Oecologia (2004) 139: 30–34
DOI 10.1007/s00442-003-1470-6

PLANT ANIMAL INTERACTIONS

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Cold temperature increases winter fruit removal rate of a bird-dispersed shrub

Received: 15 June 2003 / Accepted: 12 November 2003 / Published online: 10 January 2004
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Abstract We tested the hypothesis that winter removal rates of fruits of wax myrtle, *Myrica cerifera,* are higher in colder winters. Over a 9-year period, we monitored *M. cerifera* fruit crops in 13 0.1-ha study plots in South Carolina, U.S.A. Peak ripeness occurred in November, whereas peak removal occurred in the coldest months, December and January. Mean time to fruit removal within study plots was positively correlated with mean winter temperatures, thereby supporting our hypothesis. This result, combined with the generally low availability of winter arthropods, suggests that fruit abundance may play a role in determining winter survivorship and distribution of permanent resident and short-distance migrant birds. From the plant's perspective, it demonstrates inter-annual variation in the temporal component of seed dispersal, with possible consequences for post-dispersal seed and seedling ecology.

Keywords Avian seed dispersal · Frugivory · Seed predation · Winter food · Yellow-rumped warbler.

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Introduction

Fruits are an abundant but seasonal resource in most temperate and tropical forests (van Schaik 1993; Jordano 2000) and their importance in maintaining populations of frugivorous vertebrates has long been asserted (Snow 1971; Terborgh 1983). Evidence for the importance of fruits to vertebrates includes positive correlations of fruit and frugivorous bird abundances across time and space (i.e., "tracking", Loiselle and Blake 1991; Levey and Stiles 1992; Rey 1995; Kinnaird et al. 1996), declines in frugivore visits to experimental plots where fruits have been removed (Parrish 2000; Moegenburg and Levey 2003), high biomass of frugivores in forests with high fruit production (Terborgh 1986; Gentry 1990), and almost complete consumption of many fruit crops (McCarty et al. 2002). An alternative perspective is that fruit is an unpredictable and nutritionally unbalanced resource, containing secondary compounds with detrimental effects on consumers (Herrera 1982; Izhaki and Safriel 1989; Cipollini and Levey 1997). Thus, fruit may be little more than a supplemental, though not necessarily unimportant, resource, at least in the temperate zone (reviewed in Snow and Snow 1988). In support of this view, a study of fruiting plants and frugivorous birds in Spain found "extensive decoupling of the long-term temporal dynamics of fruits and frugivores, and a remarkable 'indifference' of frugivores to variations in the fruit supply...." (Herrera 1998, p. 511).

As with most ecological interactions, it is likely misguided to frame the importance of fruits to frugivores in a dichotomous way; fruits are probably a supplemental

resource in some situations and a critical resource in others. The challenge is one of clearly identifying both ends of a continuum. We present a long-term dataset on a relatively simple study system and provide a straightforward test of the dependency of fruit-eating birds on fruit. In particular, we test the hypothesis that the winter removal rate of fruits from a common shrub, *Myrica cerifera*, is fastest in years when ambient temperatures are low. These conditions both increase the energy demands of birds (Calder and King 1974) and reduce the availability of insects (Thompson and Willson 1979). We argue that fruit may be especially important to birds wintering in temperate zones because energetic costs of foraging and maintenance are unusually high at precisely the time when most other resources are unusually scarce.

Materials and methods

Plant species

Wax myrtle, *Myrica cerifera* L. (hereafter, "*Myrica*"), is a small to mid-sized clonal dioecious shrub that is commonly found in many habitats of the southeastern coastal plain, U.S.A. (Godfrey 1988). It flowers in May and June (Radford et al. 1968), and female plants produce wax-coated drupes (hereafter "fruits") that ripen in November and can persist for several months. Large individuals can produce ≥10,000 one-seeded fruits, which are 2–3 mm diameter and, at our study site, contain 0.003 g of pulp (dry mass) when ripe. These fruits are consumed by a wide variety of birds, including many that are insectivorous at other times of year (Martin et al. 1951). Some species appear to specialize on *Myrica* fruit in the fall and winter (Place and Stiles 1992).

Study site

Our study was conducted in managed pine stands at the U.S. Department of Energy's Savannah River Site, a National Environmental Research Park in Aiken and Barnwell counties, South Carolina, U.S.A. We chose three types of stands: (1) mature loblolly pine (*Pinus taeda*), (2) mature longleaf pine (*P. palustris*), and (3) young longleaf pine, planted after clearing (hereafter, "regeneration stands"). All of these stand types contained fruiting *Myrica* (typically between 2–4 m in height), which is one of the only winter-fruiting species at our site (McCarty et al. 2002). Mature loblolly and longleaf pine stands had a sparse canopy layer of pines, scattered shrubs and trees (e.g., *Vaccinium arboreum*, *Quercus* spp.), and a sparse ground layer of shrubs (e.g., *V. stamineum*, *Rhus toxicodendron*), vines (e.g., *Vitis rotundifolia*, *Smilax* spp.), and herbs (e.g., *Panicum* spp., *Carex* spp.). Regeneration stands were cut just prior to the start of this study and initially contained short, second-growth vegetation. By 2002, these stands had a "canopy" of longleaf pine (to 6 m tall) and well-developed shrub and ground layers, including *Myrica*, *Opuntia compressa*, *Prunus* spp., *Rhus copallina*, *R. toxicodendron*, *Rubus* spp., and *Vaccinium stamineum*. Regeneration stands were typified by successional development and a general increase in *Myrica* shrub volume and fruit production through time. *Myrica* shrubs in regeneration stands did not produce fruits for the first 2 years of this study.

Field methods

As part of a long-term study addressing spatial and temporal patterns of fruit production, 56 study plots each 0.1 ha (50x20 m) were established in the summer of 1994. Because fruiting *Myrica* shrubs only occurred in managed pine stands, this study pertains solely to those stands. Thirteen plots were placed in mature loblolly stands, 13 in longleaf stands, and 10 in regeneration stands that were cleared and planted with longleaf seedlings in 1993. In plots that contained fruiting *Myrica* (n=13), we counted and recorded unripe, ripe, and damaged *Myrica* fruits on each individual shrub each month from the fall of 1994 through April 2003. We defined individual shrubs as those with stems not obviously joined underground and spatially distinguishable canopies. When possible, all fruits on a given shrub were counted; otherwise, extrapolations were made from counts taken from randomly chosen branches.

Data and statistical analysis

We first investigated whether the mean time to *Myrica* fruit removal differed among years. We used November fruit censuses as start dates for removal times each year because *Myrica* fruit most commonly ripens then. Removal time (in months) of *Myrica* fruit within plots was inferred by comparing the number fruits in a plot to the number in the same plot the previous month. Removal of missing fruits was assumed to have occurred at the midpoint between successive monthly counts, and removal time was the difference in months between that midpoint and the date of the November fruit census (e.g., if a fruit was removed between December and January censuses, its time to removal was 1.5 months). We assumed that missing *Myrica* fruits had been consumed because *Myrica* fruits are rarely found on the ground beneath fruiting shrubs at our study site (McCarty et al. 2002; C. Kwit, personal observation). We included both ripe and damaged fruits in our removal estimates, because damaged fruits are sometimes consumed (Buchholz and Levey 1990). Few *Myrica* fruits (<10%) were categorized as damaged during any monthly fruit census and their exclusion from analyses did not alter the significance of any relationship.

We ascribed a gamma distribution to the time of *Myrica* fruit removal. Such a distribution is appropriate for fruits that exhibit a lag in consumption and therefore no constant decay rate. We used plots with fruiting *Myrica* (including all stand types) within years as sampling units, and pooled data from multiple shrubs within plots (n_{max}=10 shrubs/plot). We did so because: (1) fruit removal from shrubs within plots was presumably not independent, (2) some plots contained only one fruiting shrub, and (3) in a few sampling periods only one plot of a given stand type contained fruiting *Myrica*. Thus, measures of fruit removal reflect a stand-level spatial scale. We acknowledge that fruit removal rates can be a function of fruiting plant density, neighborhood, and habitat variables (Denslow 1987; Sargent 1990; Willson and Whelan 1993). However, our data do not provide the opportunity to simultaneously factor out numerous potential sources of variation. Analysis on the effects of year on mean time to *Myrica* fruit removal was conducted using the GLIMMIX macro in SAS (Littell et al. 1996).

We next examined whether "winter temperature" differed among years during our study. Winter temperature (°C) for each year was based on mean daily temperatures (the average of a daily low and high temperature) at the Savannah River Site for all days of the 3-month period from the beginning of November through the end of January. This corresponded to the coldest time periods when ripe *Myrica* fruits were first available through the period when the "average" fruit had been consumed (see Results). A winter was labeled according the year of its winter solstice (e.g., the winter of 1995–1996 was attributed to 1995). We used ANOVA (MIXED procedure) to test for differences in mean winter temperature among years (SAS Institute 1994). Finally, we examined whether the mean time to *Myrica* fruit removal was associated with mean winter temperature using correlation analysis (CORR procedure; SAS Institute 1994).

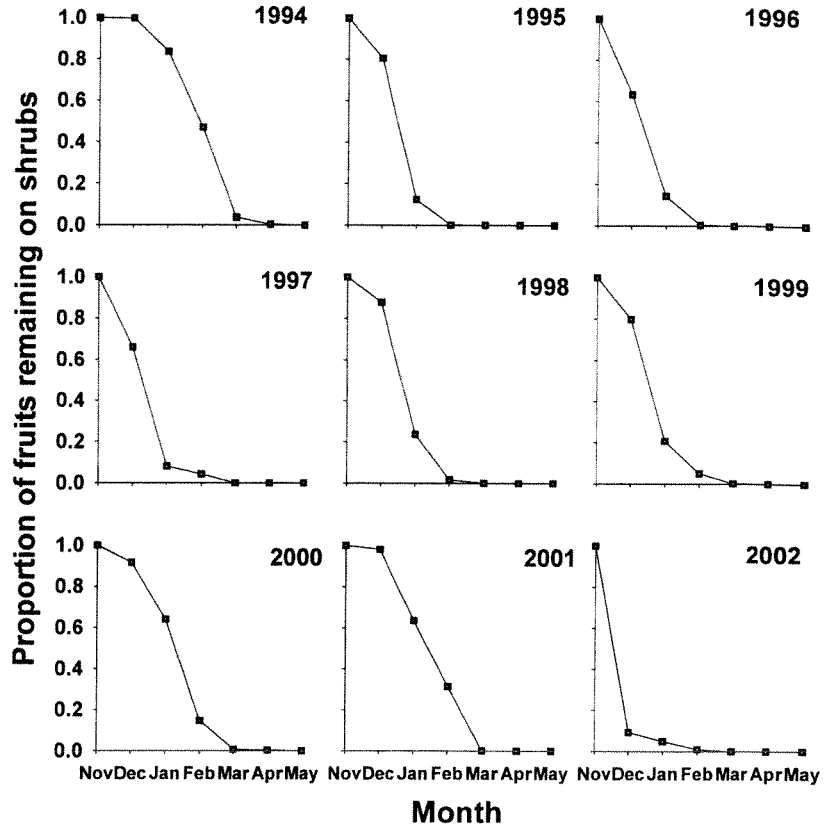

Fig. 1 Proportion of *Myrica cerifera* fruits on shrubs in 0.1-ha study plots at monthly intervals in each year of the study. To obtain monthly proportions, fruit counts from monthly censuses were pooled across all shrubs in all study plots within years. Years correspond to winter solstice date

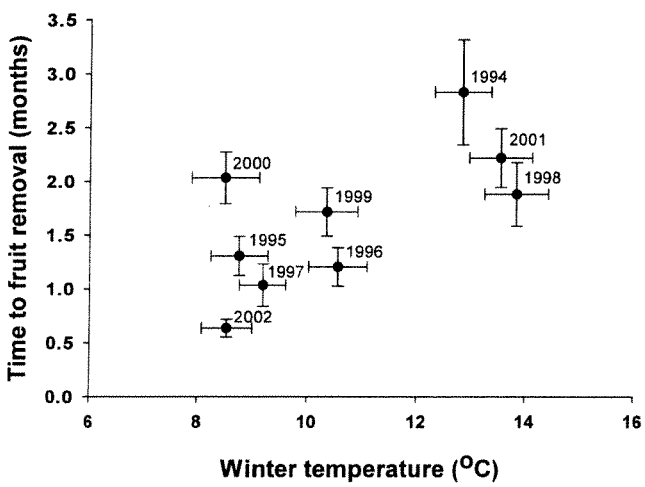

Fig. 2 Plot of relationship between mean time to *Myrica cerifera* fruit removal (±SE) and mean winter temperature (±SE) from 0.1-ha study plots across 9 years. Estimation of fruit removal times and winter temperatures are described in Materials and methods

Results

We followed the fate of approximately 780,000 *Myrica* fruits over 9 years. In each year, fruit crops ripened synchronously, such that peak abundance of ripe fruits occurred in November. *Myrica* removal rates were generally low until December and January. By February of most years, >90% of the fruit crop was depleted and by April of every year all fruits had disappeared (Fig. 1).

Mean time to fruit removal ranged from under 1 month in 2002 to almost 3 months in 1994 (Fig. 2), and differed among years ($F_{8,69}$=12.64, P<0.0001). Mean winter temperatures ranged from 8.5°C in 2000 to 13.8°C in 1998 (Fig. 2), and also differed among years ($F_{8,819}$=16.56, P<0.0001). As predicted, mean winter temperatures were positively correlated with mean time to *Myrica* fruit removal (r=0.67, P=0.025; Fig. 2), indicating that *Myrica* fruits were generally removed more quickly in colder winters. Indeed, the three warmest winters accounted for three of the four years with lowest removal rates (high mean time to removal) and except for an anomalously low removal rate in 2000, the three coldest winters accounted for three of the four highest removal rates (Fig. 2).

Discussion

In support of our hypothesis, removal rates of *Myrica* fruits were higher in colder winters. A combination of three mechanisms likely generated this pattern. Most obviously, birds are forced to increase rates of food consumption to meet increased energetic demands when ambient temperature drops (Calder and King 1974). The

major consumer of *Myrica* fruits is the yellow-rumped warbler (*Dendroica coronata*: Martin et al. 1951), which often forage exclusively on *Myrica* fruits at our study site during winter months (S. Pearson, unpublished data). We suspect increased foraging intensity of yellow-rumped warblers in cold winters may largely account for the increased rates of *Myrica* fruit consumption that we observed.

A second mechanism that likely contributed to the positive correlation of temperature and time to fruit removal is diet switching by primarily insectivorous birds. As elsewhere in the temperate zone, species richness and abundance of arthropods at our site reach their lowest annual levels in winter (Skorupa and McFarlane 1976; Hanula and Franzreb 1998), forcing many permanent resident species and short distance-migrants to include fruit in their diets (Martin et al. 1951). *Myrica* fruits are low in water content, high in lipids, and can persist for months on the plant (Place and Stiles 1992). Such fruits are especially prominent in diets of birds that are primarily insectivorous (Fuentes 1994). Examples of these types of bird species at our site include pine warblers (*Dendroica pinus*), ruby-crowned kinglets (*Regulus calendula*), and tufted titmice (*Parus bicolor*: S. Pearson, unpublished data). Colder winters may increase reliance by these species on *Myrica* fruit.

Finally, higher removal rates of *Myrica* fruits may result if fruit-eating birds are locally more abundant in colder winters. Although regional movements of winter frugivores in North America remain unexplored, colder temperatures in the northern part of a species' winter range may result in high population densities of that species in the southern part of its winter ranges (see Koenig 2001).

Regardless of the mechanism behind faster fruit removal during colder winters, one consequence is that seeds are dispersed more quickly during colder winters. These seeds are therefore exposed to environmental conditions and potential hazards, including colder temperatures and seed predation, for longer periods of time during cold winters. Cold stratification increases germination probabilities of many species, including those of *Myrica* spp. (Barton 1932; Heit 1968). However, any such advantage may be offset by an increased probability of seed predation because seeds dispersed quickly are vulnerable to terrestrial seed predators for a longer period. We note that the cold temperatures presumably driving high fruit consumption and rapid seed dispersal by birds may identically drive high rates of seed consumption by seed predators. As opposed to spatial aspects of seed dispersal (Howe and Miriti 2000; Jordano 2000), such temporal aspects of seed dispersal have rarely been considered (but see Gryj and Dominguez 1996).

Our results lend support to the notion that fruit is an important dietary component for wintering birds in North America. Until recently (Li et al. 1999; McCarty et al. 2002), the importance of fruit for North American birds has centered on the time periods just prior to and during migration (Loiselle and Blake 1991; Parrish 1997; Rivera et al. 1998; Suthers et al. 2000), or on the overwinter period of long-distance migrants on their tropical wintering grounds (Howe and DeSteven 1979; Greenberg 1981; Holmes et al. 1989; Blake and Loiselle 1992; Greenberg et al. 1995; Wunderle 1995; Latta and Faaborg 2002). The relative lack of species in North America that depend solely on fruit year-round may suggest that fruit does not play the role of critical resource analogous to the situation in the Neotropics. However, the results we present do not support the alternative that fruit is an unimportant supplement. Rather, we suggest that fruit in the temperate zone may act as a critical supplement. Persistent fruits such as *Myrica* are available for a number of insectivorous and omnivorous birds during the winter when insect prey are at their most scarce. For numerous permanent resident and short-distance migrants that winter in the southeastern United States, fruit may be critically important for winter survivorship. Future management plans need to consider ensuring adequate levels of fruit production not only during the fall at pre-migration and migratory stopover sites (see Parrish 2000), but also during the winter.

Acknowledgements We thank John I. Blake and the U.S. Forest Service for long term logistical and finanacial support of this study, and the Department of Energy for supplying weather data. Support was also provided by the Department of Energy-Savannah River Operations Office through the U.S. Forest Service Savannah River under Interagency Agreement DE-IA09–76SR00056. K. Borgmann, A. Brinton, R. Busser, C. Deppe, N. Khalil, M. Reiskind, C. Renk, T. Roof, and E. Uramkin assisted with fruit censuses, and C. Whelan and two anonymous reviewers provided valuable comments and suggestions.

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