Fruit availability and consumer demand within a major migration stopover area: The Lower Delmarva Peninsula

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Cover Photo: Mosaic of fruiting grape, bayberry, autumn olive, and devil's walking stick. Photos by Barton J. Paxton

The Center for Conservation Biology is an organization dedicated to discovering innovative solutions to environmental problems that are both scientifically sound and practical within today's social context. Our philosophy has been to use a general systems approach to locate critical information needs and to plot a deliberate course of action to reach what we believe are

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EXECUTIVE SUMMARY

The lower Delmarva Peninsula is one of the most significant migration bottlenecks in eastern North America where large numbers of birds become concentrated within a relatively small land area. Habitats on the peninsula receive extremely high use by migrant landbirds during the fall months and are considered to have some of the highest conservation values on the continent. Over the past 20 years blocks of private land have been acquired by state and federal agencies for the stated purpose of restoring habitat for migratory land birds. This activity represents a sea change in both the character and purpose of this landscape and has the potential to improve the survivorship of many species of conservation concern. How to manage these lands to achieve maximum benefit to migrants continues to be an important question.

Resource agencies have identified two management endpoints including mature forest and maintained shrubland intended to improve conditions for migrants on the lower Delmarva Peninsula. An important question within this landscape is what resources these conservation endpoints will provide to migrants. Fruit is an essential component of habitat quality for fall migrants. We performed more than 2,000 vegetation assays during the fall of 2014 to evaluate the composition and density of fruiting plants and the density of fruit production within reference forest and shrub patches. We monitored nearly 500 fruiting branches (12 species) supporting more than 24,000 fruits weekly during the study period to assess patterns in fruiting phenology. These branches were included in an exclusion experiment (bagged vs unbagged) that we used to evaluate rates of fruit loss, fruit consumption, and fruit preference.

The seasonal schedule of fruit ripening varied dramatically between species such that the availability of ripe fruits changed during the migration period. Some of the fruits including American holly and hackberry matured too late to have relevance for most migrants. Based on the exclusion experiment, an index of consumption varied significantly between fruit species. Sassafras, devil’s walking stick, fox grapes and autumn olive had consumption rates of more than 15%/wk compared to hackberry, beautyberry and bayberry that were less than 5%/wk. Based on the first two months of the migratory period fruit species fall into three preference categories including high demand, medium demand and low demand.

The two management endpoints (mature forest vs shrub) differ dramatically with respect to the composition of the fruiting plant community, plant density, fruit density and the extent to which they support preferred fruit species. Although fruit density within shrub habitat was more than ten-fold higher than forest patches, 95% of the crop is of low demand or is produced by an exotic invasive. Shrub patches should be managed to broaden out the fruiting plant community to include preferred fruit species. Management prescriptions should be developed that drive the footprint of the less desirable plants down and expand the more desirable elements. The reference forest patches used in this study are of high quality but atypical habitats within the lower Delmarva landscape. Most of the forest patches within the study area are much younger, have closed canopies, support fewer fruit-producing plants and should be managed within an open-canopy system in order to mimic the reference patches and produce higher fruit densities.

BACKGROUND

The vast majority of nearctic-neotropical migratory birds are physically incapable of carrying enough energy to complete non-stop flights between their breeding and wintering areas (e.g., Berthold 1975, Dawson et al. 1983, Pettersson and Hasselquist 1985). To overcome this problem, migrants make periodic stops en route to replenish energy reserves. Once in stopover areas, migrants encounter unfamiliar landscapes where they must maintain a positive energy balance often under severe time constraints and uncertain conditions. Individuals that are able to successfully negotiate these conditions presumably increase their probability of successfully completing migration by maximizing their rate of energy deposition. Since successful migration is a prerequisite for future breeding, habitat use decisions made within stopover areas have profound fitness consequences for migrants.

The lower Delmarva and Cape May peninsulas are the most significant migration bottlenecks in eastern North America, concentrating large numbers of birds within relatively small land areas. Habitats on these peninsulas receive extremely high use by migrant landbirds during the fall months and are considered to have some of the highest conservation values on the continent. Along the lower Delmarva Peninsula, fall migrants “fall out” in the early morning hours as they reach the mouth of the Chesapeake Bay and form a steep density gradient extending south to north within the lower 20 km (Watts and Mabey 1993, 1994). This pattern suggests that lands near the peninsula tip have very high conservation value. Research has documented significant levels of resource depression within this concentration area (Watts et al., Unpublished) suggesting that habitat availability/quality may directly influence the condition of migrants during stopover periods and presumably their likelihood of surviving migration.

Within limits, the availability and quality of stopover habitats encountered by migrants within the lower Delmarva Peninsula are under management control. Over the past 20 years blocks of private land have been acquired by state and federal agencies for the stated purpose of restoring habitat for migratory land birds. This activity represents a sea change in both the character and purpose of this landscape and has the potential to improve the survivorship of many species of conservation concern. How to manage these lands to achieve maximum benefit to migrants continues to be an important and unresolved question.

Resource agencies have identified two management endpoints intended to improve conditions for migrants on the lower Delmarva Peninsula (Watts and Wilson 2013). These include maintained shrublands and forests. Because shrublands are an intermediate seral stage within a successional trajectory, long-term sustainability requires periodic management intervention. Because old-growth reference forests represent the end of the successional trajectory, once attained they do not require periodic management. However, when restoring habitat from agricultural fields, shrublands may be established very rapidly whereas establishment of reference forests would require several decades. The relationships between management costs and migrant benefits for these two endpoints have not been fully evaluated. An important question within this management puzzle is what resources will these conservation endpoints provide to migrants.

Fruit is an essential element contributing to habitat quality for fall migrants. Many passerine species that migrate along the Western Atlantic Flyway switch from a predominantly insect diet on the breeding grounds to a fruit-based diet during migration (Parrish 1997). Many fall fruits are high in fats and carbohydrates (White 1989, Smith et al. 2007) and their consumption facilitates migratory fattening (Bairlein and Simons 1995, Stevens 1996). A key question for habitat managers is what fruits do forest and shrublands provide within the lower Delmarva Peninsula. A related question is how do migrating birds respond to the fruits available within these habitats.

OBJECTIVES

Addressing general questions about fruit production, fruit availability and migrant fruit consumption habitats intended to represent management endpoints provides a necessary foundation on which to make management decisions. Our objectives in this field investigation were 1) to quantify the density of fruiting plants and fruit production within reference forest and shrub patches, 2) to examine patterns of fruiting phenology, 3) to quantify fruit consumption and 4) to examine fruit preferences within the lower Delmarva Peninsula.

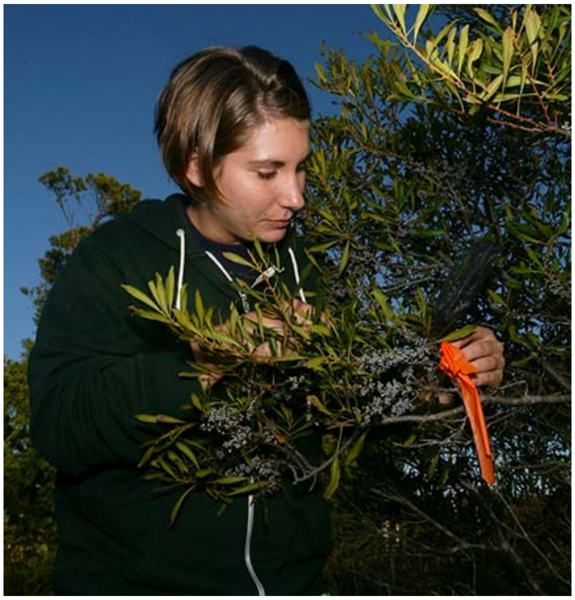
METHODS

Study Area

We measured the density of fruiting plants, fruiting phenology and consumption of fruit by birds within the lower Delmarva Peninsula in Northampton County, Virginia (Figure 1) during the fall (15 August to 25 November) of 2014. The Delmarva Peninsula separates the Atlantic Ocean and the Chesapeake Bay. The southernmost 100 km of the peninsula is a narrow land mass averaging less than 10 km in width. The rural landscape has been used for agriculture for generations, is highly dissected, and composed of alternating farm fields and forest fragments. Forest tracts are generally small and isolated with mixed vegetation. Canopy trees are dominated by loblolly pine (*Pinus taeda*), Virginia pine (*P. virginiana*), red maple (*Acer rubrum*), and various oaks (*Quercus spp.*), and hickories (*Carya spp.*). Understory trees are dominated by black cherry (*Prunus serotina*), and American holly (*Ilex opaca*). During the fall migration period, active a gricultural fields contain vegetable and row crops or bare ground. In recent decades, several open tracts have been

Technician, Sarah Rosche, counting the fruit of a beautyberry.

acquired by government agencies and conservation organizations and are being "allowed" via natural succession or "assisted" via plantings to transition to habitats supporting woody vegetation (Watts and Wilson 2013).



Technician, Arianne Millet, counting the fruit of a bayberry.

The lower Delmarva Peninsula supports a diversity of fruit-producing plants that are used heavily by birds during fall migration. Local trees that produce fall fruits include sassafras (*Sassafras albidum*), devil's walking stick (*Aralia spinosa*), American Holly, and hackberry (*Celtis occidentalis*). Once a significant component of the understory vegetation flowering dogwood (*Cornus florida*) has declined precipitously over the past three decades and no longer makes a significant contribution to the fall fruit crop. Understory shrubs including bayberry (principally *Myrica cerifera* and *M. pennsylvanica*) and beautyberry (*Callicarpa americana*) are widespread and produce large fruit crops. In addition to the native shrubs, Chinese privet (*Ligustrum sinense*) and autumn olive (*Elaeagnus umbellata*) have been established within the landscape and produce significant fruit crops where they occur - typically within early successional patches. Fruiting vines including fox grapes (*Vitus Labrusca*), frost grapes (*V. vulpina*), poison ivy (*Toxicodendron radicans*) and Virginia creeper (*Parthenocissus quinquefolia*) are common and produce significant fruit crops during most years.

Study Patches

We quantified fruiting plants within forest (n = 10) and shrub (n = 8) patches located within the southern 15 km of the Delmarva Peninsula (Figure 1). We selected habitat patches for inclusion that represent examples of management endpoints within the study area (Watts and Wilson 2013). Forest patches chosen were generally greater than 100 years old. From previous work within the study area (Watts and Mabey 1994) these forest patches are known to support the highest densities of fall migrants among all forest patches regardless of geographic position. Loblolly patches of this age class have older, well-established understory trees that support high fruit production and due to ongoing senescence have broken crowns that lead to the development of hardwood canopy trees and dense understories. Similarly, the shrub patches chosen represent the oldest and most well-established patches within the study area supporting mature stands of shrub species that produce large fruit crops during the fall period.

Fruiting Plants

We measured fruiting plant density and diversity within randomly selected vegetation plots in all study patches. The number of vegetation plots varied per patch from 2 to 16 according to patch size (Table 1). We quantified the coverage of fruiting plants within each survey plot using a

Technicians, Sarah Rosche and Arianne Millet, collecting vegetation data at a shrub plot.

variation of the vertical-line intercept technique (MacArthur and Horn 1969) referred to as the "pole method" (Mills et al. 1991). We used an 8-m telescopic pole marked in 0.5 m intervals to measure an index of vegetation (see Mills et al. 1991). In each survey plot, we randomly selected one transect intersecting the plot center and a second perpendicular to the first. We sampled vegetation at 5 m intervals along each transect (N = 20 samples/plot). Within each sampling station, the pole was held vertically through the vegetation and each fruiting species that entered the 0.5-m radius cylinder was recorded. For patches with vegetation exceeding 8 m in height the pole was used as a guide to sight up through the vegetation and record "hits" of fruiting plants. Fruiting plants that entered sample cylinders were examined and classified according to fruiting status (fruiting, not fruiting). All fruits detected within sample stations were identified and counted. We sampled vegetation between 21 August and 30 September, 2014.

We used vegetation samples to estimate fruit and fruiting plant density across the study area by habitat type. Occupancy of pole samples by fruit plants was used to project plants onto the ground surface and estimate plant coverage at the plot level (each vegetation plot sampled 20 cylinders or 15.71 m^2 of surface area). Plot information was used to estimate sample statistics (mean, standard deviation, standard error, coefficient of variation) for plant density in units of plants/100 ha and fruit density in units of fruit/ha. The number of fruit plant species per plot was used as a measure of community breadth. Two-tailed, independent sample t-tests were used to compare mean densities between forest and shrub patches. Frequency statistics were used to compare the proportion of plants that were fruiting during the study year between habitat types.

Figure 1. Shrubland and forest study patches located on the lower Delmavara peninsula of Virginia.

Table 1. Forest patches used for vegetation sampling on the lower Delmarva Peninsula (Northampton County, VA) in the fall of 2014.

Patch Type	Patch	Vegetation Plots (N)	Latitude	Longitude
Forest	Eastern Shore of Virginia, NWR - Firing Range	5	-75.949169	37.133135
Forest	Eastern Shore of Virginia, NWR - Bunker	2	-75.959881	37.130201
Forest	Magothy Road	16	-75.950364	37.154435
Forest	Kiptopeke North	6	-75.971823	37.168767
Forest	Kiptopeke South	14	-75.974888	37.158311
Forest	Devils Ditch Forest	3	-75.989702	37.182835
Forest	Morris Tract	6	-75.986688	37.189756
Forest	Cape Charles North	12	-76.012174	37.259596
Forest	Cape Charles South	4	-76.017251	37.26014
Forest	Sunset Beach	12	-75.969486	37.130611
Shrub	Eastern Shore of Virginia , NWR - Shrub East	2	-75.958604	37.131915
Shrub	Eastern Shore of Virginia , NWR - Shrub West	2	-75.963225	37.129796
Shrub	Eastern Shore of Virginia, NWR - Butterfly Trail North	4	-75.962945	37.134104
Shrub	Eastern Shore of Virginia, NWR - Butterfly Trail South	4	-75.964815	37.131725
Shrub	Seaside Road North	4	-75.964876	37.141518
Shrub	Seaside Road South	4	-75.963023	37.138178
Shrub	Fisherman Island East	3	-75.973939	37.090304
Shrub	Fisherman Island West	3	-75.978375	37.094818

Fruit Phenology and Consumption

We quantified fruit dynamics using a focal-branch approach (Drummond 2005, Smith et al. 2007). We randomly selected and marked with colored and labeled flagging tape branches on fruiting plants of twelve species and followed fruit on the branches weekly to assess the number and condition of fruit (Table 2). We selected a companion branch and enclosed the fruiting portion of the branch with translucent netting to ensure that netted branches were exposed to weather conditions but protected from foraging birds. Branches were selected and initial fruit counts were made between 21 August and 23 September, 2014 depending on the plant species and counts were made weekly following establishment. Plants included in the intensive fruit sampling were within study plots located on the lower 5 km of the peninsula (primarily on the Eastern Shore of Virginia National Wildlife Refuge).

Table 2. Sample sizes of fruiting branches and fruits monitored to evaluate fruit dynamics on the lower Delmarva Peninsula (Northampton County, VA) in the fall of 2014.

Species	Unbagged Branch	Bagged Branch	Beginning Fruit
American Holly	21	21	1,032
Autumn Olive	20	20	2,413
Bayberry	20	20	3,860
Beautyberry	20	20	3,432
Chinese Privet	20	20	1,759
Devil's Walking Stick	20	20	4,881
Fox Grapes	20	20	362
Frost Grapes	20	20	1,129
Hackberry	20	20	1,550
Pokeweed	14	14	1,135
Sassafras	34	34	859
Virginia Creeper	20	20	1,716
Total	**249**	**249**	**24,128**

Fruit Phenology

We classified the condition of fruit on all selected branches weekly to assess fruit seasonality. We evaluated fruit ripeness based on color and integrity. Fruits that were greater than 50% green were classified as unripe. Fruits that were less than 50% green and maintained a firm texture were considered ripe. Fruits that were discolored, brown or had a flaccid appearance were considered beyond their peak condition or rotten. The pattern in condition of fruits across time periods was used to estimate seasonality in ripeness. Data from bagged branches only was used to assess fruit phenology patterns because these fruits were protected from predation and so were allowed to progress through stages of ripeness. It should be noted that for some species in high demand this phenology does not represent availability of ripe fruit since birds are capable of consuming significant portions of the fruit crop as the fruit becomes ripe.

Fruit Loss or Consumption

We compared the number of fruits on branches across weeks with the initial number counted to evaluate patterns in loss (bagged branches) and loss/consumption (unbagged branches). We estimated the changes in fruit over time by calculating the proportion of fruit remaining weekly for both bagged and unbagged branches. We performed an arcsine transformation of the proportional data and evaluated the temporal pattern using a repeated-measures ANOVA with week as the grouping parameter. We calculated a fruit consumption index (Drummond 2005) by dividing the proportion of fruit remaining on unbagged branches by those on bagged branches. This ratio was subtracted from one to produce an index in which greater values reflect higher cumulative consumption over time. We used a repeated-measures ANOVA to analyze the arcsine transformed index to evaluate changes in the index over the season.

Fruit Preference

We used the index of fruit consumption as an indicator of preference between fruiting species with the assumption that high mean values of the index are related to levels of demand or desirability. We compared mean values for the index between fruit species during the eighth week (first week of November) of the study. We used this time period because most species were ripe by this date and it is late in the migratory season for the majority of passerines passing through the study area (Watts and Maybe 1993). We compared arcsine transformed index values between species using a one-way ANOVA.

RESULTS

Plant and Fruit Densities

We examined more than 2,100 fruit-producing plants in forest (1727) and shrub (421) patches while conducting greater than 2,000 pole samples (Table 3). The overall proportion of plants that were fruiting was relatively low (22.2%) and was significantly higher (Chi-square = 42.7, df = 2, p< 0.001) in shrub patches compared to forest patches. Fruiting rates varied considerably between species and habitats. Species such as poison ivy and Virginia creeper had consistently low fruiting rates while others including American holly, hackberry and Chinese privet seemed to have consistently high fruiting rates. Eight of the ten species that occurred in both habitats had higher fruiting rates in shrub patches possibly reflecting better access to sunlight. An exception was poison ivy. This pattern may reflect the influence of shrub management on plant age structure and associated fruiting.

Fruiting plant density was significantly higher in forest compared to shrub patches (Table 4). The composition of the fruiting plant community was dramatically different between the two habitat types with forest patches being dominated by American holly and shrub patches being dominated by bayberry. American holly and wild grapes accounted for more than 66% of the overall plant density in forest patches while bayberry and Virginia creeper accounted for more than 69% in shrub patches. The six plant species that had significantly higher densities by habitat were evenly split between forest and shrub.

Overall fruit density was more than ten fold higher in shrub patches compared to forest patches (Table 5). However, the overwhelming majority (84%) of fruit in the shrub patches was produced by bayberry with an additional 13% produced by autumn olive. Despite the overall low plant density, devil's walking stick produced 72% of the fruit in forests followed by 13% contributed by American holly. More than 14% of the fruit produced in shrub patches was produced by invasive autumn olive and Chinese privet. Greater than 11% of fruits produced in forests were from vines compared to less than 2% in shrub patches supporting the notion that patch age may contribute to vine development and productivity.

Table 3. Fruiting plants examined during pole samples within forest and shrub patches on the lower Delmarva Peninsula (Northampton County, VA) in the fall of 2014. Table presents number of plants examined, number of examined plants that were fruiting and the percentage of fruiting plants by habitat.

Plant Species	Forest N	Forest Fruiting	Forest %	Shrub N	Shrub Fruiting	Shrub %
Autumn Olive	2	0	0.0	21	20	95.2
American Holly	758	211	27.8	30	9	30.0
Beauty Berry	8	6	75.0	0	0	-----
Bayberry	41	8	19.5	170	74	43.5
Devil's Walking Stick	120	26	21.7	0	0	-----
Hackberry	4	2	50.0	3	1	33.3
Poison Ivy	169	11	6.5	20	0	0.0
Chinese Privet	20	9	45.0	17	9	52.9
Pokeweed	3	1	33.3	6	6	100.0
Sassafras	63	9	14.3	8	2	25.0
Virginia Creeper	145	2	1.4	111	22	19.8
Wild Grape	394	36	9.1	35	15	42.9
Total	**1,727**	**321**	**18.6**	**421**	**158**	**37.5**

Table 4. Summary statistics (mean + standard error) and statistical comparisons (two-tailed t-tests for independent samples) for fruit-producing plant species within forest and shrub patches. Presented are mean number of plants/100 ha.

Plant Species	Forest	Shrub	t-statistic	p-value
American Holly	47.1±3.43	5.2±2.88	6.7	<0.001
Autumn Olive	0.1±0.09	4.0±1.80	3.8	<0.001
Beautyberry	0.5±0.28	0	-----	-----
Bayberry	2.6±0.71	32.7±6.82	7.4	<0.001
Devil's Walking Stick	7.5±2.03	0	-----	-----
Hackberry	0.3±0.20	0.6±0.42	0.8	0.439
Poison Ivy	10.6±1.68	1.5±1.15	3.1	<0.01
Chinese Privet	1.3±0.52	3.3±0.96	1.9	0.06
Pokeweed	0.2±0.11	1.2±1.15	1.4	0.157
Sassafras	3.9±1.14	1.5±0.72	1.2	0.244
Virginia Creeper	9.1±1.58	21.3±3.49	3.6	<0.001
Wild Grape	24.6±2.18	6.7±1.83	4.5	<0.001
Total	**107.8±2.25**	**78.0±4.75**	**3.5**	**<0.001**

Table 5. Summary statistics (mean + standard error) and statistical comparisons (two-tailed t-tests for independent samples) for fruit within forest and shrub patches. Presented are mean number of fruits/ha.

Plant Species	Forest	Shrub	t-statistic	p-value
American Holly	20,746±3,145	51±50	3.6	<0.001
Autumn Olive	0	248,173±152,084	-----	-----
Beautyberry	2,743±1,701	0	-----	-----
Bayberry	5,965±3,579	1,615,277±396,635	7.4	<0.001
Devil's Walking Stick	111,661±48,201	0	-----	-----
Hackberry	212±212	0	-----	-----
Poison Ivy	14,027±6,647	0	-----	-----
Chinese Privet	2,986±1,583	25,869±18,147	2.2	<0.05
Pokeweed	149±149	12,553±12,550	1.8	0.075
Sassafras	228±140	229±184	0	0.996
Virginia Creeper	0	15,964±7,773	-----	-----
Wild Grape	2,868±1,583	3,488±1,701	0.3	0.802
Total	**154,513±49,253**	**1,923,055±389,335**	**7.6**	**<0.001**

Fruit Phenology

The seasonal schedule of fruit ripening varied dramatically between species such that the availability of ripe fruits changed during the study period (Figure 2). Plants generally fall within three fruiting categories including early, middle and late fruiters. Early fruiting species include sassafras, autumn olive, pokeweed and Virginia creeper. Middle producers include devil's walking stick, bayberry, and both grape groups. Late fruiting plants include American holly, Chinese privet, hackberry and beautyberry. For some of these late ripening species such as hackberry or privet that primarily represent late fall and winter foods, the proportion of fruit in the ripe category remained low during the duration of the study period.

Fruit Loss and Consumption

We monitored nearly 500 fruiting branches supporting more than 24,000 fruits weekly during the study period to assess patterns in fruit loss. Fruit numbers declined significantly (repeated-measures ANOVA, all F-statistics >450 and p-values <0.001) over the study period for all combinations of species and treatment (bagged vs unbagged). However, the fruit loss rates varied dramatically between species (Figure 3). Sassafras, autumn olive and pokeweed reached 50% loss levels during the first month of the study while devil's walking stick, privet and both grapes reached 50% depletion during the second month. Remaining species never reached 50% losses. Of all fruits evaluated, sassafras appears to be in the most demand, being cropped out very early in the season.

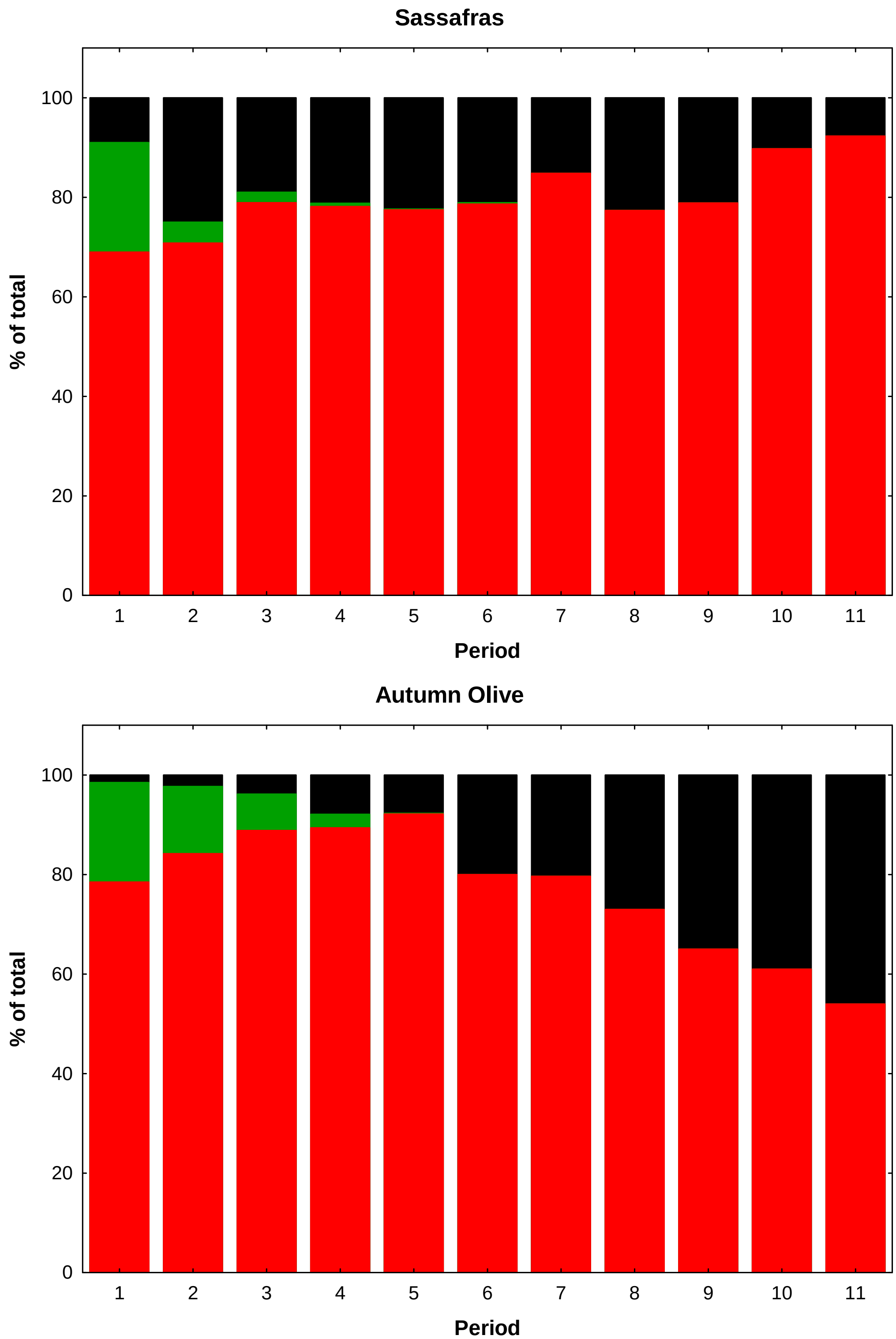
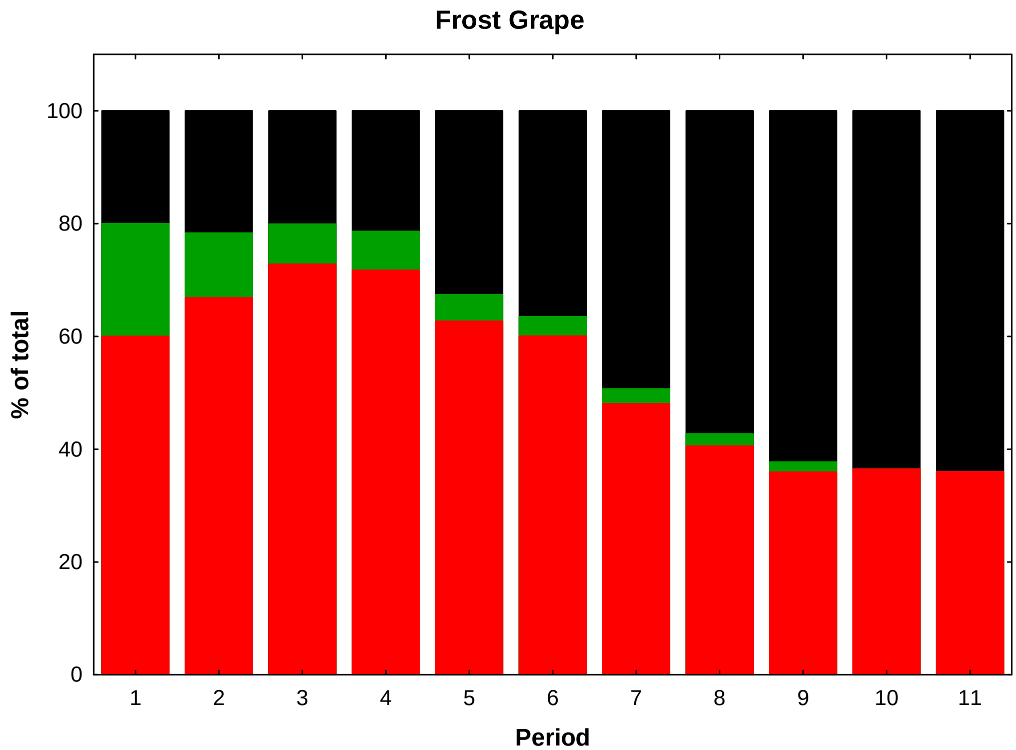
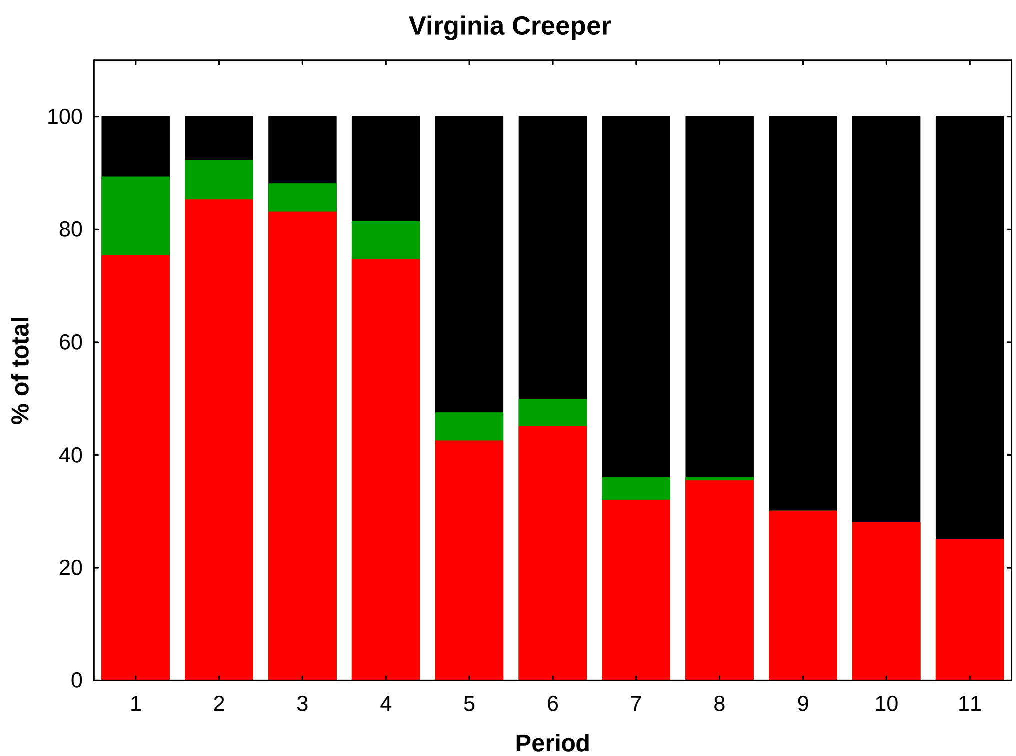


Figure 2. Phenology of fruit condition for plant species assessed on the lower Delmarva Peninsula (Northampton County, VA) during the fall of 2014. Green=Unripe, Red=Ripe, Black=Rotten.





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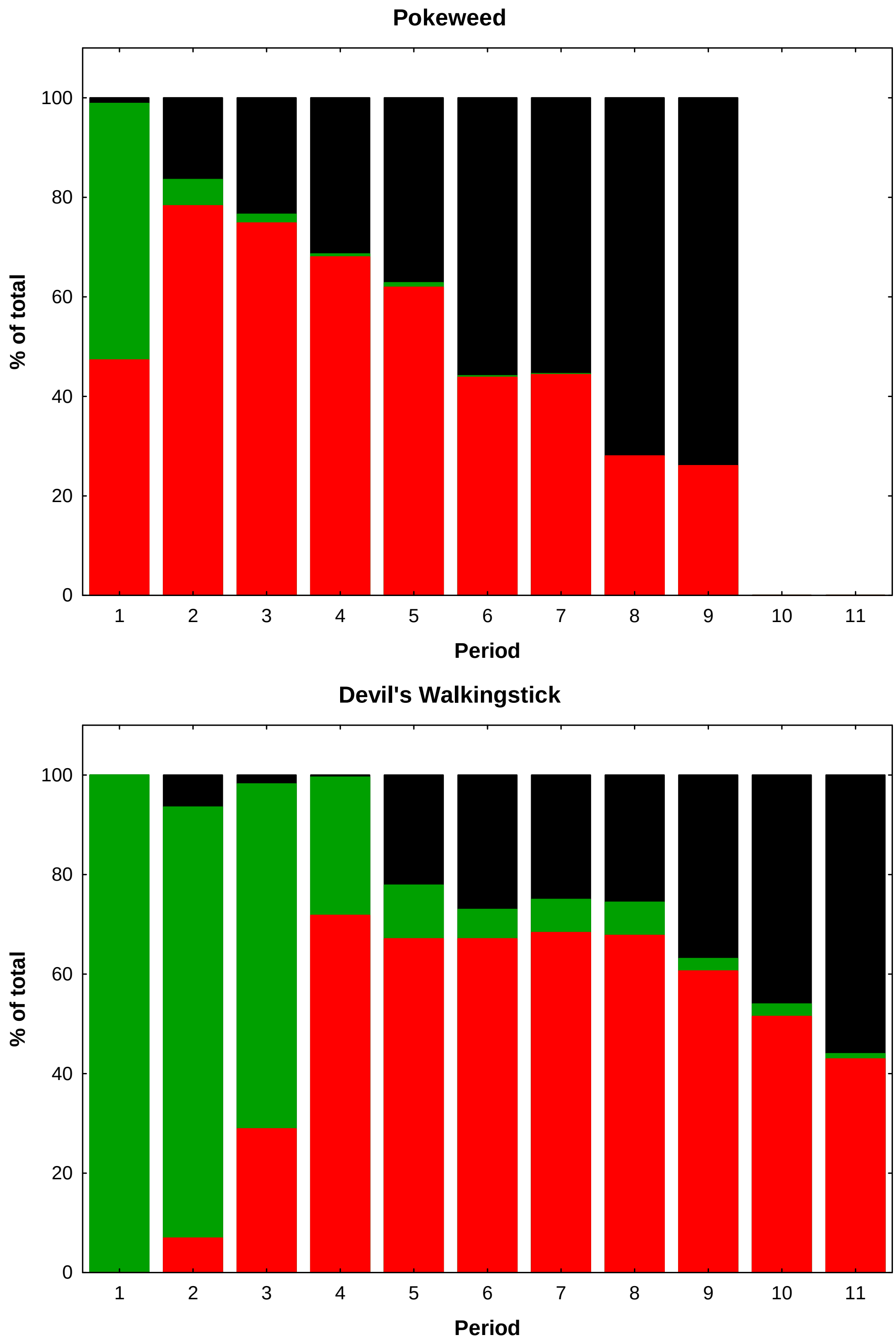

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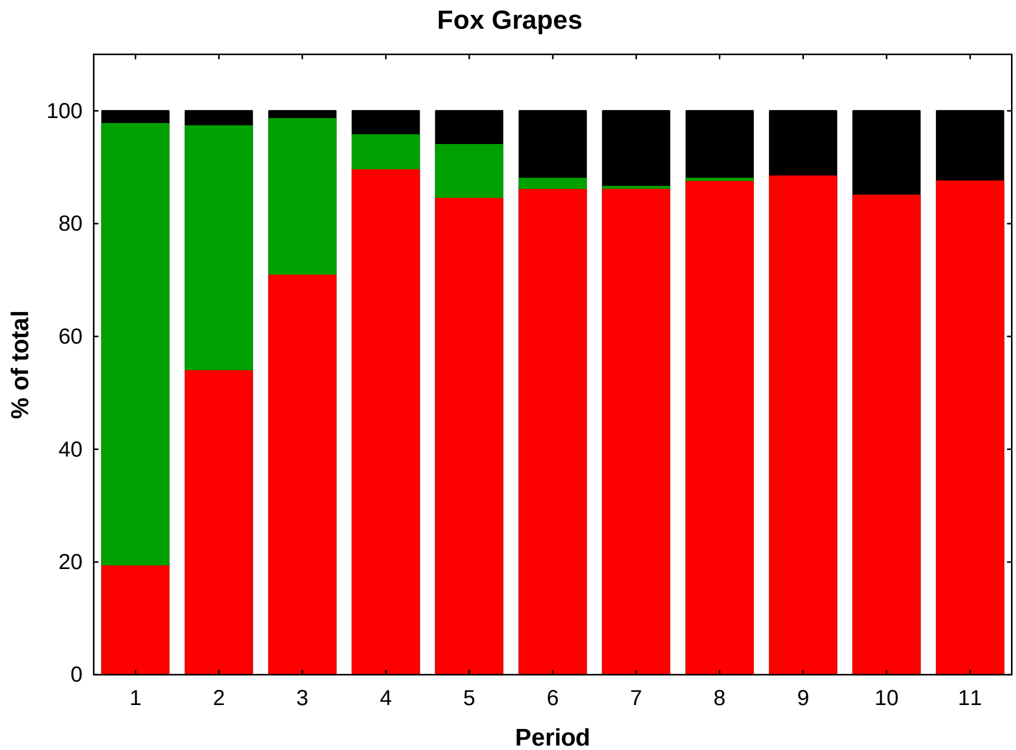

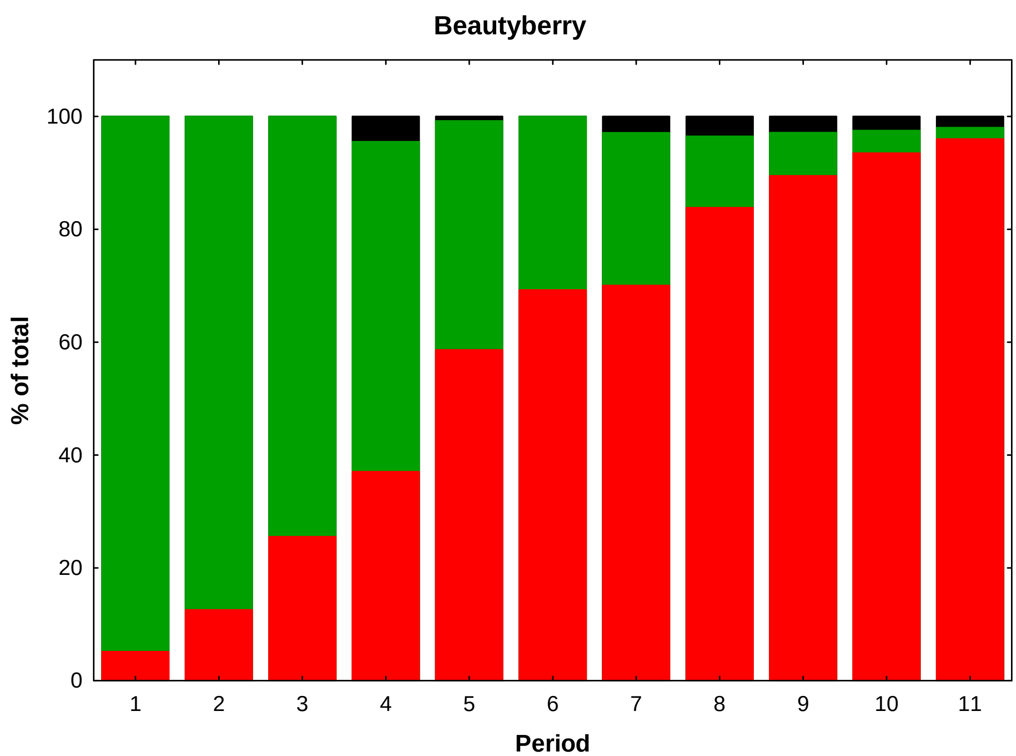

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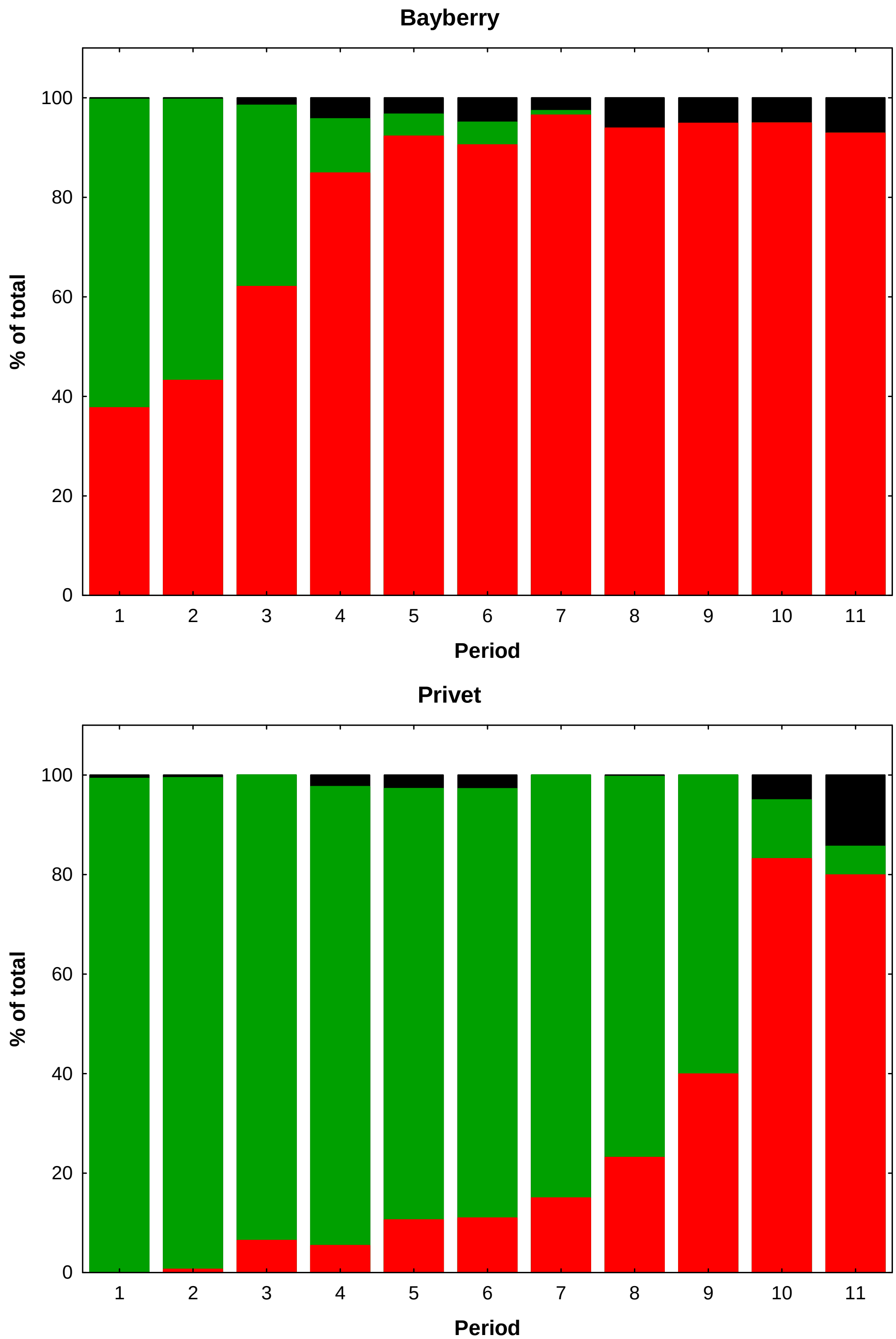

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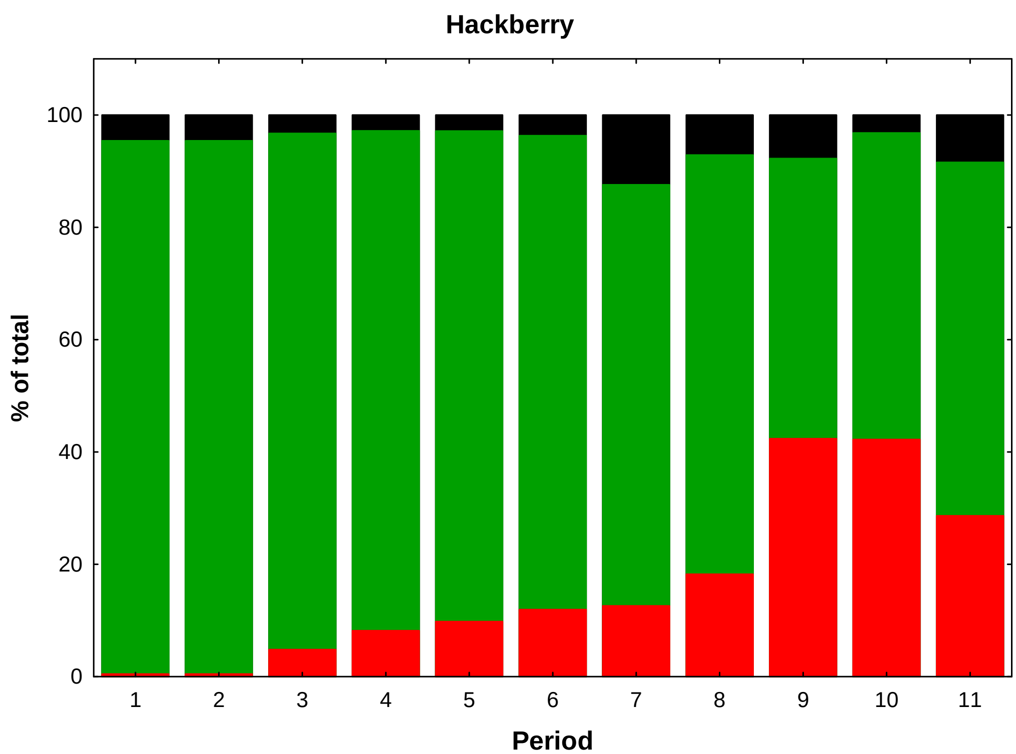

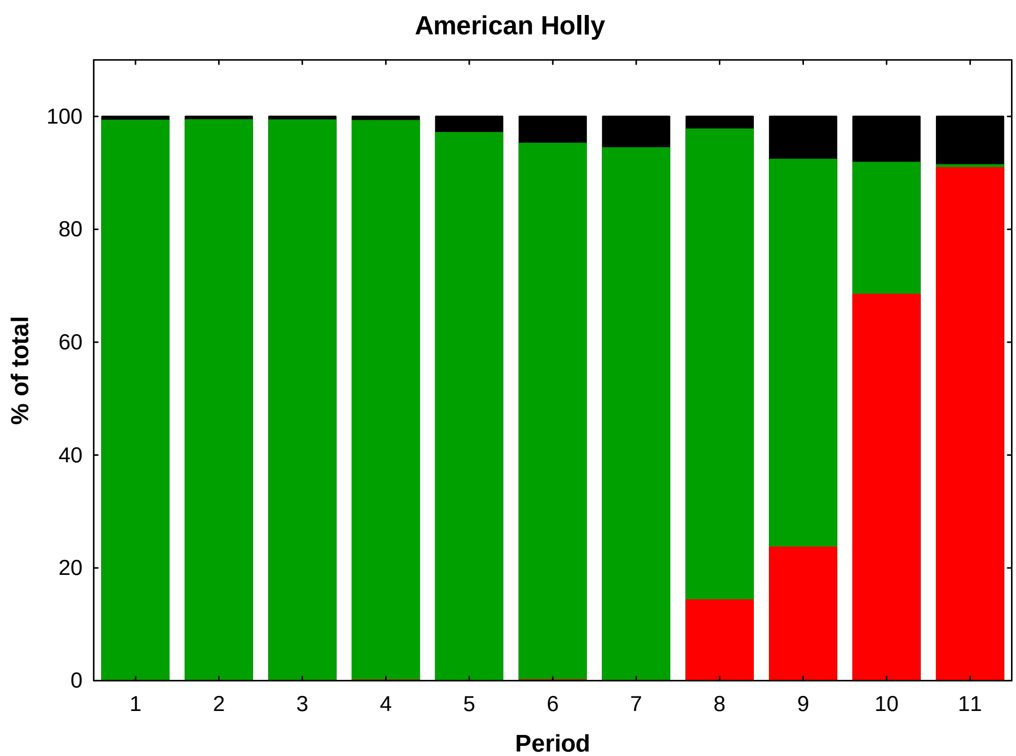

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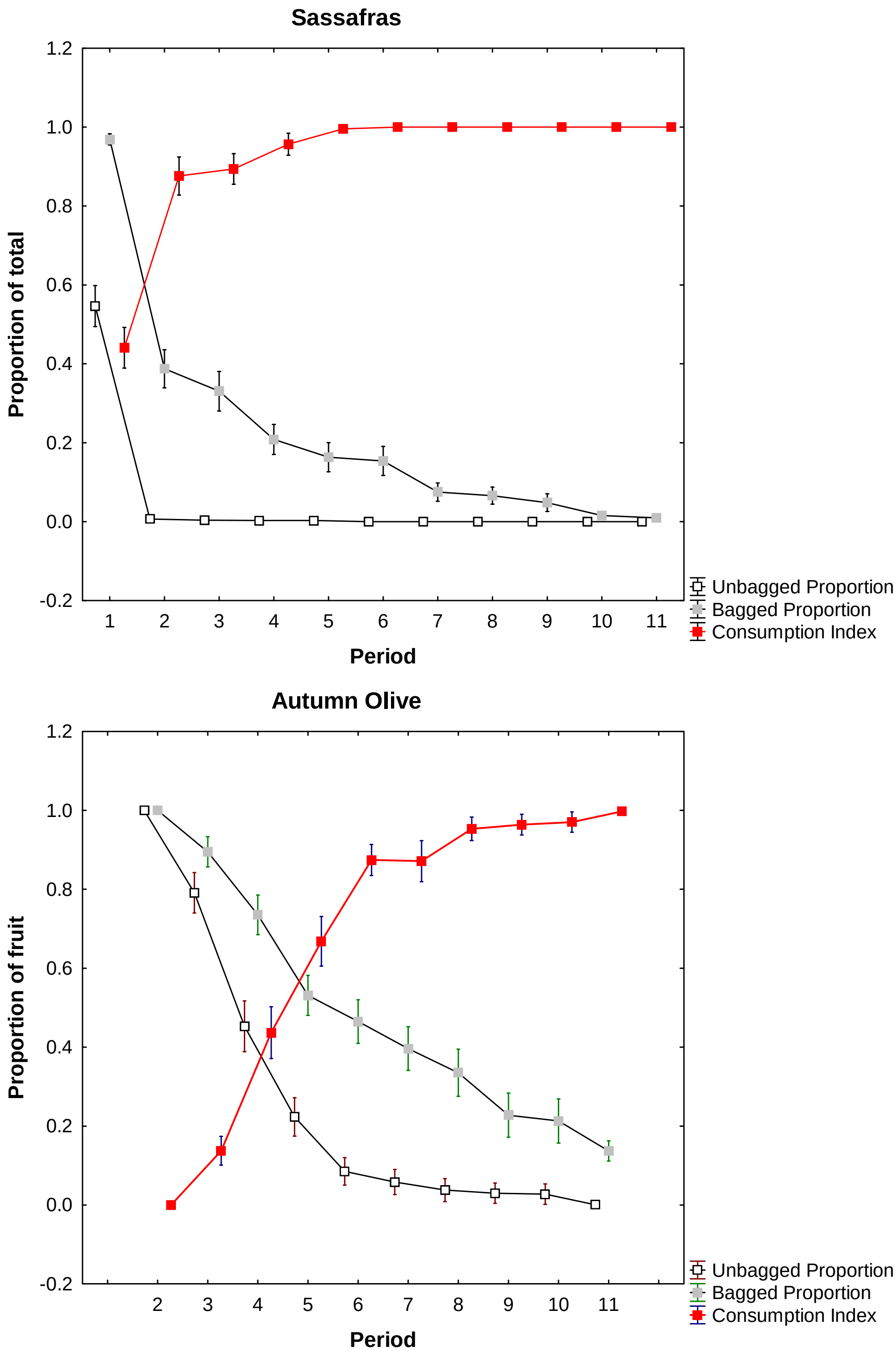


Figure 3. Seasonal fruit loss and consumption (mean + SE) for plant species assessed on the lower Delmarva Peninsula (Northampton County, VA) during the fall of 2014. Loss/Consumption values represent proportions of initial counts (bagged and unbagged branches). Consumption index = 1 – [% fruit remaining on unbagged branches divided by % fruit remaining on bagged branches). Fruits with index values closer to 1 have the higher cumulative consumption.

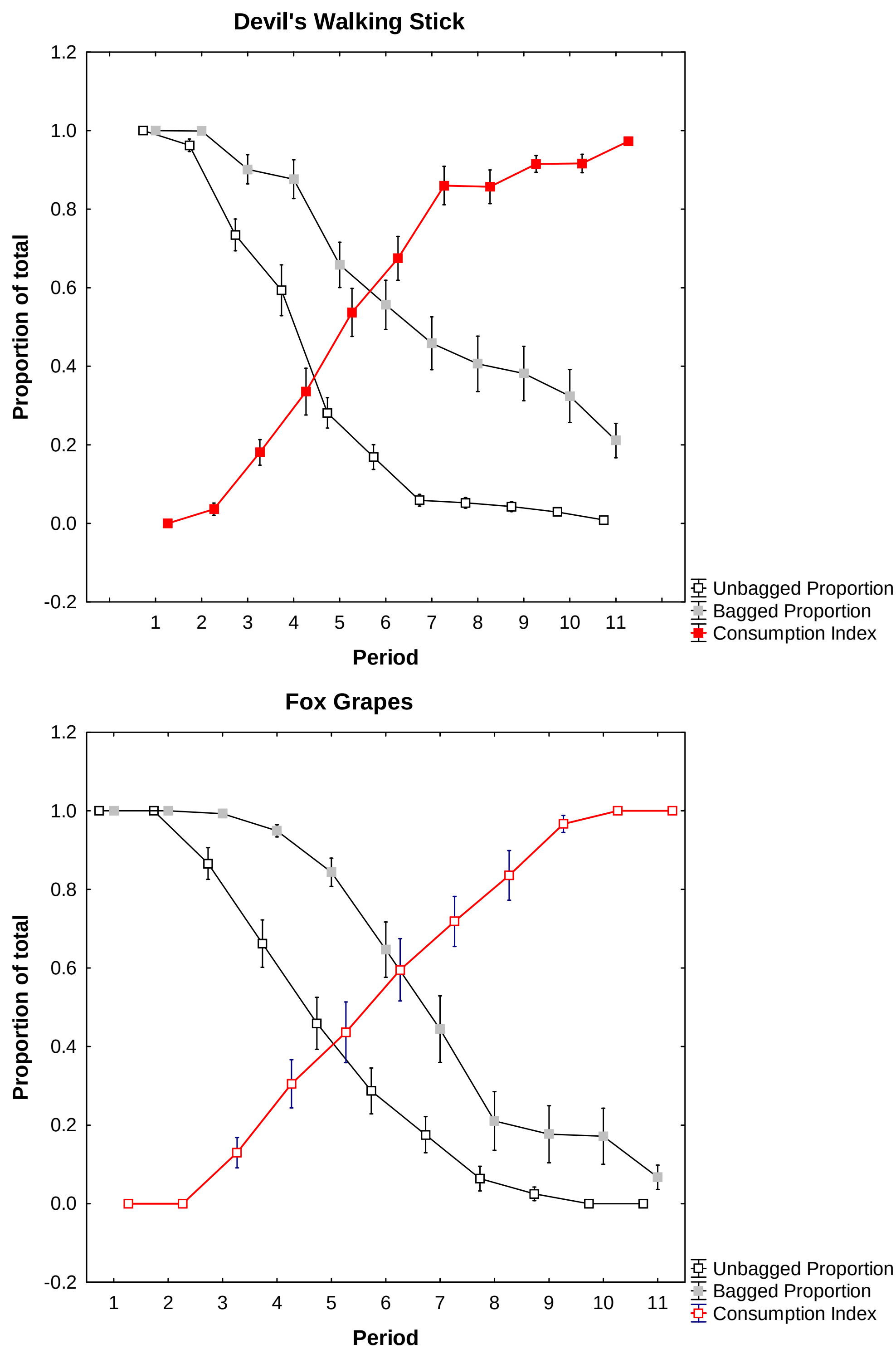
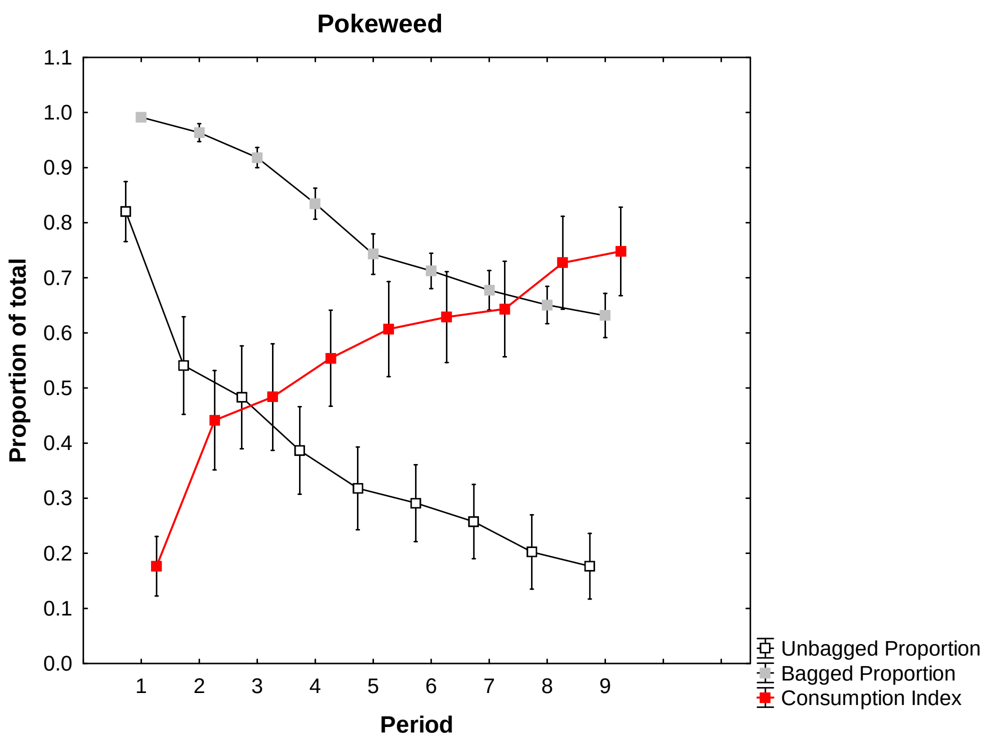


Figure 3. Seasonal fruit loss and consumption (mean ± SE) for plant species assessed on the lower Delmarva Peninsula (Northampton County, VA) during the fall of 2014. Loss/Consumption values represent proportions of initial counts (bagged and unbagged branches). Consumption index = 1 – [% fruit remaining on unbagged branches divided by % fruit remaining on bagged branches). Fruits with index values closer to 1 have the higher cumulative consumption. (continued)



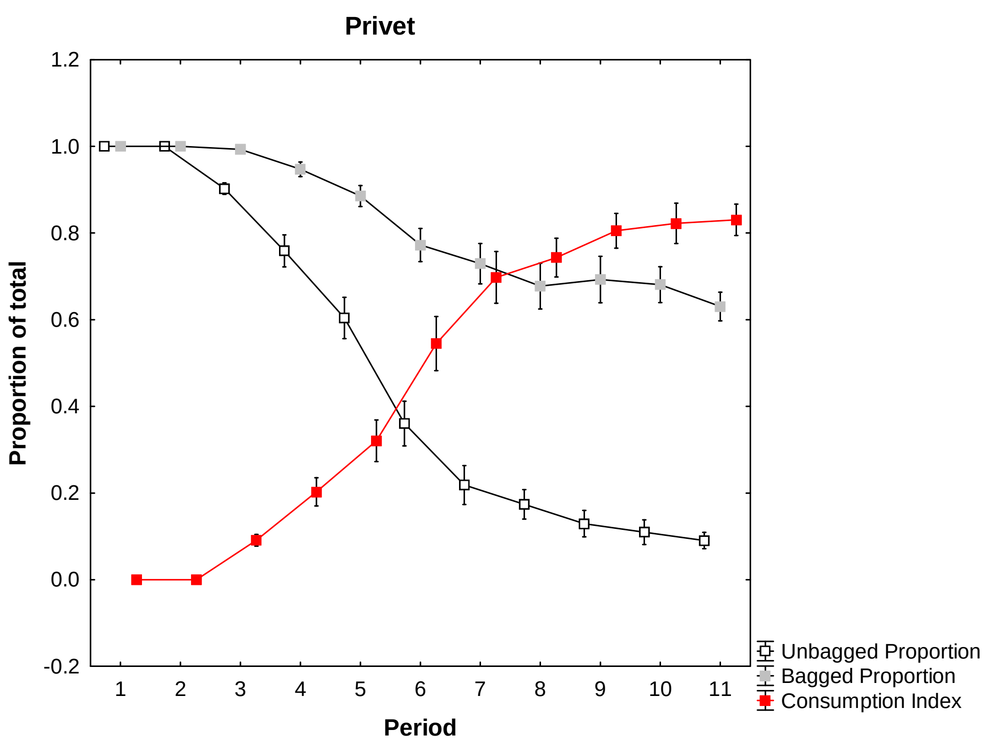


Figure 3. Seasonal fruit loss and consumption (mean ± SE) for plant species assessed on the lower Delmarva Peninsula (Northampton County, VA) during the fall of 2014. Loss/Consumption values represent proportions of initial counts (bagged and unbagged branches). Consumption index = 1 – [% fruit remaining on unbagged branches divided by % fruit remaining on bagged branches). Fruits with index values closer to 1 have the higher cumulative consumption. (continued)

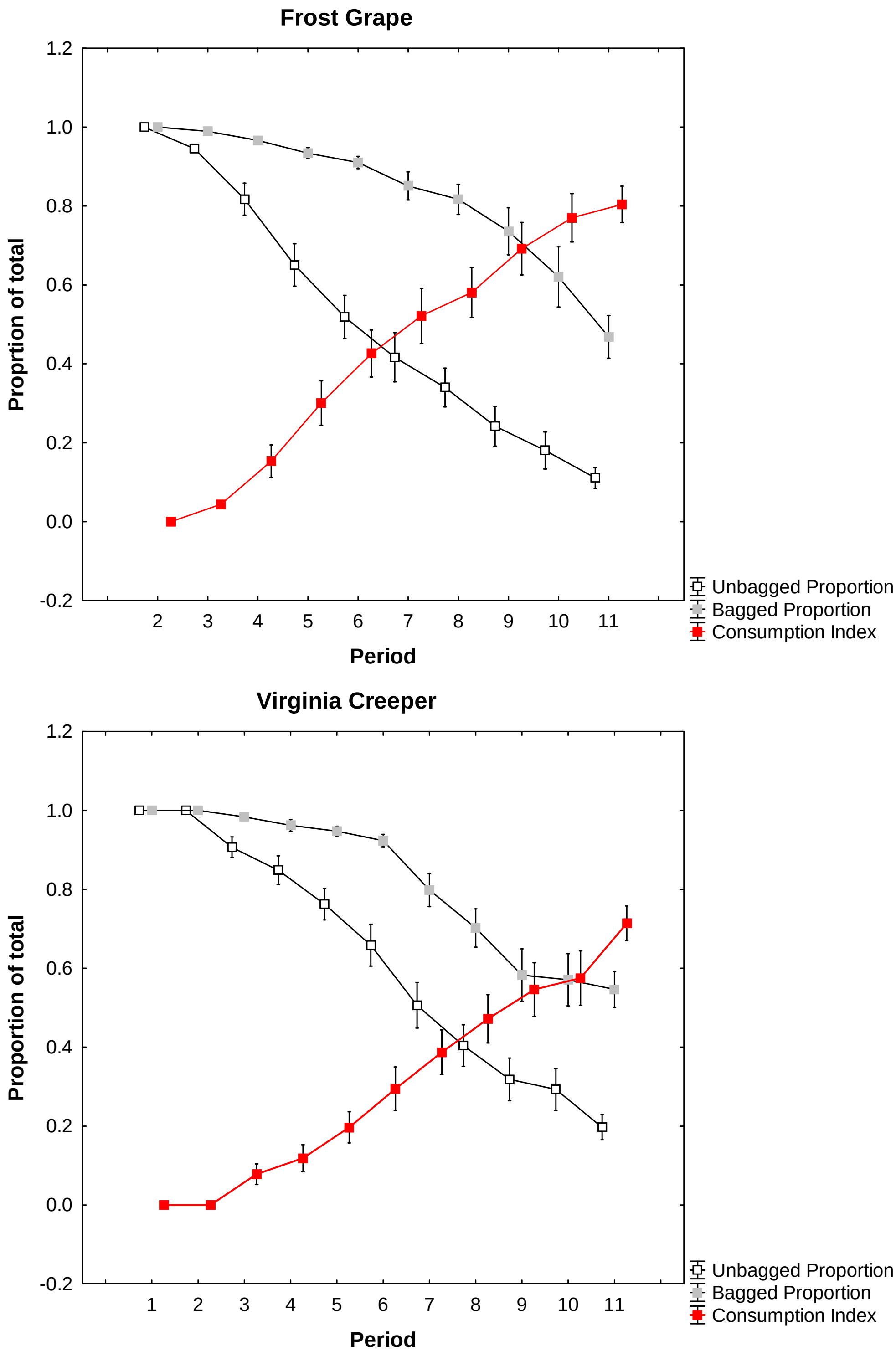


Figure 3. Seasonal fruit loss and consumption (mean $\pm$ SE) for plant species assessed on the lower Delmarva Peninsula (Northampton County, VA) during the fall of 2014. Loss/Consumption values represent proportions of initial counts (bagged and unbagged branches). Consumption index = 1 – [% fruit remaining on unbagged branches divided by % fruit remaining on bagged branches). Fruits with index values closer to 1 have the higher cumulative consumption. (continued)

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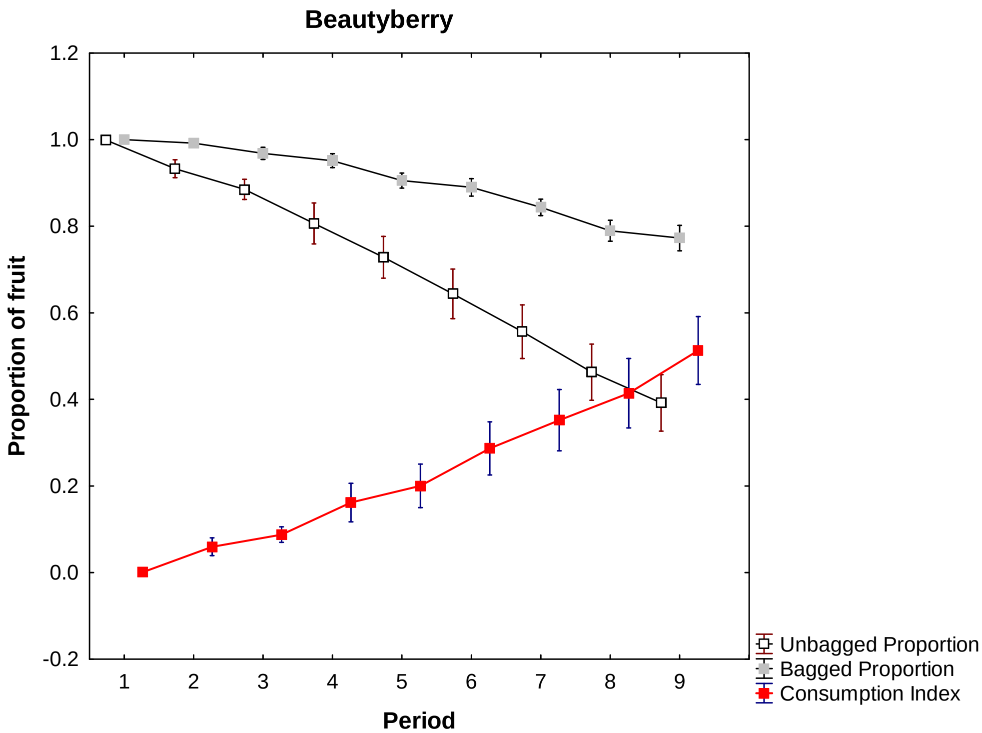


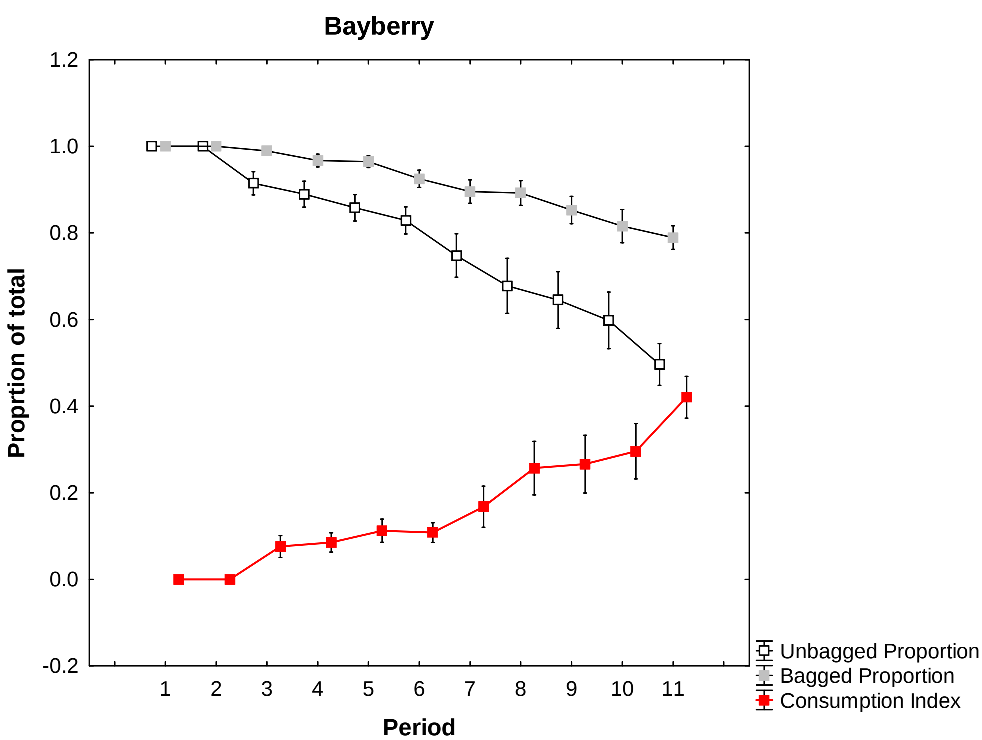
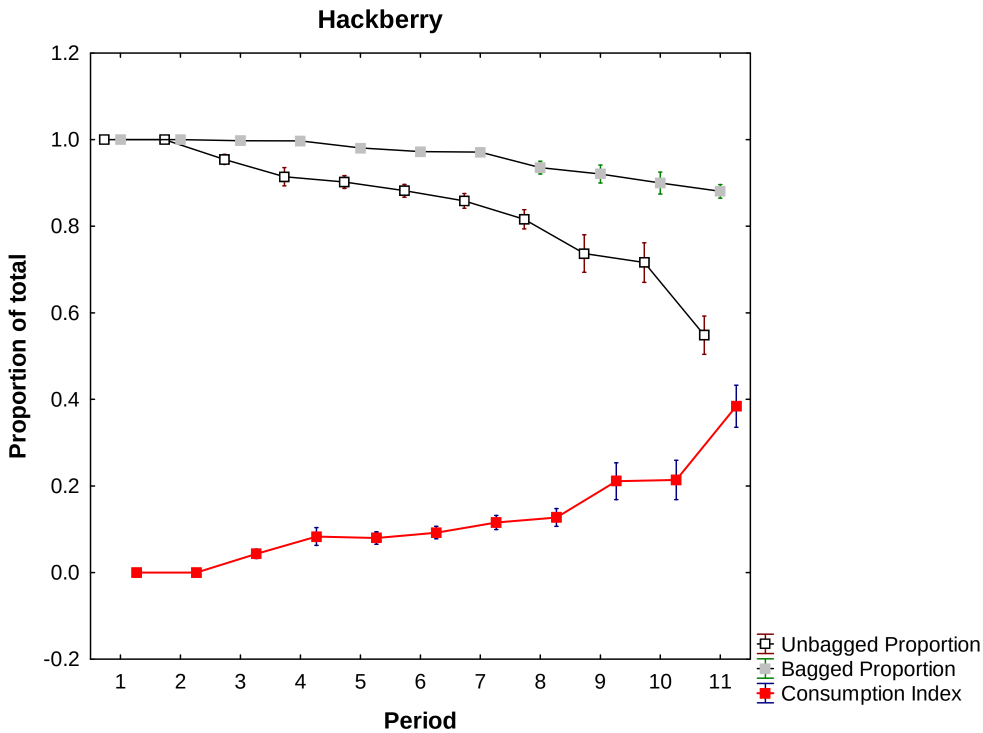
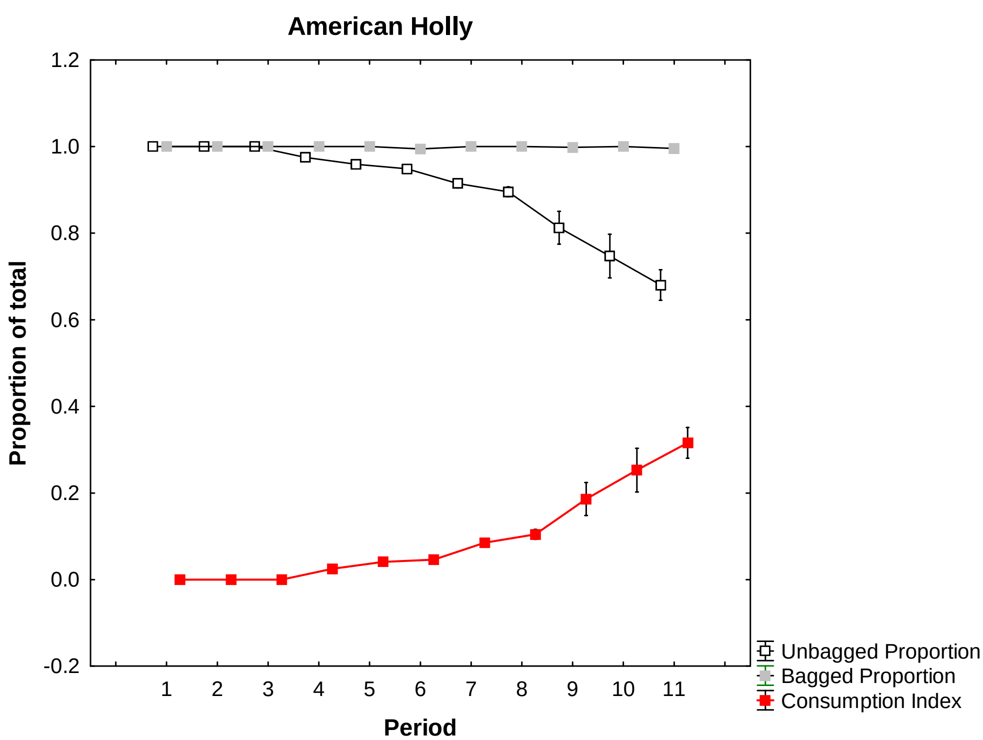


Figure 3. Seasonal fruit loss and consumption (mean ± SE) for plant species assessed on the lower Delmarva Peninsula (Northampton County, VA) during the fall of 2014. Loss/Consumption values represent proportions of initial counts (bagged and unbagged branches). Consumption index = 1 – [% fruit remaining on unbagged branches divided by % fruit remaining on bagged branches). Fruits with index values closer to 1 have the higher cumulative consumption. (continued)





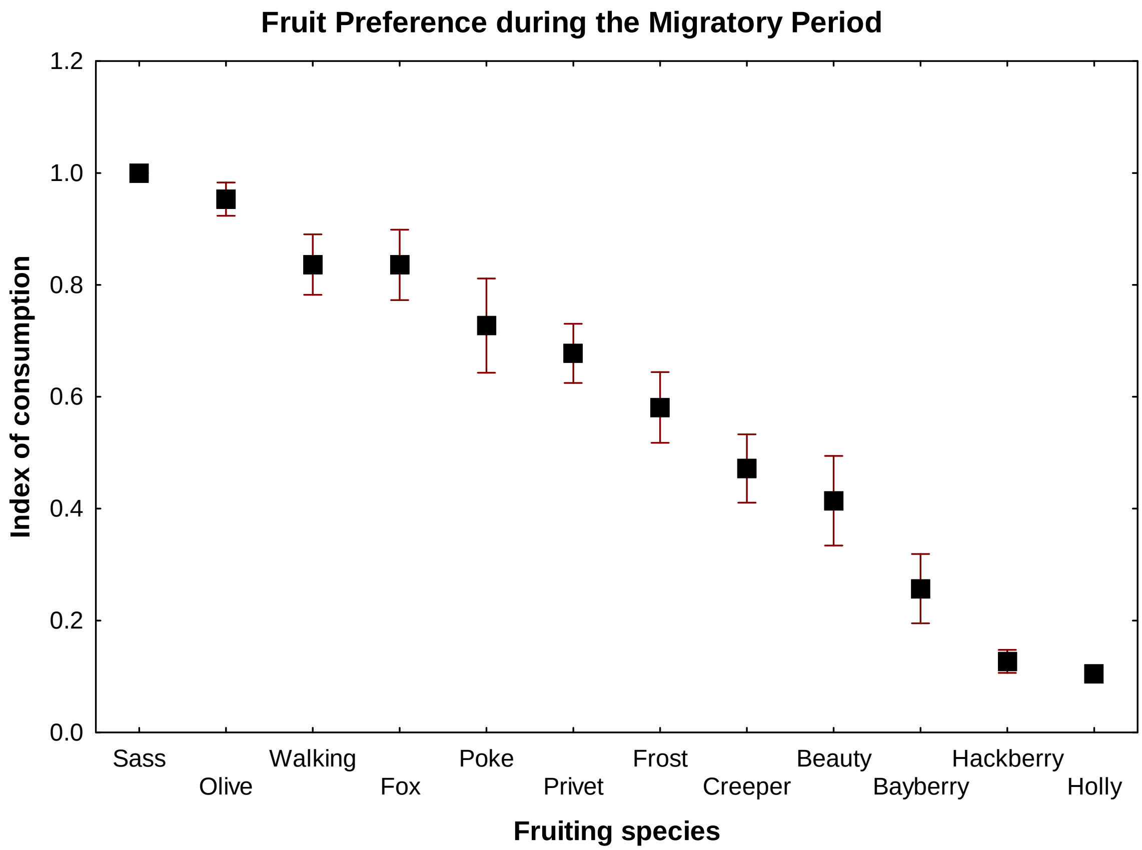
Reflecting the decline in fruit stocks, the index of consumption for all species measured increased significantly (repeated-measures ANOVA, all F-statistics >450 and p-values <0.001) over the study period. However, species varied dramatically in their rate of consumption. The index of consumption had the highest slopes during the first two months for sassafras, devil's walking stick, fox grapes and autumn olive, increasing more than 15% per week. Sassafras was in a class by itself with an average weekly increase of nearly 20%. On the other end of the spectrum is American holly, hackberry, beautyberry, bayberry and Virginia creeper that exhibited a much slower rate of increase of below 5% per week.

Fruit Preference

Arcsine transformed consumption indices varied significantly (one-way ANOVA, df = 1,11, F-statistic = 1,446, p<0.001) between species during the eighth week of the study (Figure 4). Over the course of the first two months of the migratory period, fruit species fall into three preference categories including high demand, medium demand and low demand. Species that appear to be most sought after include sassafras, autumn olive, devil's walking stick and fox grapes. Species that fall into the medium category of desirability include pokeweed, Chinese privet, frost grapes, Virginia creeper and beautyberry. Species with the lowest demand include bayberry, hackberry and American holly.

Devil's walking stick study sample, showing berries stripped from unbagged branches.

Figure 4. Mean consumption indices during the eighth week (late October) of the study for plant species assessed on the lower Delmarva Peninsula (Northampton County, VA) during the fall of 2014.



DISCUSSION

The influence of fruit availability on habitat selection by fall migrants has been documented within many landscapes (e.g., Martin et al. 1986, Moore et al. 1995, Parrish 1997, Suthers et al. 2000, Rodewald and Brittingham 2004). Within the lower Delmarva Peninsula, reference forest and shrub patches differed dramatically in the composition and overall density of the fruiting plant community, as well as, the overall density of fruits produced. Not surprisingly, shrub patches were dominated by sun-loving plants such as bayberry, autumn olive and pokeweed that are quick to colonize open patches and capable of producing enormous fruit crops. In contrast, older forest patches support a community of fruiting plants such as American holly, devil's walking stick, sassafras and beautyberry that are more shade-tolerant and that take longer periods to become established. Despite the fact that forest patches supported significantly higher densities of fruiting plants, shrub patches produced more than ten-fold higher densities of fruit.

The actual fruit crops produced by both forest and shrub patches were numerically dominated by few species. More than 95% of the fall fruit crop within shrub patches was produced by bayberry and autumn olive while more than 85% of the crop within forest patches was produced by devil's walking stick and American holly. Devil's walking stick is particularly interesting because it represented only 7% of the fruiting plant density in forest patches but produced 72% of the fruit. Also interesting is that more than 10% of the fruit crop produced in forest patches came from vines. The older (>100 years) forest patches used as reference samples in this study were senescent and had broken crowns that allow for good light penetration to the forest floor. These conditions have led to the development of dense vine mats that produce large fruit crops.

Timing is an important component in meeting energetic demands for migrating birds. In order for fruit to be relevant to migration it must be ripe when migrants are staging and in need of energy. The phenology patterns presented here suggest that some fruits reach peak condition early in the season and are available as fuel when the earliest migrants begin to arrive while others are just becoming ripe as the last migrants pass through. American holly, Chinese privet and hackberry are late developing fruits and likely have more relevance to wintering species than to most fall migrants.

All fruits do not appear to be equally desirable or relevant as fuel for fall migrants. Consumption of some species was out of sync with availability. The most obvious example of this pattern was sassafras. Sassafras ripens early and is in high demand by migrants during the first third of the migratory season. This plant species forms dense stands along the Holocene dunes and ridges along the Bayside of the Delmarva. As the earliest migrants including eastern kingbirds (*Tyrannus tyrannus*), northern orioles (*Icterus galbula*) and orchard orioles (*I. spurius*) appear in mid to late August they descend on these stands and quickly strip the fruit from in just a few days. Sassafras accounted for a small percentage of the fruiting plants and fruit crop but is clearly sought after by migrants. As devil's walking stick ripens in mid fall period it is rapidly consumed by American robins and a variety of other bird taxa. As robins, blue jays, common flickers and other thrushes arrive they move through forest patches and strip the dense fruiting heads. Robins, in particular, move through in large flocks that are capable of stripping large quantities of devil's walking stick very rapidly. Both of the grape species considered here also appear to be very desirable and are consumed rapidly as they ripen.

Both American holly and bayberry stand out as being underutilized by migrants when compared to availability. Holly is a late ripening fruit that was only beginning to reach peak condition as the study ended. This species is known to be an important resource during the winter period but it does not appear to have a great deal of relevance to fall migrants in general and virtually no relevance to early migrants. Bayberry is a prolific fruit producer and accounted for most of the fruit documented in shrub patches. Bayberry fruits are coated with a wax consisting primarily of saturated long-chain fatty acids. With the exception of a few highly adapted species like the yellow-rumped warbler (*Setophaga coronate*), most species cannot readily process these fruits effectively (Place and Stiles 1992). Except for yellow-rumped warblers and tree swallows (*Tachycineta bicolor*) which are certainly important migrants within the study area, bayberry is not a preferred fruit species.

MANAGEMENT RECOMMENDATIONS

The results presented here have some implications for management decisions within the lower Delmarva Peninsula as they pertain to fall migrants. The two management endpoints (mature forest vs shrub) differ dramatically with respect to fruiting plant density, fruit density and the extent to which they support preferred fruit species. Although fruit density within shrub habitat was more than ten-fold higher than forest patches, the removal of bayberry reduces the difference to a factor of two and removal of the invasive autumn olive reduces fruit density to only 30% of forest patches examined. Bayberry is an important cover plant within this landscape and should be maintained as a component of the fruiting community. However, its lack of relevance to most migrants that depend on the area as a stopover site suggests that its footprint should be reduced in favor of more desirable species. Although autumn olive was shown to be an attractive food plant for migrants, the fact that it is an exotic invasive precludes its recommendation as a species to promote within conservation lands. Autumn olive should be eliminated from the landscape in favor of other desirable species.

Shrub patches should be managed to broaden out the fruiting plant community to include preferred fruit species. Although these patches currently support most of these species they exist as minor components. Management prescriptions should be developed that drive the footprint of the less desirable plants down and expand the more desirable elements. The clear management quandary with shrub habitat is that disturbance frequency must be high enough to maintain an open structure but the use of high frequency disturbance precludes the establishment of certain species or prevents them from maturing enough to produce fruit. A possible solution to this problem would be to establish narrow treelines where desirable plants such as sassafras, poison ivy and devil's walking stick may be encouraged over the longterm while maintaining the balance of the habitat as open shrub.

The reference forest patches used in this study are atypical habitats within the lower Delmarva landscape. They are over mature and support well-developed understories with older fruit-producing plants. Most of the forest patches within the study area are much younger, have closed canopies and support fewer fruit-producing plants. All forest patches should be managed within an open-canopy system in order to mimic the reference patches and produce higher fruit densities until they mature into older age classes.

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