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Yellow Jackets (*Vespula* spp.) Disperse Trillium (spp.) Seeds in Eastern North America

ABSTRACT.—Approximately 70 plant families worldwide have ant-dispersed seeds (myrmecochory). In this putative ant-plant mutualism, ants are attracted to and disperse seeds that have a lipid-rich elaiosome. We observed yellow jackets (*Vespula* spp.) dispersing seeds of three elaiosome-bearing species—*Trillium cuneatum, T. undulatum* and *T. catesbaei*—in the Blue Ridge Mountains of North Carolina and South Carolina. Moreover, we estimated the mean distance yellow jackets dispersed seeds *of T. cuneatum* by placing intact fruits on index cards and recovering dispersed seeds on sheets placed on the ground surface. Of the seeds presented, 41% were recovered and the average dispersal distance was 1.4 m (range 0.1–2.6 m). Some yellow jackets carrying *Trillium* seeds flew out of sight and probably dispersed seeds farther (perhaps 20 m or more). To our knowledge, this is the first report of yellow jackets dispersing elaiosome-bearing seeds in eastern North America. Although the fate of vespid-dispersed seeds is unknown, seed dispersal by yellow jackets might benefit plants by increasing the dispersal distance of seeds and, therefore, potentially reducing density-dependent mortality and expanding species ranges.

INTRODUCTION

More than 3000 ant-dispersed plant species (myrmecochores) are found worldwide (Handel and Beattie, 1990). Plants common to mesic forests in the eastern United States that have ant dispersed seeds include trilliums (*Trillium* spp.), violets (*Viola* spp.) and bloodroot (*Sanguinaria canadensis*) (Pearson *et al.*, 1998). Myrmecochores possess seeds with a lipid-rich attachment (elaiosome) that attracts ants. Ants carry the seeds to their nests where the elaiosome is consumed, and the intact seed is discarded in trash piles (Handel, 1976). In western North America, both ants and yellow jackets disperse elaiosome-bearing seeds of *Vancouveria hexandra* (Pellmyr, 1985) and *Trillium ovatum* (Jules, 1996).

We report that yellow jackets in North Carolina and South Carolina also disperse seeds of three myrmecochorous trilliums—*Trillium cuneatum* Rafinesque, *T. undulatum* Willdenow and *T. catesbaei* Elliott (Liliaceae). Moreover, we estimate the mean distance that yellow jackets dispersed seeds of *T. cuneatum.*

MATERIALS AND METHODS

Sweet betsy, *Trillium cuneatum,* is a sessile-flowered trillium that occurs on rich wooded slopes throughout the southeastern United States (Case and Case, 1997). *Trillium catesbaei* (Catesby's trillium) and *T. undulatum* (painted trillium) have pedicellate flowers. *Trillium catesbaei* occurs in a variety of habitats, from sunny slopes to shaded coves, whereas *T. undulatum* is restricted to forests with rich, acidic soils (Case and Case, 1997).

In June 1998 we presented seeds of *Trillium cuneatum* on index cards to ants at Oconee State Park in Oconee Co, SC and subsequently observed yellow jackets (*Vespula flavopilosa* Jacobson) (Hymenoptera: Vespidae) removing these seeds. We also observed yellow jackets stealing seeds from ants (*Aphaenogaster carolinensis*). One month later, yellow jackets were seen removing seeds of *T. undulatum* and *T. catesbaei* from index cards placed in a moist forest at the High Hampton Inn Resort (Cashiers, NC—Jackson Co). Although we never noticed yellow jackets foraging on seeds from intact capsules, Jules (1996) observed *V. vulgaris* removing seeds from *T. ovatum* fruit in Oregon.

To determine the mean dispersal distance of vespid-dispersed seeds, we used seed capsules of *Trillium cuneatum* collected in June 2000. The capsules were refrigerated at 4 C, and were used in this experiment conducted on 27 July 2000, in Seneca, SC (Oconee Co.) near the base of a north-facing slope in an oak-hickory forest. Dogwoods (*Cornus florida*) and sourwood (*Oxydendrum arboreum*) were common understory species, and the herbaceous layer included Solomon's seal (*Polygonatum biflorum*) and crane-fly orchid (*Tipularia discolor*). No natural trillium populations existed at this site; however, the myrmecochores wild ginger (*Hexastylis arifolia*) and bloodroot (*Sanguinaria canadensis*) were present.

Because the entire seed capsule of *Trillium cuneatum* is shed upon ripening, we wanted to determine how yellow jackets respond to intact fruits. Three intact fruits of *T. cuneatum* were placed 0.3 m from

each other on the forest floor. Within 5 min, yellow jackets (*Vespula maculifrons* Buysson) had discovered the fruits, chewed through the pericarp and extracted the seeds. We determined the dispersal distance of removed seeds by placing 100 seeds of *T. cuneatum* on a white index card and allowing vespids to remove seeds for 1 h. Each yellow jacket used all six legs to grasp a seed and either flew out of our sight range or flew to the lowest branches (0.5–3 m above the ground) of one of two nearby understory trees (*Prunus serotina* and *Fagus grandifolia*). Yellow jackets perched on branches chewed off the elaiosome, dropped the seed, and flew away with the elaiosome in its mandibles. To locate discarded seeds and record their dispersal distance, two tan (206 × 244 cm) bed sheets were placed under the two nearby trees mentioned previously. All recovered seeds were examined microscopically for evidence of seed coat scarification and embryo damage.

Voucher specimens of *Trillium cuneatum, T. undulatum* and *T. catesbaei* were deposited in the Clemson University Herbarium, and specimens of the yellow jackets (*Vespula flavipilosa* and *V. maculifrons*) were deposited in the Clemson University Arthropod Collection.

Results and Discussion

Of 100 *Trillium cuneatum* seeds presented to *Vespula maculifrons,* 41 were recovered on the sheets, and only 6 seeds were not removed from the index card by the yellow jackets; 53 seeds were unrecovered. Some seed-carrying yellow jackets flew out of our sight range (~20 m). The yellow jackets possibly were transporting seeds to a nest because they all flew in the same direction, however we were unable to locate the nest. Based on seeds recovered on sheets, *V. maculifrons* dispersed *T. cuneatum* seeds an average of 1.4 m (range 0.1–2.6 m) from the index cards. However, because some vespids appeared to carry seeds 20 m or more (as discussed above), our calculated average clearly underestimates the actual value. Our calculated average dispersal distance of trillium seeds taken by yellow jackets is still much greater than that of ant-dispersed seeds because ants carry seeds only short distances (mean global distance is 0.96 m) (Gómez and Espadaler, 1998).

We found that vespids discovered seeds and began removing them within 5 min. From 1 to 9 conspecifics foraged on seeds at any one time during the experiment, and most (94%) seeds were removed within 1 h. This rapid seed removal might reduce pre-dispersal seed predation from predators such as rodents (Smith *et al.*, 1989) and ground beetles (Ohkawara and Higashi, 1994).

Because long-distance dispersal is a selective advantage for myrmecochores (Anderson, 1988; Handel, 1976; Higashi *et al.*, 1989), dispersal by yellow jackets can potentially benefit plants. If vespids increase dispersal distance, density-dependent mortality, such as post dispersal seed (and seedling) predation, could be reduced. Long-range seed dispersal by vespids might also increase range expansion and possibly contribute to gene flow. Furthermore, long-range dispersal and subsequent seedling establishment increases the ability of populations to recover from isolated small-scale disturbances that can lead to local extinctions (Peterson *et al.*, 1998).

Yellow jackets removed the elaiosomes from 95.7% of the 47 seeds recovered, and only 17% of the recovered seeds were scarified near where the elaiosome was attached. None of the 47 seeds had visible signs of embryo damage. While seed handling by vespids does not appear to damage seeds directly, its effect on seed germination and seedling establishment is unknown.

Jules (1996) suggests that the elaiosomes of seeds taken into yellow jacket nests are fed to developing larvae, and the seeds are subsequently discarded. Most yellow jackets live in subterranean colonies, and wastes are either discarded in the soil beneath the nest or incorporated into its construction (Akre *et al.*, 1980). Therefore, discarded *Trillium* seeds are likely to be left inside the nest. The spherical nests of *Vespula* have an average diameter (and therefore depth) of 8–15 cm (Akre *et al.*, 1980). At present, we do not know how seed burial in these nests might affect seed germination and seedling emergence.

Jules (1996) uses the term *vespicochory* to describe seed dispersal by vespid wasps, and he suggests that yellow jackets disperse seeds of myrmecochorous plants wherever their ranges overlap. Our study is the first known documentation of vespicochory in the eastern United States. The interaction between ants and plants with elaiosome-bearing seeds is generally considered to be a true mutualism (Handel and Beattie, 1990). Additional research is needed to discover whether the interaction between such plants and vespid wasps is also a mutually beneficial relationship.

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