Notes and Discussion

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Yellow Jackets (Vespula vulgaris) as a Second Seed Disperser for the Myrmecochorous Plant, Trillium ovatum

ABSTRACT.—Fleshy appendages attached to seeds (elaiosomes) can aid in seed dispersal by ants. This mode of dispersal (myrmecochory) occurs in over 3000 species in 70 different plant families and is found on every continent except Antarctica. I have observed that a vespid wasp (the common yellow jacket *Vespula vulgaris*) forages for the seeds of the elaiosome-bearing plant *Trillium ovatum* in Oregon and returns to the nest with seeds and attached elaiosomes. Yellow jackets consume elaiosomes but not seeds, thus this event represents effective seed dispersal. Upon inquiry, it was learned that similar observations have been made for *T. ovatum* in California and the UK, and for *Vancouveria hexandra* in Washington state. Given the ubiquity of yellow jackets, seed dispersal by yellow jackets (here termed "vespicochory") quite likely occurs in other elaiosome-bearing plants. Yellow jackets forage for much greater distances than ants, and therefore they will influence both the dispersal ability of plants and the genetic and demographic structure of populations.

Over 3000 species in 70 different plant families produce seeds with fleshy lipid-rich appendages (elaiosomes) which are attractive to ants and are thought to be an adaptation for effective seed dispersal (=myrmecochory; Berg, 1975; Hanzawa *et al.*, 1988; Handel and Beattie, 1990). Ants can transport seeds to their nest, remove the elaiosome and feed it to their developing larvae, and then discard the intact seed within the nest (Culver and Beattie, 1980; Beattie, 1985). Here I report that a vespid wasp (the common yellow jacket *Vespula vulgaris* L.) is also attracted to elaiosomes and provides long-distance dispersal of seeds. Because yellow jackets and the guild of myrmecochorous plants share large range distributions, this novel dispersal mechanism (here termed "vespicochory") almost certainly occurs in other plants as well. If true, vespicochory has significant ecological and evolutionary consequences for many of the well-studied plants previously thought to be dispersed solely by ants.

Western trillium, *Trillium ovatum* Pursh. (Liliaceae), is a common herbaceous perennial in mesic forests of western North America. Adult plants produce fleshy capsules that split along three sides, revealing 1–150 seeds (Mesler and Lu, 1983). Seeds bear elaiosomes which attract ants that disperse the seeds (Mesler and Lu, 1983). During the past 4 summers (1992–1995) I have been studying the dynamics of *T. ovatum* populations in the Siskiyou Mountains of southwestern Oregon (*see* Whittaker, 1960, for description of the Siskiyous). While ants may disperse seeds in this region, I have never observed ants foraging for, or carrying, *T. ovatum* seeds in the Siskiyous. However, I have observed yellow jackets actively foraging for the seeds of *T. ovatum* and returning to their nests with seeds and attached elaiosomes.

On 17 August 1993 I noticed a yellow jacket perched on the fruit of *Trillium ovatum*. The yellow jacket entered the dehisced fruit wall and spent approximately 30 sec pulling one seed from its position among the other seeds. The insect carried the seed to the outside of the fruit and then flew just beneath the forest canopy for as far as I could observe (approximately 30 m), carrying the seed and attached elaiosome. Five more yellow jackets appeared at the same fruit 1 min later. Four waited outside the fruit while the fifth removed another seed and flew in the same direction as the first yellow jacket. The remaining four behaved precisely the same, each entering alone and removing a seed. The final yellow jacket removed the last remaining seed in the fruit, which appeared large enough to encase 30 seeds. Before flying away with the seed, this yellow jacket perched on the leaf of the plant and spent 5 min eating a very small portion of the elaiosome. It did not, however, attempt to damage the seed coat.

One wk later this observation was repeated near a known yellow jacket ground-nest, 3 km from where I had made my initial observation. Approximately 20 m from this nest there is a small stand of alders (*Alnus sinuata*) on which many yellow jackets alight in late afternoon. A yellow jacket was introduced to seeds by gently tipping a leaf so that one individual fell onto a wood platform containing many fresh *Trillium ovatum* seeds. As soon as the yellow jacket encountered a seed while walking on the platform, it seized the seed and flew back toward the nest. I repeated this observation three more times within 15 min.

Extensive studies of yellow jacket diets demonstrate that adults use liquid food sources (*e.g.*, nectar and sap) for themselves and masticated insect parts to feed larvae. No seeds have been reported from yellow jacket nests or from intercepted foragers returning to nests (Evans and Eberhard, 1970; Spradbery, 1973; Harris and Oliver, 1993). Thus it appears that yellow jackets, like ants, can not break the hard seed coat of *Trillium ovatum* seeds and that they use the elaiosome as a source of carbohydrate. Most nests of *Vespula vulgaris* are below ground (Spradbery, 1973). Seeds transported into these nests will have their elaiosomes removed and/or eaten, and then be left in the nest (which will be abandoned in autumn) or dragged back out of the nest and deposited near the entrance. Either case represents effective dispersal of seeds; *T. ovatum* seeds passively dispersed onto the soil surface from a fruit can become established (Mesler and Lu, 1983), and seeds remaining in the nest have the same advantages thought to be possessed by seeds transported into ant nests. These advantages include reduced intraspecific competition, escape from seed predators and dispersal to superior germination sites (Hanzawa *et al.*, 1988).

Dispersal of seeds by yellow jackets is apparently not a rare or geographically restricted event. Pellmyr (1985) observed yellow jackets dispersing the elaiosome-bearing seeds of *Vancouveria hexandra* (Berberidaceae) in Washington state (Lewis Co.). His is the first known account of seed dispersal by yellow jackets. The yellow jackets carried seeds a few meters and landed on a branch where they removed the elaiosome and dropped the seed before flying away. S. Baughman (pers. comm.) has observed a yellow jacket eating the elaiosomes of several *Trillium ovatum* seeds in a redwood forest in Marin Co., California. After 5 min, the yellow jacket flew away carrying a seed with the attached elaiosome. M. R. Mesler (pers. comm.) has seen a yellow jacket eating an elaiosome of *T. ovatum* in the redwoods of Humbolt Co., California, though the insect did not remove the seed from his experimental seed depot. During the summer 1994 I again observed, on two separate occasions, a yellow jacket removing a seed from a *T. ovatum* fruit. In addition, the removal of trillium seeds has been observed many times at the Royal Botanical Gardens, Edinburgh, the Botanical Gardens at St. Andrew, Fife, and in a garden in Edinburgh (BBC Wildlife, August 1985, p. 360; pers. comms. to O. Pellmyr). The genus *Trillium* is not native to the UK; nevertheless, there are many elaiosome-bearing plants in the European flora.

Seed dispersal by yellow jackets will have a great influence on the population structure of myrmecochorous plants such as *Trillium ovatum.* Dispersal distance, along with breeding structure and selective mortality, greatly influence genetic variation within and among populations (Hamrick and Loveless, 1986). Ants can move seeds distances up to 70 m (Handel and Beattie, 1990), but usually they transport seeds less than 5 m (Anderson, 1988). Conversely, species of *Vespula* are capable of foraging up to 900 m from their nests (Spradbery, 1973). Since even an occasional immigration by seed dispersal into a population can significantly affect the rate and direction of population differentiation (Lacy, 1987), yellow jacket dispersal of seeds may serve to reduce variation among populations from the level expected from ant dispersal alone.

In addition, the colonization ability of myrmecochorous plants will be increased by the occasional dispersal of seeds by yellow jackets. Since yellow jackets nest in both forested and open disturbed sites (Harris and Oliver, 1993), and they move farther than ants, seeds will be carried from forested sites to early successional sites more often. In the Siskiyou region much of the landscape is in early successional stages following timber harvesting. *Trillium ovatum* is almost entirely absent from these sites (Jules, pers. observ.), since *T. ovatum* individuals do not tolerate dry conditions typical of deforested sites in southern Oregon. As cooler and moister conditions arise when a new forest canopy is formed, *T. ovatum* will become established in these sites given that seeds are dispersed from surrounding forests. The rate at which *T. ovatum* colonizes young forests will be significantly aided by yellow jackets.

More work is obviously needed to determine the effectiveness and frequency of seed dispersal by yellow jackets. There is however inferential evidence that yellow jackets act as seed dispersers of *Trillium ovatum* in the Siskiyou Mountain region, and in other areas as well. And although vespicochory has been observed for one other species (*Vanvouveria hexandra*), nothing is known about its occurrence for other elaiosome-bearing plants. Yellow jackets are ubiquitous across North America, Europe, Asia and Japan (Miller, 1961), and elaiosome-bearing plants are found on every continent except Antarctica

(Handel and Beattie, 1990). It is possible that other plants have yellow jacket-dispersed seeds and studies of elaiosome-bearing plants ought to include observations to determine if such an interaction is occurring. Specifically, vespicochory should be given careful consideration in studies that examine the fate of marked seeds where some seeds are never recovered in the limited search range of the study (*e.g.*, Bossard, 1990), or where seed dispersal by ants is estimated by removal rates of seeds from depots, but where the removal event is not actually observed (e.g., Gunther and Lanza, 1989; Smith *et al.*, 1989).

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Literature Cited

ANDERSON, A. N. 1988. Dispersal distance as a benefit of myrmecochory. *Oecologia,* **75**:507–511.

BEATTIE, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge Univ. Press, Cambridge. 182 p.

BERG, R. 1975. Myrmecochorous plants in Australia and their dispersal by ants. *Aust. J. Bot.,* **23**:475–508.

BOSSARD, C. C. 1990. Tracing of ant-dispersed seeds: a new technique. *Ecology,* **71**:2370–2371.

CULVER, D. C. AND A. J. BEATTIE. 1980. The fate of *Viola* seeds dispersed by ants. *Am. J. Bot.,* **67**:710–714.

EVANS, H. E. AND M. J. W. EBERHARD. 1970. The wasps. Univ. of Michigan Press, Ann Arbor. 265 p.

GUNTHER, R. W. AND J. LANZA. 1989. Variation in attractiveness of *Trillium* diaspores to a seed-dispersing ant. *Am. Midl. Nat.,* **122**:321–328.

HAMRICK, J. L. AND M. D. LOVELESS. 1986. The influence of seed dispersal mechanisms on the genetic structure of plant populations, p. 211–223. *In:* A. Estrada and T. H. Fleming (eds.). Frugivores and seed dispersal. W. Junk, Dordrecht, Netherlands.

HANDEL, S. N. AND A. J. BEATTIE. 1990. Seed dispersal by ants. *Sci. Am.,* **262**:76–83.

HANZAWA, F. M., A. J. BEATTIE AND D. C. CULVER. 1988. Directed dispersal: demographic analysis of an ant-seed mutualism. *Am. Nat.,* **131**:1–13.

HARRIS, R. J. AND E. H. OLIVER. 1993. Prey diets and population densities of the wasps *Vespula vulgaris* and *V. germanica* in scrubland-pasture. *N. Z. J. Zool.,* **17**:15–12.

LACY, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, selection and population subdivision. *Cons. Bio.,* **1**:143–158.

MESLER, M. R. AND K. L. LU. 1983. Seed dispersal of *Trillium ovatum* (Liliaceae) in second-growth redwood forest. *Am. J. Bot.,* **70**:1460–1467.

MILLER, C. D. F. 1961. Taxonomy and distribution of Nearctic *Vespula. Can. Entomol. Suppl.,* **22**:1–52.

PELLMYR, O. 1985. Yellow jackets disperse *Vancouveria* seeds (Berberidaceae). *Madroño,* **32**:56.

SMITH, B. H., P. D. FORMAN AND A. E. BOYD. 1989. Spatial patterns of seed dispersal and predation of two myrmecochorous forest herbs. *Ecology,* **70**:1649–1656.

SPRADBERY, J. P. 1973. Wasps: an account of the biology and natural history of solitary and social wasps. Univ. of Washington Press, Seattle. 408 p.

WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Eco. Monogr.,* **30**:279–338.

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