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

PLANT ANIMAL INTERACTIONS

**Charles Kwit · Douglas J. Levey ·
Cathryn H. Greenberg · Scott F. Pearson ·
John P. McCarty · Sarah Sargent**

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

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.

C. Kwit (✉) · D. J. Levey · S. F. Pearson · J. P. McCarty ·
S. Sargent
Department of Zoology, University of Florida,
Box 118525 Gainesville, FL 32611, USA
e-mail: kwit@srel.edu
Tel.: +1-803-7255925
Fax: +1-803-7253309

C. H. Greenberg
Southern Research Station, USDA Forest Service,
Asheville, NC 28806, USA

Present address:
C. Kwit
Savannah River Ecology Laboratory,
P.O. Drawer E Aiken, South Carolina 29802, USA

Present address:
S. F. Pearson
Washington Natural Areas Program, Washington Department of Natural Resources,
1111 Washington Street S.E.,
Olympia, Washington 98504, USA

Present address:
J. P. McCarty
Department of Biology, University of Nebraska at Omaha,
Omaha, Nebraska 68182, USA

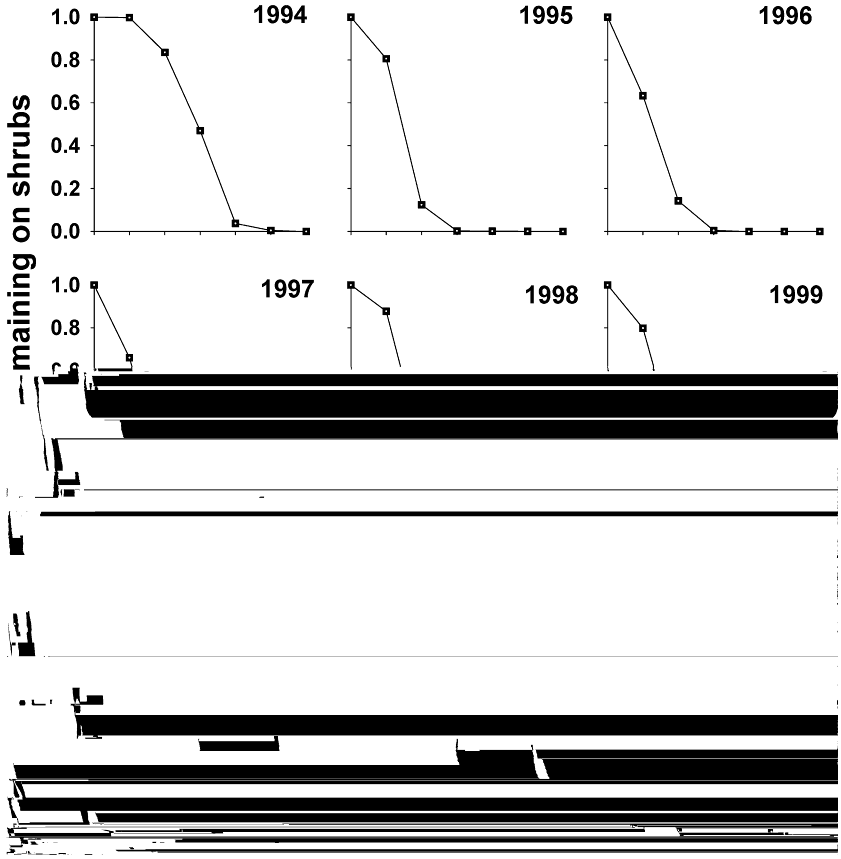
Present address:
S. Sargent
Department of Biology, Allegheny College,
Meadville, Pennsylvania 16335, USA

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.

Fig. 1 Proportion of Myrica cerifera c3



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

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