning but none were observed feeding on sugar.

Discussion

The evolution of nectarivory and frugivory in birds has resulted in concomitant changes in the sugar composition of nectar and fruit and the digestive enzymes of birds. In the Western Hemisphere, plants pollinated by hummingbirds are characterized by nectars with high concentrations of sucrose whereas most passerine-pollinated flowers tend to be rich in monosaccharide sugars (Martínez del Rio *et al.* 1992, Stiles and Freeman 1993, Baker *et al.* 1998). The association between pollinator type and sugar composition of nectars, however, is not clear-cut (references in Lotz and Schondube 2006). Many nectar-feeding birds also exploit homopteran honeydew, a complex cocktail of sugars, amino acids, and secondary plant products (Way 1963). Sugar composition of honeydew depends on the plant and homopteran species, but most honeydews contain a mixture of monosaccharides, disaccharides including sucrose, and oligosaccharides composed of three to six monosaccharides (Fischer and Shingleton 2001).

Animals that lack intestinal sucrases experience osmotic diarrhea after ingesting sucrose (Sunshine and Kretchmer 1964) and may exhibit a behavioral aversion to sucrose-rich fruit and nectar (Brugger and Nelms 1991). Sucrases have been reported in several non-passerine and passerine bird families (Lotz and Schondube 2006), but little is known about the taxonomic extent of sucrase activity within avian clades. Likewise, the degree to which sucrase secretion is seasonally modulated or varies with diet is also poorly known (Afik and Karasov 1995, Levey *et al.* 1999). Exploratory studies suggest that many groups of nine-primaried oscines such as wood warblers (*Oreothypis*, *Setophaga*), flower-piercers (*Diglossa*), and icterids (*Icterus*, *Cacicus*) exhibit moderate to high levels of sucrase activity (Martínez del Rio 1990, Afik and Karasov 1995, Levey *et al.* 1999, Schondube and Martínez del Rio 2004). Other taxonomic groups in the Western Hemisphere such as thrushes (*Catharus*, *Hylocichla*, *Turdus*), mimids (*Dumetella, Mimus*), and furnariids (*Cinclodes*) apparently lack sucrases and the ability to efficiently assimilate sucrose (Martínez del Rio 1990, Malcarney *et al.* 1994, Witmer and Martínez del Rio 2001, Sabat and Gonzalez 2003, Gatica *et al.* 2006). Passerine species with rapid gut passage rates may also have difficulty in assimilating sucrose (Martínez del Rio 1990).

Fig. 1. Black-throated Blue Warbler (*Setophaga caerulescens*) feeding on granulated unrefined sugar. Grains of sugar are adhering to the tip of the warbler's bill (photograph by Gary R. Graves).

Avian sugar preference and assimilation efficiency vary with solute concentration (Schondube and Martínez del Rio 2003). Most laboratory studies of sucrose consumption have been conducted with relatively dilute sugar solutions (< 30 % weight/volume). The ability to effectively assimilate very high concentrations of sucrose, as exemplified by granulated cane sugar, has been inferred only from a few anecdotal observations. Red-crowned Woodpecker (*Melanerpes rubricapillus*), Bananaquit (*Coereba flaveola*), White-lined Tanager (*Tachyphonus rufus*), Blue-gray Tanager (*Thraupis episcopus*), and the Lesser Antillean Bullfinch (*Loxigilla noctis*) have been observed to eat cane sugar directly from sugar bowls in the Caribbean (Hundley and Mason 1965, Reader *et al.* 2002). An undocumented mention of refined sugar consumption also appeared in the species account for the Black-throated Blue Warbler (Holmes *et al.* 2005).

My observation of sugar consumption in the Black-throated Blue Warbler adds to the body of knowledge that suggests many if not all species of wood warblers (*Mniotilta*, *Oreothlypis*, *Setophaga*, *Basileuterus*, *Cardellina*, *Myioborus*) are able to efficiently digest sucrose-rich nectars and homopteran honeydew (Wunderle 1978, Fraga 1989, Remsen *et al.* 1989, Greenberg *et al.* 1993, Afik and Karasov 1995, Wunderle 1995, Rogers 1997, Levey *et al.* 1999, Latta *et al.* 2001, Schondube and Martínez del Rio 2004, Peter 2008, Gamper and Koptur 2010). The extent to which digestive enzymes are co-evolved with taste receptors in wood warblers and other birds is unknown. In vertebrates, sweet tastes are sensed by G protein-coupled receptors that usually cluster in taste buds (Shi and Zhang 2006). Sensitivity to sucrose is known in some avian species but has been lost in others such as the domestic chicken (*Gallus gallus*; Shi and Zhang 2006, Baldwin *et al.* 2014). Unfortunately, the functional expression of taste receptors in songbirds to the diverse array of naturally occurring sugars in nectars and fruit has not yet been investigated. Nevertheless, it is probable that the Black-throated Blue Warbler and other nine-primaried oscines are able to taste sucrose. Otherwise it would be difficult to explain how individuals observed eating granulated cane sugar were able to identify this novel substance as eatable.

Avian ecologists have long been intrigued by the capacity of migratory passerines to insinuate themselves during the nonbreeding season into species-rich avian communities in the Neotropics (Keast and Morton 1980). Avian community dynamics undoubtedly shift when millions of migratory wood warblers annually flood into the Caribbean basin and Central America but remarkably little research has been conducted on seasonal variation in competitive partitioning of fruit and nectar resources among facultative and obligate nectarivores and frugivores. Several authors have commented on the importance of homopteran honeydew and flower nectar as food resources for wintering wood warblers (Greenberg *et al.* 1993, Wunderle 1995, Latta *et al.* 2001, Latta and Faaborg 2002, Gamper and Koptur 2010), yet the mechanistic connections between the evolution of digestive enzymes, resource exploitation, and interspecific competition have not been explicitly addressed in the voluminous literature on the community ecology of avian assemblages in the Caribbean and elsewhere. Nonetheless, the implications of laboratory and field observations are clear. The ability to efficiently assimilate disaccharides and complex oligosaccharides may give wintering populations of wood warblers a competitive edge over species that lack digestive enzymes necessary to exploit sucrose-rich nectar, honeydew, and fruit. Moreover, clade-specific differences in the digestive physiology may result in resource use patterns in avian communities that mimic the outcome of interspecific competition. Species with reduced sucrase activity and rapid gut passage rates (e.g., thrushes) may naturally avoid sucrose-rich fruit and nectar (Brugger and Nelms 1991) regardless of potential or actual competitive interactions with other species. A full understanding of resource use patterns in migratory and resident Caribbean birds will require knowledge of the sugar composition of nectar and fruit as well as the array of digestive enzymes present in resource consumers.

Acknowledgments

I thank the James Bond Fund of the Smithsonian Institution and the Smoketree Trust for support and two reviewers for comments on the manuscript.

Author Information

Department of Vertebrate Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013, USA; and Center for Macroecology, Evolution and Climate, University of Copenhagen, 2100 Copenhagen Ø, Denmark; e-mail: gravesg@si.edu

Literature Cited

Afik, D., and W.H. Karasov. 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. Ecology 76:2247–2257.

Baker, H.G., I. Baker, and S.A. Hodges. 1998. Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. Biotropica 30:559–586.

Baldwin, M.W., Y. Toda, T. Nakagita, M.J. O'Connell, K.C. Klasing, T. Misaka, S.V. Edwards, and S.D. Liberles. 2014. Evolution of sweet taste perception in hummingbirds by transformation of the ancestral umami receptor. Science 345:929–933.

Brugger, K.E., and C.O. Nelms. 1991. Sucrose avoidance by American Robins (*Turdus migratorius*): implications for control of bird damage in fruit crops. Crop Protection 10:455–460.

Fischer, M.K., and A.W. Shingleton. 2001. Host plant and ants influence the honeydew sugar composition of aphids. Functional Ecology 15:544–550.

Fraga, R.M. 1989. Interactions between nectarivorous birds and the flowers of *Aphelandra sinclairiana* in Panama. Journal of Tropical Ecology 5:19–26.

Gamper, H.A., and S. Koptur. 2010. Honeydew foraging by birds in tropical montane forests and pastures of Mexico. Journal of Tropical Ecology 26:335–341.

Gatica, C.D.L., S.P. González, R.A. Vásquez, and P. Sabat. 2006. On the relationship between sugar digestion and diet preference in two Chilean avian species belonging to the Muscicapoidea superfamily. Revista Chilena de Historia Natural 79:287–294.

Greenberg, R., C. Macias Caballero, and P. Bichier. 1993. Defense of homopteran honeydew by birds in the Mexican highlands and other warm temperate forests. Oikos 68:519–524.

Holmes, R.T., N.L. Rodenhouse, and T.S. Sillett. 2005. Black-throated Blue Warbler (*Setophaga caerulescens*). *In* The Birds of North America Online, no. 87 (A. Poole, ed). Cornell Laboratory of Ornithology, Ithaca, NY. bna.birds.cornell.edu/bna/species/087.

Hundley, M.H., and C.R. Mason. 1965. Birds develop a taste for sugar. Wilson Bulletin 77:408.

Keast, A., and E.S. Morton. 1980. Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation. Smithsonian Institution Press, Washington, DC.

Kilham, L. 1953. Warblers, hummingbird, and sapsucker feeding on sap of yellow birch. Wilson Bulletin 65:198.

Latta, S.C., and J. Faaborg. 2002. Demographic and population responses of Cape May Warblers wintering in multiple habitats. Ecology 83:2502–2515.

Latta, S.C., H.A. Gamper, and J.R. Tietz. 2001. Revising the convergence hypothesis of avian use of honeydew: evidence from Domincan subtropical dry forest. Oikos 93:250–259.

Levey, D.J., A.R. Place, P.J. Rey, and C. Martínez del Rio. 1999. An experimental test of dietary enzyme modulation in Pine Warblers *Dendroica pinus*. Physiological and Biochemical Zoology 72:576–587.

Lotz, C.N., and J.E. Schondube. 2006. Sugar preferences in nectar- and fruit-eating birds: behavioral patterns and physiological causes. Biotropica 38:3–15.

Malcarney, H.L., C. Martínez del Rio, and V. Apanius. 1994. Sucrose intolerance in birds: simple nonlethal diagnostic methods and consequences for assimilation of complex carbohydrates. Auk 111:170–177.

Martínez del Rio, C. 1990. Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. Physiological Zoology 63:987–1011.

Martínez del Rio, C., H.G. Baker, and I. Baker. 1992. Ecological and evolutionary implications of digestive processes: bird preferences and the sugar constituents of floral nectar and fruit pulp. Experientia 48:544–551.

Niemuth, N.D. 1997. Black-throated Blue Warbler (*Dendroica caerulescens*) feeds at hummingbird feeder. Passenger Pigeon 59:233–234.

Peter, J. 2008. Nectar-feeding by a Nashville Warbler. Ontario Birds 26:69–71.

Reader, S.M., D. Nover, and D.L. Lefebvre. 2002. Locale-specific sugar packet opening by Lesser Antillean Bullfinches in Barbados. Journal of Field Ornithology 73:82–85.

Remsen, J.V., Jr., M. Ellerman, and J. Cole. 1989. Dead-leaf-searching by the Orange-crowned Warbler in Louisiana in winter. Wilson Bulletin 101:645–648.

Rogers, L.L. 1997. Nectar-feeding by Cape May, Tennessee, and Nashville Warblers in Minnesota. Loon 69:55–56.

Sabat, P., and S.P. Gonzalez. 2003. Digestive enzymes in two species of marine cinclodes (Passeriformes: Furnariidae). Condor 105:830–833.

Schondube, J.E., and C. Martínez del Rio. 2003. Concentration-dependent sugar preferences in nectar-feeding birds: mechanisms and consequences. Functional Ecology 17: 445–453.

Schondube, J.E., and C. Martínez del Rio. 2004. Sugar and protein digestion in flowerpiercers and hummingbirds: a comparative test of adaptive convergence. Journal of Comparative Physiology B 174:263–273.

Shi, P., and J. Zhang. 2006. Contrasting modes of evolution between vertebrate sweet/umami receptor and bitter receptor genes. Molecular Biology and Evolution 23:292–300.

Stiles, F.G., and C.E. Freeman. 1993. Patterns in floral nectar characteristics of some bird-visited plant species from Costa Rica. Biotropica 25:191–205.

Sunshine, P., and N. Kretchmer. 1964. Intestinal disaccharidases: absence in two species of sea lions. Science 144:850–851.

Way, M.J. 1963. Mutualism between ants and honeydew-producing homoptera. Annual Review of Entomology 8:307–344.

Witmer, M.C., and C. Martínez del Rio. 2001. The membrane-bound intestinal enzymes of waxwings and thrushes: adaptive and functional implications of patterns of enzyme activity. Physiological and Biochemical Zoology 74:584–593.

Wunderle, J.M., Jr. 1978. Territorial defense of a nectar source by a Palm Warbler. Wilson Bulletin 90:297–299.

Wunderle, J.M., Jr. 1995. Population characteristics of Black-throated Blue Warblers wintering in three sites on Puerto Rico. Auk 112:931–946.

Cite this article as:

Graves, G.R. 2014. Questions raised by the consumption of cane sugar by a Black-throated Blue Warbler (*Setophaga caerulescens*). Journal of Caribbean Ornithology 27:27–30.