New England Plant Conservation Program

Conservation and Research Plan

*Corydalis flavula* (Raf.) D C
Yellow Corydalis

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SUMMARY

*Corydalis flavula* or Yellow Corydalis (Raf.) D C (Fumariaceae), occurs in only four populations spanning five towns in New England, all clustered in south-central Connecticut. Recent estimates put the total size of the region-wide population on the order of 4000 plants. Because ecological studies are lacking, it is unclear whether this number represents a viable level for the taxon in New England. *Corydalis flavula* is listed in the *Flora Conservanda: New England* as a Division 2, regionally rare species. It has a global rank of G5. The taxon is listed as Threatened (S1) in Connecticut. Elsewhere in North America, *Corydalis flavula* is listed as critically imperiled (S1) in Delaware and Nebraska, imperiled (S2) in Michigan and Ontario, and watch-listed (S3 or S4) in New York and Georgia. It is reported from 22 other southeastern and mid-western states, and is common in the Virginias, Pennsylvanian, and the Carolinas. With intensive surveys, several new populations of *C. flavula* have been located in New York, and there is good potential for new discoveries in southern New England.

In North America generally, *C. flavula* occurs either in mesic floodplains and rich woods, or on dry to xeric circumneutral montane bedrock outcrops. *Corydalis flavula* reaches the northeastern limit of its range-wide distribution in central Connecticut, where it is highly restricted to a narrow belt of open outcrops and sparsely wooded summits of sub-acidic basalt ridges. These "trap-rock" ridges have been impacted by quarrying and deforestation since colonial settlement, and relatively intact examples are rare in the state. Trap-rock ridges support several specialized and rare plant and animal species, and are of high conservation importance regionally. Thus, securing protection for *C. flavula* populations will result in enhanced protection for a variety of threatened species.

*Corydalis flavula* is a winter annual whose capacity to form a persistent seed bank is unknown for New England populations. It relies on a combination of insect pollination and cleistogamy to reproduce, and on insects to disperse its seeds to safe sites for germination. The taxon is potentially vulnerable to drought, trampling by hikers, competition with other plant species, pollinator limitation, and climatic change.

Conservation objectives include: 1) maintaining the four extant populations with 500-1000 stems each, of which 75% are reproductive; 2) maintaining at least three sub-populations per site; 3) evaluating population viability by monitoring demographic parameters, identifying limits to fecundity through ecological studies, and bolstering seedling establishment where needed. New populations should be searched for and more complete information assembled on the biogeography and ecology of the species in New England and New York. Invasive shrubs inhibit plant growth at one site; experimental thinning should be attempted. Trampling and damage from all-terrain vehicles may threaten plants at three of four sites; precise impacts should be assessed. One population is protected by a conservation organization, and another is managed cooperatively by two towns, but the others remain in ownership without explicit conservation objectives. Management agreements should be negotiated with these landowners.
This document is an excerpt of a New England Plant Conservation Program (NEPCoP) Conservation and Research Plan. Full plans with complete and sensitive information are made available to conservation organizations, government agencies, and individuals with responsibility for rare plant conservation. This excerpt contains general information on the species biology, ecology, and distribution of rare plant species in New England.

The New England Plant Conservation Program (NEPCoP) is a voluntary association of private organizations and government agencies in each of the six states of New England, interested in working together to protect from extirpation, and promote the recovery of the endangered flora of the region.

In 1996, NEPCoP published "Flora Conservanda: New England," which listed the plants in need of conservation in the region. NEPCoP regional plant Conservation Plans recommend actions that should lead to the conservation of Flora Conservanda species. These recommendations derive from a voluntary collaboration of planning partners, and their implementation is contingent on the commitment of federal, state, local, and private conservation organizations.

NEPCoP Conservation Plans do not necessarily represent the official position or approval of all state task forces or NEPCoP member organizations; they do, however, represent a consensus of NEPCoP's Regional Advisory Council. NEPCoP Conservation Plans are subject to modification as dictated by new findings, changes in species status, and the accomplishment of conservation actions.

Completion of the NEPCoP Conservation and Research Plans was made possible by generous funding from an anonymous source, and data were provided by state Natural Heritage Programs. NEPCoP gratefully acknowledges the permission and cooperation of many private and public landowners who granted access to their land for plant monitoring and data collection.

This document should be cited as follows:


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I. BACKGROUND

INTRODUCTION

*Corydalis flavula* (Raf.) D C (Fumariaceae), also known as Yellow corydalis, is a diminutive spring ephemeral characteristic of basalt trap-rock ridges in New England. While secure in several parts of the mid-west and southeastern states, *C. flavula* is restricted to a very narrow habitat in Connecticut, along with other specialist species of mineral-rich basalt mountains. Its known distribution spans five towns and eleven miles in the state, and totals some four thousand stems. First recorded in the state in 1926 (Clark 1926), its presence in Connecticut is something of a mystery, because its known occurrences are over fifty miles from the nearest documented populations in New York and occupies such a seemingly confined area. It is possible that more intensive searches for this species will reveal more populations.

Little is known of the ecology of *Corydalis flavula*, especially within its New England range. However, studies of its similar congeners suggest much about its requirements for survival. It is self-compatible and occasionally cleistogamous, but likely depends on insects (especially bees) for pollination, out-crossing, and the maintenance of genetic heterogeneity (Mitchell 1983). Its seeds, produced in May-June, show unusual dormancy characteristics, germinating in the fall and producing seedlings that overwinter (Baskin and Baskin 1994, Farnsworth unpublished data). These seeds have conspicuous, fatty elaiosomes attractive to ants that transport the propagules to nutrient-rich nest sites favorable for germination (Beattie et al. 1979). Its annual life history -- and uncertainty about its capacity to form a long-lived seed bank -- engender concern that this species is vulnerable to local extinction in years of poor resource availability, heavy disturbance (such as fire, trampling, and collection), late onset of spring, and early and long winters. All observed plants in one population, for example, died before fruiting during an unusual spring drought in Spring 2001. Thorough study of the demography of these populations and the factors that influence fecundity, mortality, and dispersal, is needed in order to understand the population trends and habitat requirements of *C. flavula* and to predict and plan for its long-term survival.

Because three of the four known *Corydalis flavula* populations in Connecticut occur within a few meters of the popular Mattabesett hiking trail, the plant faces several potential anthropogenic threats. All-terrain vehicles and irresponsible handling of fire can impact these populations negatively. More consistent monitoring of all sites is needed to determine how large a problem these factors may be. At two sites, the canopy is closing due to forest succession, but the impacts of shade on *C. flavula* are as yet unknown. A recent study at one site indicates that plant size and reproductive output are positively correlated with light availability (Farnsworth, unpublished data), so a minimum amount of light may be important to maintain vigorous populations. Inappropriate land uses, specifically timbering, may also threaten *C.
flavula at certain sites. Two of the four sites receive moderate conservation protection (although no active management). Management agreements should be forged with landowners at the other two sites (as well as a large municipal landowner abutting one of the protected areas). This Conservation and Research plan reviews in detail the conservation status of \textit{C. flavula}, its biology, its biogeography, and the actions that are necessary to ensure its persistence in New England.

**DESCRIPTION**

\textit{Corydalis flavula} is a delicate, herbaceous annual, growing 1-3 dm tall. It has a sympodial architecture, with its primary green or lightly glaucous main stem giving rise to many axillary branches. It often becomes prostrate as it grows. Its soft, fragile stems, are susceptible to breaking. Its 2-5 cm-long leaves are finely, bipinnately dissected into linear or oblong, sometimes cuneate or acute segments (Britton and Brown 1970). Its lower leaves are borne on slender petioles up to 10 cm long, while the upper leaves are nearly sessile.

Flowers occur in racemes borne on thin pedicels, which are not generally longer than the leaves. The bracts enclosing the racemes of 6-10 flowers are ovate, leaf-like and 3-8 mm long. Each flower is borne on a pedicel (0.5-) 1-1.5 cm long. The sepals are minute. The four-petaled corolla is pale yellow (hence the species' common name) and is 7-9 mm long, including a characteristic, 1-2 mm long, curved nectar spur. The flowers are strongly irregular and asymmetrical (Gleason and Cronquist 1991). The crest of the upper, keeled petal is usually toothed. The two inner, lateral petals are similarly keeled and come together over the 2-lobed stigma. The genus \textit{Corydalis} is so-named from the Greek meaning "crested lark," because the bent nectar spur resembles the hind claw of the European crested lark (Stevens 1961).

The fruit of \textit{C. flavula} is a spreading or drooping, 1.5-2 cm long, 3 mm wide, unilocular, thin capsule (resembling a small pod). The fruit dehisces its 6-12 seeds through two elongate valves. A persistent replum (remnant of the placenta) remains on the pedicel after the seeds have dispersed. The seeds are lenticular, round, dimpled, shiny and black, about 2 mm wide, with sharp margins, and a wrinkled, white aril (Mitchell 1983, Gleason and Cronquist 1991, Stern 1997).

On trap-rock ridges of Connecticut, \textit{C. flavula} can occur with a few close relatives in the Fumariaceae, including its congener, \textit{Corydalis sempervirens}. Several features distinguish it from \textit{C. sempervirens}, as Table 1 summarizes. Although the mature plants of \textit{C. flavula} and \textit{C. sempervirens} are distinctive, separating seedlings and immature plants can be problematic in the field (C. Mangels, personal observation). In New York, it reportedly co-occurs with \textit{Corydalis aurea} (R. Zaremba, The Nature Conservancy, personal communication)
Table 1. Characters distinguishing *Corydalis flavula* from *Corydalis sempervirens* (Gleason and Cronquist 1991, Kartesz and Meacham 1999)

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Corydalis flavula</em></th>
<th><em>Corydalis sempervirens</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall size of plant</td>
<td>1 to 3 dm</td>
<td>3 to 8 dm</td>
</tr>
<tr>
<td>Life history</td>
<td>Annual</td>
<td>Biennial, perennial, annual</td>
</tr>
<tr>
<td>Growth form</td>
<td>Prostrate</td>
<td>Erect</td>
</tr>
<tr>
<td>Flowering time (in Connecticut)</td>
<td>Begins in April</td>
<td>Begins in mid-May</td>
</tr>
<tr>
<td>Corolla color</td>
<td>Pale yellow</td>
<td>Rose to pink-purple</td>
</tr>
<tr>
<td>Seed size and shape</td>
<td>2 mm wide, acute margin</td>
<td>1 mm wide, obtuse margin</td>
</tr>
</tbody>
</table>

Other members of the Fumariaceae that can occur in sub-acidic/circumneutral, shallow-to-bedrock areas (but only infrequently co-occur with *C. flavula*) are *Dicentra cucullaria* (Dutchman's breeches) and *Dicentra canadensis* (Squirrel corn). However, this genus possesses bilaterally symmetrical flowers and only superficially resembles species of the genus *Corydalis* (Gleason and Cronquist 1991).

**TAXONOMIC RELATIONSHIPS, HISTORY, AND SYNONYMY**

The genus *Corydalis* is placed in the subfamily Fumarioideae of the Fumariaceae (Fumitory family), and includes approximately 320 species of herbaceous plants. These taxa are found chiefly in the temperate northern hemisphere, with a few species occurring in the mountains of eastern and southern Africa (Cullen 1993). Ten species occur in North America (Gleason and Cronquist 1991, Stern 1997). Four of these species, all Western, form a group of perennial species, while the other are annuals or biennials. Various taxonomic treatments segregate the latter, 'non-perennial' group on the basis of the color, size, and shape of the corolla, as well as seed size (Weber 1991).

Most North American members of this genus are distinct and morphologically homogeneous within taxa, and hybridization is uncommon or unknown (Ownbey 1947). However, some variation in corolla size, correlated with a prevalence of cleistogamous (closed, internally pollinated) flowers and a relatively lax and diffusely branched habit, has been noted in *C. flavula* (Mitchell 1983), indicating the possibility of hybridization with *C. sempervirens*, its sympatric congener. Slight differences in the timing of flowering are thought to maintain reproductive isolation between these species (Mitchell 1983), but detailed breeding studies are needed to address this hypothesis.
The species *Corydalis flavula* (Refinesque ex. Desv.) De Candolle was first described in 1808 (Rafinesque-Schmaltze 1808). The taxon has variously been ascribed to the genera *Fumaria* (the basionym selected by Rafinesque) and *Capnoides* (cf. Kuntze 1891), and has been synonymized in the literature as *Corydalis aurea* var. *flavula* Wood, *Corydalis flavidula* Chapm., *Corydalis geyeri* Fedde, and *Neckeria flavula* Millsp. (Ownbey 1947, W3-TROPICOS 2000). Despite the early malleability of the taxon, the nomenclature has settled down with the analysis provided by a 1947 monograph (Ownbey 1947) and added information on its karyotype and other informative characters (Hill 1992; sporophyte count $2n = 16$).

**SPECIES BIOLOGY**

*Life history*

*Corydalis flavula* is an annual species, and this life history has several important implications for its ecology and its persistence on the landscape. First, a population must reproduce itself every year, since mature plants do not over-winter. In "bad" years of low resource availability or high disturbance rates, the population can shrink to precipitously low numbers if mature plants suffer high mortality before they are able to reproduce. A spring drought in 2001, for example, appears to have killed a majority of plants before reproduction at one site in Connecticut (CT .002; Farnsworth, personal observation).

Second, a population of *C. flavula* relies solely on floral reproduction because it has no perennating structures like rhizomes or stolons that enable it to propagate itself vegetatively. Therefore, *C. flavula* is particularly vulnerable to factors influencing the success of sexual reproduction, including the abundance of pollinators, the ability of those pollinators to effect out-crossing, and the availability of nutrients and water for producing and maturing viable seeds.

Third, the seeds of *C. flavula* must find their way to safe sites for subsequent germination, usually via insect dispersers (see below). Finally, it is uncertain whether *C. flavula* can maintain a persistent seed bank (Baskin and Baskin 1994); if not, it may be doubly vulnerable to environmental vagaries during a given growing season.

*Phenology*

*Corydalis flavula* matures and flowers very early in the frost-free season. It is documented as flowering in April and fruiting in May through June in New England (Magee and Ahles 1999, data from Connecticut Natural Diversity Data Base, and personal observation) and in New York (Young 2000). In fact, the species shows characteristics of an early "spring ephemeral" throughout its range, reaching reproductive maturity in March through April in North Carolina, Tennessee, and Virginia (Wofford 1989). Where spring ephemerals like *C. flavula* occur in a forest understory, early maturity is viewed as adaptive for taking advantage of fleeting
spring light, water, and nutrient flushes before leaf-out of a dense canopy (Brown et al. 1985, Masarovicova and Elias 1986). On moderately exposed trap-rock ridges, where *C. flavula* occurs in Connecticut, plants may respond to early warming on dark, sunny rocks in the spring. The summits of trap rock ridges can be significantly warmer than the valleys in early spring. It is of interest that the occurrences of *C. flavula* in Connecticut fall within the sector of the 50-51°F mean annual temperature isopleths that exhibits the earliest average date (April 2) of extended daily temperatures exceeding 43°F (Brumbach 1965 and William Moorhead, Consulting Botanist, personal communication). Such early emergence, however, can render plants vulnerable to sudden cold temperatures in April, as well as to very warm temperatures that can occur in May (Rogers 1983, Farnsworth et al. 1995). By flowering early, *C. flavula* relies on the equally early emergence of pollinators, and, like other *Corydalis* species, simultaneously may provide a critical nectar source for foragers early in the growing season.

**Pollination: selfing and outcrossing**

Species of the genus *Corydalis* have flowers that are specialized for pollination by insects, generally bees. The specific importance of entomophily to *C. flavula* has not studied. A brief study at one Connecticut site in April 2001 (Farnsworth, unpublished data) witnessed visits to *C. flavula* by honeybees (*Apis* spp.), flies (to be identified), and, most conspicuously, the falcate orange-tip butterfly (*Anthocaris midea*), whose range overlaps and does not extend north of the range of the plant in Connecticut. Several closely-related members of the genus with similar flower morphology have received more attention in the literature, and bear comparison to *C. flavula*. The primary pollinators of other *Corydalis* species are solitary bumblebee queens (*Bombus* spp.) that emerge and forage early in the spring (Ohara and Higashi 1994, Oleson and Knudsen 1994, Olesen 1996, Yasaka et al. 1998). Honey bees (*Apis mellifera*) have also been noted as visitors to *Corydalis ambigua* (Higashi et al. 1988). To access nectar at the end of the long nectar spur, insects must have a long proboscis or work arduously to part the petals and penetrate the spur. A few pollinators (Hymenoptera: Anthophoridae) with specialized probosci are common pollinators of *Corydalis cava* in Europe (Olesen 1996). The majority of pollinators, however, employ an alternative strategy: robbing *Corydalis* nectar by piercing the spur directly and sucking nectar out of the hole (Higashi et al. 1988). While nectar-robbing would seem detrimental to the plant (and the behavior is the subject of many studies on evolutionary trade-offs among mutualists), the robber species actually effect pollination a significant proportion of the time. For example, Higashi et al. (1988) reported that nearly 60% of *Corydalis ambigua* plants that were exclusively visited by "illegitimate foragers" (robbers) set seed. In fact, robbing does not substantially reduce seed set in many other plant species that have been studied (Darwin 1841, Inouye 1983). Oleson (1996) observed that plants at the edge of their range (such as *C. flavula*) can benefit from opportunistic nectar robbers that can circumvent a specialized flower morphology and obviate the need for a single, specialized pollinator. He notes that marginal populations of *Corydalis cava* that occur outside the range of its specific pollinator, *Anthophora acervorum*, were visited and pollinated by opportunistic robbers (*Bombus terrestris*). In fact, these bumble-bee queens increased their foraging efficiency over the 38-day flowering period of the plants, and
became entirely dependent upon *Corydalis* for nectar during this time. It is conceivable that *Corydalis flavula* is being pollinated by an unusual array of insect visitors at the edge of its range in Connecticut, and further studies are warranted.

The quality of the flower influences the success of insect pollination in *Corydalis* species. Pollinators of *Corydalis* species respond positively to a larger inflorescence size, visiting larger flowers more frequently, and spending more time per visit, resulting in higher fecundity (Ohara and Higashi 1994). Flower color and scent are also powerful cues for *Corydalis* pollinators (Olesen and Knudsen 1994). The degree of size, color, and scent polymorphism has not been assessed within and among *Corydalis flavula* populations, but may influence its pollination success. Likewise, Yasaka et al. (1998) showed that high temperatures shorten the life-span of opened flowers of *Corydalis ambigua*. Of interest is whether marginal populations of *C. flavula* growing in dry, warm hilltops like those of Connecticut and New York exhibit less showy and shorter-lived flowers than other populations, potentially leading to pollinator-limitation. Flower production at one site in Connecticut (CT .001 Middletown) spanned a brief, 10-15 day period during May 2001. Fruit production was positively correlated with flower production at this site ($r^2 = 0.64$; Farnsworth, unpublished data). Fruit production was copious at the site, with over 90% of one sub-population producing an average of 18 fruits with an estimated mean of > 90 seeds per plant (Farnsworth, unpublished data). Such fruiting activity indicates a high efficiency of pollination and/or cleistogamy in this population.

Unlike many of its congeners, which are self-incompatible, *Corydalis flavula* relies on a combination of entomophily and cleistogamy to produce seed (Mitchell 1983). A study of the relative fitness of progeny from selfed versus out-crossed plants of *Corydalis sempervirens* detected a slight short-term advantage among the out-crossed cohort (Cartier 1985). To fully understand the reproductive dynamics and possible limitations to seed set and seed viability of *C. flavula*, it will be necessary to positively identify its pollinators and to compare the relative contributions of out-crossing and self-fertilization to its total reproductive success.

**Seed dormancy**

Once seeds are produced by *Corydalis flavula*, they enter a period of specialized dormancy. A study of Kentucky populations of *C. flavula* revealed that the plants behave as winter annuals (Basking and Baskin 1994). The embryos are “underdeveloped” that is, they are incapable of germination without undergoing additional growth and hormonally-mediated maturation after release (Martin 1946). When these seeds are released in May, high summer temperatures both inhibit growth and act as a cue for the embryos to become physiologically dormant. The seeds require a dormancy period of several weeks and a specific temperature cue of the cooler August-September temperatures of 25°-30°C during the day and 15°-20°C at night to resume embryogeny and to germinate (Baskin and Baskin 1994). In Kentucky populations, the majority of *C. flavula* seeds germinate in the autumn of the year they are produced, and the seedlings themselves overwinter. Seeds collected in June, 2001 from two
Connecticut populations exhibited similar behavior, germinating copiously in both the greenhouse and field in September (Farnsworth, unpublished data). Because the species exhibits this 'nondeep morphophysiological dormancy' (sensu Baskin and Baskin 1994), *C. flavula* is not expected to maintain a large persistent seed bank, although a small proportion of seeds may remain viable for over a year. However, the precise seed-banking capacity of New England populations of *Corydalis flavula* has not been studied, and dormancy and germination dynamics in this region may differ importantly from those of more southern populations. The strict temperature requirement of hot summer temperatures followed by cool (but not cold) autumn nights for germination may in part explain why the range of *C. flavula* does not extend farther north in New England, even though trap-rock ridges reach northward into Massachusetts.

**Seed dispersal and predation**

Seeds of *Corydalis flavula*, like those of its congeners, exhibit a conspicuous elaiosome, which presumably attracts potential seed dispersers, especially ants. The function of the elaiosome in other species of *Corydalis* has been well-studied as a means to understand the evolution and importance of myrmecochory in temperate floras (Beattie and Culver 1981, Hanzawa et al. 1985, Nakanishi 1994). Beattie and Culver (1981) documented that 80% of the seeds of *C. flavula* were dispersed by ants (*Aphaenogaster rudis*) in the mountains of West Virginia. They saw no evidence that *C. flavula* is dispersed by agents other than ants. Many workers have suggested that ants facilitate seed germination and seedling establishment by moving seeds to nutrient-rich nests and burying intact seeds once they have consumed the elaiosome (Beattie et al. 1979, Hanzawa 1986). A study of the evolution of myrmecochory in seven *Corydalis* species of Japan suggests the potential importance of ants to the dispersal and survival of propagules of annuals like *C. flavula*. *Corydalis* species that rely exclusively on ant dispersal are generally annuals or biennials (without a persistent seed bank) that inhabit warm-temperate Japan (Nakanishi 1994), with life-histories and habitat preferences that resemble *Corydalis flavula*. Thus, *C. flavula* may depend almost entirely on ants to bring its seeds to scattered safe sites for germination. The identity and behavior of ants dispersing *C. flavula* in Connecticut remain to be studied, but eight species of ants have been observed actively foraging or nesting near plants at CT .003 (Berlin) and CT .001 (Middletown) in May, June, and October 2001: *Aphaenogaster rudis*; *Camponotus herculeanus*; *Camponotus nearcticus*; *Formica neogagatus*; *Formica subsericea*; *Leptothorax longispinosus*; *Myrmica punctiventris*; and *Tapinoma sessile* (Farnsworth, unpublished data).

The elaiosome of *Corydalis aurea* serves a dual function, promoting dispersal by ants while repelling herbivory by its main seed predator, *Peromyscus manulatus*, the deer mouse (Hanzawa et al. 1985). In the sand country of Illinois, the horned lark (*Eremophila alpestris*, an early nesting species) reportedly eats the seeds of *C. flavula* (Wharton and Barbour 1971), and other birds may consume it in New England as well. Turkey scratching, which may be accompanied by seed predation or otherwise damage seeds, has been noted at certain traprock glades in New England (W. Moorhead, personal communication), and turkeys have been
observed by the author at CT .002. The importance of seed predation in reducing the potential survivorship of *C. flavula* in Connecticut is currently unknown. Seeds with sticky elaiosomes tend to clump following dispersal, making them particularly apparent and vulnerable to predators, if ants do not separate and transport the seeds before they are consumed. Secondary chemicals in the elaiosome may serve as additional protection in *C. flavula*, but the role of the elaiosome in this species has yet to be determined.

**Herbivory**

Being conspicuous, succulent, and one of the earliest plants to emerge in the spring, *Corydalis flavula* ought to attract a host of herbivores including rodents and deer. Young over-wintering seedlings should be particularly vulnerable. This is particularly true on the trap-rock ridges of Connecticut, where deer can abound. Many members of the genus *Corydalis* are known for producing a host of secondary compounds in leaves, stems, and roots that show pharmacological activity, and *C. flavula* is likely to be no exception. However, herbivory has not been noted as a threat by botanists visiting the Connecticut sites to date. Visits in early spring 2001 to two sites in Connecticut (CT .001 and CT .002) did not reveal evidence of either significant mammal browsing or insect predation on these plants (Farnsworth, personal observation). However, a small proportion of stems (<10%) appeared to have been bitten off, probably by a small rodent in a sub-population at CT .003 in June 2001. Only parts of plants were being consumed, so it is unlikely that this herbivory was substantially impacting the population.

**HABITAT/ECOLOGY**

**Range-wide habitat**

*Corydalis flavula* exhibits a curious, bi-modal distribution in terms of its apparent habitat preferences throughout its range. In much of the mid-west and south-east, *C. flavula* occurs in mesic to damp woods, floodplains, and bottomlands. Where it moves up in elevation along the Alleghenies, Blue Ridge, and southern Appalachian belt, the species occupies cliffs, rocky outcrops, ledges, and other comparatively dry habitats. These rocky, montane habitats more closely resemble the very limited area where *C. flavula* is found in Connecticut, namely exposed trap-rock ridges. Table 2 summarizes the wide variety of ecosystems in which *C. flavula* has been reported from around North America, based on herbarium records and regional floras. The common denominator among all these habitats appears to be the presence of circumneutral or rich (often alluvial) soils.
Table 2. Habitats in which *Corydalis flavula* is found throughout its North American range. Sources are given in Literature Cited, except where "NYBG" followed by a collection date denotes record from the Herbarium of the New York Botanical Garden (NYBG data collected by C. Mangels)

<table>
<thead>
<tr>
<th>STATE (locality if known)</th>
<th>HABITAT</th>
<th>SOURCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arkansas (Newton County)</td>
<td>Northwest-facing limestone cliffs and ledges with much seepage</td>
<td>NYBG (12 June 1955)</td>
</tr>
<tr>
<td>Arkansas (Newport County)</td>
<td>Common in woods</td>
<td>NYBG (18 April 1902)</td>
</tr>
<tr>
<td>Connecticut</td>
<td>Summits of trap-rock ridges, with open grassy glade vegetation</td>
<td>G. S. Torrey Herbarium records and Natural Heritage data</td>
</tr>
<tr>
<td>Florida (Liberty County)</td>
<td>Floodplains of the Apalachicola River; moist shady river banks</td>
<td>Clewell (1985): page 305; Ward 1974</td>
</tr>
<tr>
<td>Georgia</td>
<td>Rocky alluvial woods and floodplains often on calcareous sites</td>
<td>Wofford (1989): page 232</td>
</tr>
<tr>
<td>Illinois (Havana County)</td>
<td>Open sandy woods</td>
<td>NYBG (21 April 1935)</td>
</tr>
<tr>
<td>Illinois (Hutsonville County)</td>
<td>Slopes above flooded area</td>
<td>NYBG (3 May 1996)</td>
</tr>
<tr>
<td>Indiana</td>
<td>Rich, moist, sandy soil in woodland, usually on slopes and the wooded bluffs of streams</td>
<td>Deam 1984: page 484</td>
</tr>
<tr>
<td>Indiana (Covington Hills, Montgomery County)</td>
<td>River bottom</td>
<td>NYBG (2 May 1961)</td>
</tr>
<tr>
<td>Indiana (Montgomery County)</td>
<td>In alfalfa near edge of woodland</td>
<td>NYBG (28 April 1945)</td>
</tr>
<tr>
<td>Kansas</td>
<td>Woods, banks, along bluffs</td>
<td>Stevens 1961: page 119</td>
</tr>
<tr>
<td>Kansas (Bourbon County)</td>
<td>Open woods, rich soil, not common</td>
<td>NYBG (8 May 1968)</td>
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<tr>
<td>Kansas (Wyandotte County)</td>
<td>Woods; uncommon</td>
<td>NYBG (12 April 1896)</td>
</tr>
<tr>
<td>Kentucky</td>
<td>Thickets and woodland borders</td>
<td>Wharton and Barbour 1971: page 216</td>
</tr>
<tr>
<td>Kentucky (Lewis County)</td>
<td>Common in shaded roadsides</td>
<td>NYBG (12 April 1988)</td>
</tr>
<tr>
<td>Kentucky (Preston)</td>
<td>In thicket on bank of Slate Creek</td>
<td>NYBG (10 May 1941)</td>
</tr>
<tr>
<td>Location</td>
<td>Habitat Description</td>
<td>Source Date</td>
</tr>
<tr>
<td>----------------------------------</td>
<td>--------------------------------------------------------------------------------------</td>
<td>----------------------</td>
</tr>
<tr>
<td>Kentucky (Henry County)</td>
<td>Among deciduous trees along sloping ground, soil rich and damp</td>
<td>NYBG (13 May 1963)</td>
</tr>
<tr>
<td>Michigan (Madden Creek)</td>
<td>Sheltered NW-facing slope in the wet stream alluvium and along banks of stream</td>
<td>NYBG (1 May 1972)</td>
</tr>
<tr>
<td>Michigan (Jefferson County)</td>
<td>Along railroad right-of-way and along spring</td>
<td>NYBG (5 April 1942)</td>
</tr>
<tr>
<td>Mississippi</td>
<td>Alluvial woods and rocky, wooded slopes</td>
<td>Timme 1989: page 150</td>
</tr>
<tr>
<td>Missouri (Carterville)</td>
<td>Rich woods</td>
<td>NYBG (11 April 1909)</td>
</tr>
<tr>
<td>Missouri (Jackson County)</td>
<td>Common in low woods</td>
<td>NYBG (25 April 1887)</td>
</tr>
<tr>
<td>New Jersey (Hunterdon Co.)</td>
<td>Banks of Delaware River</td>
<td>NYBG (28 May 1925)</td>
</tr>
<tr>
<td>New York (Ulster County)</td>
<td>In dark woods</td>
<td>NYBG (7 May 1949)</td>
</tr>
<tr>
<td>New York (Rockland Co.)</td>
<td>East side of trail, north of summit</td>
<td>NYBG (1 May 1956)</td>
</tr>
<tr>
<td>New York (Ulster County)</td>
<td>Shawangunk Mountains</td>
<td>NYBG (coll. J. P. Allen, no date)</td>
</tr>
<tr>
<td>North Carolina (Alamanee County)</td>
<td>Alluvial woods on river</td>
<td>NYBG (10 May 1956)</td>
</tr>
<tr>
<td>Ohio (Harrison Township)</td>
<td>Dry wooded ridge-top</td>
<td>NYBG (23 April 1992)</td>
</tr>
<tr>
<td>Oklahoma (Delaware Co.)</td>
<td>North slope in rich woods</td>
<td>NYBG (1 May 1948)</td>
</tr>
<tr>
<td>Oklahoma (Sequoyah Co.)</td>
<td>Occasional in floodplain forest</td>
<td>NYBG (7 May 1955)</td>
</tr>
<tr>
<td>Ontario</td>
<td>Point and island on Lake Erie, dry, rocky ground</td>
<td>NYBG (27 May 1901 and 13 May 1882)</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>An uncommon species whose distribution is little understood</td>
<td>Taylor 1915</td>
</tr>
<tr>
<td>Pennsylvania (Lancaster Co.)</td>
<td>On banks of Susquehanna River</td>
<td>NYBG (9 May 1891)</td>
</tr>
<tr>
<td>Pennsylvania (California)</td>
<td>Wet ground</td>
<td>NYBG (May 1902)</td>
</tr>
<tr>
<td>Tennessee (Knox County)</td>
<td>Woodlands</td>
<td>NYBG (May 1897)</td>
</tr>
<tr>
<td>Tennessee (Putnam County)</td>
<td>Rich woods in vicinity of confluence of Mill and Spring Creeks</td>
<td>NYBG (6 April 1979)</td>
</tr>
<tr>
<td>Virginia</td>
<td>Banks of the Roanoke River</td>
<td>NYBG (29 May 1890)</td>
</tr>
<tr>
<td>Location</td>
<td>Habitat Description</td>
<td>Collection Date</td>
</tr>
<tr>
<td>-----------------------------------------------</td>
<td>-------------------------------------------------------------------------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Virginia (Elk Wallow Shelter)</td>
<td>Abundant on gently sloping flat area on large broken rock, depressions filled with humus, in thin mixed deciduous forest with a few evergreens</td>
<td>NYBG (6 April 1967)</td>
</tr>
<tr>
<td>Virginia</td>
<td>Shore above aqueduct bridge</td>
<td>NYBG (5 May 1895)</td>
</tr>
<tr>
<td>Virginia (Greene County)</td>
<td>Abundant in mixed growth deciduous forest</td>
<td>NYBG (10 May 1974)</td>
</tr>
<tr>
<td>Virginia (Prince William County)</td>
<td>Floodplain of Branch Run</td>
<td>NYBG (28 April 1940)</td>
</tr>
<tr>
<td>Virginia (Pass Mountain and Oventop Mountain)</td>
<td>Rocky spurs and coves; dense mats in moist forest</td>
<td>NYBG (6 March 1936)</td>
</tr>
<tr>
<td>Virginia</td>
<td>Rich, low floodplain on James River; junction of Coastal Plain and Piedmont physiographic provinces; and Ridge and Valley province in <em>Carya-Fraxinus</em> woodland on steep, dry, Brallier (calcareous) shale</td>
<td>W. Moorhead, personal communication</td>
</tr>
<tr>
<td>Virginia</td>
<td>Blue Ridge province in rich river bottom floodplain forest and rich forest on adjacent, steep, colluvial slopes with high calcium/nutrient-rich soils.</td>
<td>Rawinski et al. 1996</td>
</tr>
<tr>
<td>Virginia</td>
<td>Has been collected from 26 of 108 counties, in every physiographic province except high-elevation Allegany Mountain Province and eastern shore.</td>
<td>Harvill et al. 1992</td>
</tr>
<tr>
<td>West Virginia (Morgantown)</td>
<td>Rich woods</td>
<td>NYBG (11 April 1890)</td>
</tr>
<tr>
<td>West Virginia</td>
<td>Rocky woods</td>
<td>Strausbaugh and Core 1976</td>
</tr>
</tbody>
</table>

Closest to Connecticut, in New York, *C. flavula* occurs in shallow-to-bedrock areas that resemble trap-rock ridges both physically and ecologically. Although the New York sites encompass a wider range of basaltic to calcareous bedrock types, these outcrop habitats share similar micro-environmental conditions with the Metacomet range, and *C. flavula* occurs in similar "Rocky summit grasslands" and "Red cedar rocky summit" natural communities (Troy Weldy, New York Natural Heritage Program, correspondence with Christopher Mangels, 1999). Robert Zaremba (personal communication) describes the habitat of *C. flavula* as south-facing rocky summits of the Hudson Highlands. The New York populations tend to be small and scattered, but the number of known occurrences has significantly increased since formal inventories of the Hudson Highlands began several years ago. Ecological studies of the
numerous secure populations in eastern New York would likely yield valuable comparative information to inform the management of *C. flavula* in Connecticut.

**Habitat in Connecticut**

*Corydalis flavula* has been found exclusively in Connecticut on an eleven-mile stretch of trap-rock ridge composed of Jurassic-age basalt of the Holyoke Formation (Figure 2). This basalt is a dark-gray to orange, fine-grained extrusive igneous rock, which is commonly fractured into columns due to the fact that it was extruded and cooled underground (Bell 1985). The north-south-trending, glacier-worn summits of trap-rock ridges are typically criss-crossed with fissures and shallow cracks, into which the seeds of herbaceous plants find their way. Talus also results from glacial action, and supports soil development and colonization by plants. Holyoke basalt also commonly contains calcium-plagioclase and pyroxene (a mineral containing oxides of calcium, magnesium, iron, and sodium; Bell 1985); consequently, the meager soils from this parent rock are nearly neutral in pH (Farnsworth, unpublished data). Magnesium and calcium, in particular, are essential, limiting nutrients for plants (Salisbury and Ross 1992: 120). Hence, although soil deeper than 0.5 m is generally not found on the bare summits of these trap-rock ridges, a surprising diversity of plants exploit the mineral-rich, sub-acidic chemistry of the habitat, and many species are restricted to areas where these physical conditions prevail.

Water is in short supply on trap-rock ridges, as it is typically conducted rapidly away from the summit to seepages further downslope. Thus, seeds germinate and herbaceous plants survive only in micro-environments of the crevices where humus and soils are sufficiently developed to allow for water capture (Anderson et al. 1999). Canopy trees also grow slowly, and succession proceeds at a very leisurely rate due to a paucity of water, and the woodlands or of trap-rock summits are characteristically open and park-like. Shrubs are typically very sparse to absent in these communities.

These sparse glades or rocky balds on trap-rock ridges are recognized as distinctive natural communities in Connecticut (Dowhan and Craig 1976, Metzler and Barrett, unpublished data), Massachusetts, and New York. Currently, these natural community types are classified as the *Quercus rubra-Carya (glabra, ovata)-Ostrya virginiana/Carex pensylvanica* Forest in the *Carya (glabra, ovata)-Fraxinus americana-Quercus (alba, rubra)* Forest Alliance, I.B.2.N.a.46, and the *Juniperus virginiana-Fraxinus americana/Danthonia spicata-Poa compressa* Woodland of the *Juniperus virginiana* Woodland Alliance, II.A.4.N.b.2 (The Nature Conservancy and Association for Biodiversity Information 1999, Lundgren 2000). The latter, rare community type is ranked G2G3. Typical associates of *C. flavula* observed by C. Mangels and other biologists in these Connecticut natural communities include pignut hickory (*Carya glabra*), white ash (*Fraxinus americana*), and several oak and other hickory species, often exhibiting a stunted growth form. The herbaceous layer is patchily dominated by characteristic grasses including Canada bluegrass (*Poa compressa*), little bluestem (*Schizachyrium scoparium*), and poverty-grass (*Danthonia spicata*), as well as by lush coverage of the sedge *Carex pensylvanica*. Ferns such as ebony spleenwort (*Asplenium*...
platyneuron) and woodsia (Woodsia obtusa) may also commonly occur in these habitats. This herbaceous flora also can contain several state-rare species in addition to C. flavula, among them Virginia snakeroot (Aristolochia serpentaria), long-leaved blueet (Houstonia longifolia), long-awn hairgrass (Muhlenbergia capillaris), northern dropseed (Sporobolis heterolepis), and ragwort (Senecio pauperculus) (Metzler and Wagner 1998). Rock cress (Arabis laevigata) and several spring ephemeral species (including spring beauty, Claytonia virginica, and early saxifrage, Saxifraga virginiensis) are also common elements of the flora of trap-rock ridges. Additional plant species associated with C. flavula in Connecticut are listed in Appendix 2.

*Corydalis flavula* occupies a narrow belt on the top of trap-rock ridges between the sharp, northwest-facing cliffs and the more gently sloping flank of the ridge where microclimates are more equable and more diverse vegetation takes hold. The plant is usually found in crevices of talus and bedrock outcrops that are free of Carex pensylvanica cover. Tree cover over these areas is general sparse and park-like. Estimated light availability to *C. flavula* plants at one site (CT .001) in May, 2001 averaged 53% of total sunlight (Farnsworth, unpublished data). Both plant size and total fruit production are positively correlated with available light at this site (Farnsworth, unpublished data). These open-rock "gaps" are distributed patchily throughout the summit glade, and it is clear that *C. flavula* occupies only a small fraction of the available habitat at these Connecticut sites.

The ecological processes that drive the formation of characteristic trap-rock communities are somewhat uncertain, and may vary up and down the hundred-mile length of the Metacomet Ridge. At the four sites where *Corydalis flavula* occurs, vegetation composition appears to have stayed relatively stable for decades, persisting in a steady-state, open physiognomy without human intervention or changing land use. There is little evidence that fire has been a factor in maintaining these communities at the four mountaintops in Connecticut: no charcoal layers are evident and historical accounts do not mention summit fires (some users of the areas do build fires, however). Likewise, fire is not considered to be a primary ecological driver on trap-rock ridges generally (Anderson et al. 1999). On nearly bare bedrock, sporadic disturbances, such as windthrow and frost-heaving, interact with chronic selection pressures, such as drought and exposure, to limit recruitment to a hardy and specialized set of plant species. Consequently, an annual plant like *C. flavula* will be highly sensitive to both disturbance and changes in resource availability that occur from year to year, especially at seed and seedling stages (Silvertown 1982, Kalisz and McPeek 1992).

**General ecological questions**

The unusual set of contrasting habitat preferences on the part of *Corydalis flavula* throughout its range -- rich, mesic areas to dry ridge-tops -- begs two major questions regarding the degree of habitat specialization it exhibits, and whether its current distribution reflects strict habitat requirements that must be accounted for in planning for its conservation.
First, how can this species tolerate such environmental extremes, especially in water availability? One might hypothesize that there are, in fact, two differentiated ecotypes of *C. flavula*: one that is limited to rich, mesic areas and the other to high-elevation, relatively xeric areas. The lack of obvious, consistent morphological differences among populations drawn from these two habitat types (Ownbey 1947) would seem to weaken this hypothesis, but comparative genetic analyses and studies of transplanted populations would be needed to test this supposition directly. A simpler explanation may be that the plant requires high levels of mineral nutrients (especially calcium or magnesium), which are readily available in both types of habitats, but can tolerate a wide range of water availabilities. Together with a requirement for warm spring temperatures, this nutrient preference and broad tolerance regarding water could explain the extensive but patchy range of *C. flavula* and its restriction to the warm basalt ridge of Connecticut. Other calciphiles, such as *Elymus trachycaulus* and *Muhenbergia glomerata*, are known to occupy both droughty and very moist sites as long as they can access high levels of mineral nutrients (W. Moorhead, personal communication). High mortality caused by early spring drought at CT .002 in May 2001, however, indicates that *C. flavula* is still sensitive to extreme water shortages.

Second, why are the only New England populations of *C. flavula* restricted to a few mid-latitude trap-rock ridges in Connecticut (a small proportion of available habitat sharing similar bedrock and climatic regimes)? Three alternative hypotheses pertain: 1) *C. flavula* was once more widespread in Connecticut/New England and has since declined; 2) *C. flavula* is not restricted to these areas and we simply have not found other populations; and 3) *C. flavula* has spread into Connecticut via an unknown disperser, probably within the last century and only in a very limited area.

There is little support for the first hypothesis, at least in the historical short-term; *C. flavula* does not appear in herbarium collections from anywhere in New England but Connecticut. *Corydalis flavula* was first described from Connecticut in 1926 (Clark 1926). Moreover, the few occurrences of *C. flavula* recorded in the George Safford Torrey Herbarium for Connecticut (7 collections between 18 May 1946 and 11 May 1996) are exclusively from three mountains where the extant populations all occur (one collection by H. Bertram Lambert in 1963 from Fairfield County contained an uncertain identification as *Corydalis micrantha* Englm. (A. Gray); record supplied by Torrey Herbarium, University of Connecticut). It is conceivable that *C. flavula* was more widespread in New England during past Holocene warming events such as the Hypsithermal (9000 to 3000 years BP). The *C. flavula* populations observed today may be relictual. Palynological studies might reveal pollen of *C. flavula* in cores from more areas around southern New England (but it is unlikely to have been preserved well). Currently, it seems most parsimonious to assume that *C. flavula* has arrived in the New England flora within the past one-hundred or so years, and could even be accompanying recent climatic ('greenhouse') warming trends.

The second hypothesis demands a more thorough search of Connecticut (particularly rocky outcrops in sub-acid to circumneutral bedrock of the central and western highlands)
before it can be eliminated. *Corydalis flavula* has been collected extensively elsewhere in North America, but intensive surveys of the Metacomet Range and the western highlands in the past twenty years have not yielded additional occurrences. However, new state records of rare plant species are continually turning up with new surveys in Connecticut, and in New York, new populations of *C. flavula* have been identified recently with more systematic surveys. *Corydalis flavula* is a very small, ephemeral plant that could easily be overlooked in surveys due to its brief life span and its sparse and often cryptic distribution.

If *C. flavula* is a comparatively recent arrival, the third hypothesis regarding dispersal limitation may also be plausible. *Corydalis flavula* may have entered Connecticut only during a very constrained dispersal event or via a dispersal agent (human or animal most likely) that dropped its seed over a small area. Its most logical route of entry into Connecticut, given the present range of *C. flavula*, is from New York. Thus, it is curious that *C. flavula* does not seem to occur in the western highlands of Connecticut, where numerous other herbaceous spring ephemerals occur on mesic soils and rocky uplands. This disjunction suggests that *C. flavula* was transported to the site and may have skipped other potential colonization sites between New York and middle Connecticut. Agents of long-range dispersal are unknown as yet, but could have transported *C. flavula* overland to its present sites on the Metacomet Range. Alternatively, *C. flavula* may have arrived in Connecticut many times by various means, but has been able to establish only in a handful of sites. If this is true, the warm and mineral-rich Metacomet Range represents particularly amenable habitat for *C. flavula*.

These alternative hypotheses suggest that *C. flavula*, whether a recent or relictual member of the Connecticut flora, is restricted in its distribution to a narrow set of habitat types in this region. In fact, we may never know definitively why *Corydalis flavula* is found only in a fragile narrow belt in middle Connecticut. Until additional populations of *C. flavula* are located (and intensive searches are certainly warranted), it is most pragmatic to study the ecology of the Connecticut populations in this context, and to work to undergird populations within trap-rock ridges in the state. By doing so, many plant species in association with *C. flavula* will similarly be conserved.

**DISTRIBUTION AND STATUS**

**General status**

*Corydalis flavula* is endemic to North America. It exhibits a wide range, extending over a large portion of the eastern United States, from Louisiana and Arkansas north to Connecticut (Figure 1). As a whole, *C. flavula* exhibits a cohesive North American distribution. The species is not reported as "historic" or "presumed extirpated" from any North American regions. Overall, the taxon is ranked globally as G5 (‘demonstrably widespread, abundant, and secure’ -- see Appendix 3) and nationally as N?, with a Canadian national rank of N2 indicating it is vulnerable to extirpation from Canada (The Nature Conservancy and Association for Biodiversity Information 1999).
In the east, Delaware and Connecticut both report *C. flavula* as critically imperiled. Georgia considers it to be vulnerable, and *C. flavula* occurs in only three counties there (Jones and Coile 1988). The taxon extends along the Ozark/Appalachian belt from Virginia to Arkansas and Missouri, through to the mid-western United States, including Nebraska (where it is listed as critically imperiled at the western edge of its range). Extreme northern populations, both listed as imperiled, are found in Michigan and southern Ontario (Catling and Brownell 1999). In Michigan, *C. flavula* is now restricted to Kalamazoo and Calhoun counties in the southeast, with two populations recorded from Berrien County to the southwest along Lake Michigan (cf. Table 2, which shows more occurrences from earlier in the 1900's).

There is considerable uncertainty about the state-level conservation status of *C. flavula* throughout its range, reflected in a number of ranks bearing question marks (see Table 3, below). In the mid-west, for example, *C. flavula* remains unranked in South Dakota, Kansas, Missouri, and Oklahoma. Information on its distribution in Oklahoma and South Dakota are lacking. Herbarium records at the Missouri Botanical Garden hail from the eastern half of the state along the Missouri River (W3-TROPICOS 2000). The taxon occurs in the "east fourth"of Kansas (Stevens 1961). While it is reported from most of the south and eastern-central states, it remains unranked in Ohio, Pennsylvania, Indiana, Kentucky, West Virginia, and Illinois. Little information is available on the status of *C. flavula* in Ohio, where it is not listed. Its congener, *Corydalis sempervirens*, has been listed as "Potentially threatened" since 1990, downgraded from "threatened" status in 1980-1989 (Ohio Department of Natural Resources 2000). Given the overlapping habitats of *C. sempervirens* and *C. flavula*, it seems likely that the latter is sparsely distributed as well. Twenty-six counties record *C. flavula* in Pennsylvania, and it is apparently widespread throughout the southern half of the state (Rhoades and Klein 1993). In Indiana, *C. flavula* is reported from the south and western sectors of the state (Deam 1984). In Kentucky, *C. flavula* is found in most regions of the state except the central and northern portions (Wharton and Barbour 1971). Paul J. Harmon (Botanist, West Virginia Nongame Wildlife and Natural Heritage Programs), reports that *C. flavula* is "an extremely common herbaceous plant species in WV, occurring in possibly every county of our state, and currently vouchedered in 29 of the 55 counties...As our datamanager [sic] said, 'It's common as dirt!'" (correspondence to Christopher Mangels, 5 November 1999). *Corydalis flavula* is also presumed to be secure in North Carolina, where it occurs in 26 counties (Radford et al. 1965).

Interestingly, the species also extends to the alluvial lowlands of Louisiana, Mississippi (Timme 1989), and Florida (Clewell 1985), although specific data on occurrences are lacking because the taxon is not ranked in these states. Such a broad distribution may reflect an unusually broad tolerance for a range of sub-tropical to north-temperate climatic conditions, or considerable micro-differentiation among populations.

Closest to New England, *Corydalis flavula* is found in the highlands of the lower Hudson River Valley of New York state, where it occurs in 14 counties (6 confirmed...
occurrences, 8 suspected occurrences based on herbarium records). The counties bordering Connecticut, including Westchester, Putnam, and Dutchess, contain known occurrences of *C. flavula*. The species is presently on the Watch List of New York State (Young 2000). Steve Young (Botanist, New York Natural Heritage Program) reports that *C. flavula* recently has been observed "a lot in the Hudson Highlands where there were few historical records...so it seems to be expanding" (correspondence to Christopher Mangels, 29 October 1999). He also points out that the species is highly sensitive to changing conditions; thus, a population that was present only in low numbers one year may flourish the next, confounding attempts to assess population trends.

*Corydalis flavula* is listed in the *Flora Conservanda: New England* as a Division 2, regionally rare species (Brumback and Mehrhoff et al. 1996), because its populations number fewer than 20 in the region and reach the edge of the species range. As pointed out by Brumback and Mehrhoff et al. (1996: 243) and echoed by many conservation biologists, "it is important to conserve these edge of range occurrences as part of New England's natural heritage as well as to avoid further shrinkage of these species' entire ranges" and erosion of genetic diversity within the taxon as a whole. It is also of interest that several of the rare species listed as associates of *C. flavula* in Connecticut including *Aristolochia serpentaria*, *Houstonia longifolia*, *Muhlenbergia capillaris*, *Sporobolis heterolepis*, and *Senecio pauperculus* C are also imperiled at the northern or northeastern peripheries of their ranges (TNC and ABI 1999). This pattern suggests that similar factors may explain their common range contractions, and that efforts to conserve one may potentially ensure the protection of several rare taxa simultaneously.

Table 3 below summarizes known occurrences of the taxon range-wide. Natural Heritage state ranks designate many of these occurrences as "SR" (reported but not verified); see Appendix 3. Unverified state records ranked SR are placed in the "unverified" column, while "SR" records with additional confirmation from herbaria and floras are retained in the second column.
<table>
<thead>
<tr>
<th>OCCURS &amp; LISTED (AS S1, S2, OR T &amp; E)</th>
<th>OCCURS &amp; NOT LISTED (AS S1, S2, OR T &amp; E)</th>
<th>OCCURRENCE UNVERIFIED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Connecticut (S1): 4 current occurrences</td>
<td>Arkansas (SR)</td>
<td>Minnesota (SRF)</td>
</tr>
<tr>
<td>Delaware (S1): 1 current occurrence</td>
<td>District of Columbia (S?)</td>
<td>Alabama (SR)</td>
</tr>
<tr>
<td>Michigan (S2): 8 current occurrences</td>
<td>Florida (SR)</td>
<td>Iowa (SR)</td>
</tr>
<tr>
<td>Nebraska (S1)</td>
<td>Georgia (S3?): occurs in 3 counties</td>
<td>Louisiana (SR)</td>
</tr>
<tr>
<td>Ontario (S2)</td>
<td>Illinois (S?)</td>
<td>South Dakota (SR)</td>
</tr>
<tr>
<td></td>
<td>Indiana (SR)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Kansas (SR)</td>
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</tr>
<tr>
<td></td>
<td>Kentucky (S?)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maryland (SR)</td>
<td></td>
</tr>
<tr>
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<td>Mississippi (SR)</td>
<td></td>
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<td></td>
<td>Missouri (SR)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>New Jersey (SR)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>New York (S3): 24 occurrences</td>
<td></td>
</tr>
<tr>
<td></td>
<td>North Carolina (S4): occurs in 26 counties</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ohio (SR)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Oklahoma (SR)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pennsylvania (SR): occurs in 31 counties</td>
<td></td>
</tr>
<tr>
<td></td>
<td>South Carolina (SR): occurs in 7 counties</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tennessee (SR)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Virginia (SR)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>West Virginia (S?): occurs in 29 counties</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. North American distribution of *Corydalis flavula*. States with more than 5 known occurrences are shown in black. States with 1 occurrence (or for which occurrence numbers are unknown) are shaded in gray. There are no states in which *Corydalis flavula* is known to be historic (presumed extirpated).
Figure 2. Extant occurrences of *Corydalis flavula* in New England. Connecticut, the only New England state in which the species occurs, is shown. Towns with one occurrence are shaded in gray. Extant and historical occurrences (from herbarium records at the George Safford Torrey Herbarium, University of Connecticut) overlap completely in distribution.
Table 4. New England Occurrence Records for *Corydalis flavula*.
Shaded occurrences are considered extant.

<table>
<thead>
<tr>
<th>State</th>
<th>Element Occurrence Number</th>
<th>County</th>
<th>Town</th>
</tr>
</thead>
<tbody>
<tr>
<td>CT</td>
<td>.001</td>
<td>Middlesex</td>
<td>Middletown</td>
</tr>
<tr>
<td>CT</td>
<td>.002</td>
<td>New Haven</td>
<td>Wallingford</td>
</tr>
<tr>
<td>CT</td>
<td>.003</td>
<td>Hartford</td>
<td>Berlin</td>
</tr>
<tr>
<td>CT</td>
<td>.004</td>
<td>New Haven</td>
<td>North Branford</td>
</tr>
</tbody>
</table>

**THREATS TO TAXON**

Currently, two of the four populations occur on protected land, and another two appear relatively remote from harmful activities. Thus, no confirmed, imminent anthropogenic threats seem to face this taxon at the sites where it currently occurs in Connecticut. However, two major threats do impinge on the plants at one or more sites: drought and encroachment by vegetation, especially shrubs. The CT .002 population appears to have declined since it was observed in 1999, and in spring of 2001 had completely succumbed to an unusual, six-week-long drought with no evidence of reproduction. At the same time, available habitat for the population is shrinking at this summit, because cover of *Rosa multiflora* and *Viburnum rafinesquianum* has become significantly denser between 1999 and 2001 (confirmed by comparison of reference photos taken by Christopher Mangels and the author). Of particular concern is the prevalence of *Rosa multiflora* and *Euonymous alatus*, invasive species that can rapidly dominate an area (Clark et al. 1998, Westbrooks 1998). The author will be observing this population in future years to document its recovery and the existence of a seed bank at CT .002, but the persistence of *C. flavula* at the site appears to be precarious. The plant's highly restricted range in New England makes it vulnerable to being eliminated from the region if any of these sites are destroyed. Therefore, it is important to identify and prevent both known and potential threats before they negatively impact these few populations.

Several potential threats to *Corydalis flavula* can also be pinpointed. First is the threat of trampling due to heavy use of the Mattabesett hiking trail that passes near to the populations at CT .001, .002, and .003, and horse trails that may traverse CT .004. All-terrain vehicle (ATV) use is particularly heavy at CT .001 and .002 (and present at .003). Day hikers seem less likely to pose a threat to the plants, but foot traffic can trample individual stems. Deer hunters who use the area frequently have erected informal stands off-trail at CT .001 (according to 1999 notes of Paul Vidovich, Preserve Steward for The Nature Conservancy Connecticut Chapter), and may inadvertently trample plants. A stone cairn was found in October 2001. Horseback riding has been identified as a threat on trails within a mile of CT .004 (notes to Natural Resource File, The Nature Conservancy, Connecticut Chapter), but the proximity of horse trails to the *C. flavula* population there is unknown. Garbage has also been deposited at
CT .001 and .002 (1999 notes of P. Vidovich, TNC CTFO), but the extent to which this material harms the plants is unknown. Fire pits used by campers at CT .001 and CT .003 have been observed in the past (notes of Karen Sexton, TNC CTFO and 2001 observations of the author); an accidental fire could kill the population depending upon the time of year in which it occurs. Finally, disturbance (and possible seed predation) by turkeys could affect these plants (W. Moorhead, personal communication), but the scope of this threat remains unknown.

The second potential threat to *C. flavula* is inappropriate land use. While most of the populations occur on public or conservation land, activities adjacent to these parcels may reduce the availability of suitable habitat or be damaging as-yet-undocumented populations. For example, recent timbering near CT .001 may have destroyed potential habitat for *C. flavula*, if it was not carried out to minimize erosion and compaction. Alternatively, such clearing could produce new habitat for *C. flavula*, and this land should be surveyed thoroughly to assess its impact. Connecticut EOs .001 and .003 are relatively well protected from landscape-level alteration. Likewise, these open summits are attractive for the placement of communications towers, which can entail clearing and road-building; several exist on peaks throughout the Metacomet Range, and a tower was being considered at the CT .001 site in 1991. The land-use intentions of the private company owning CT .002 and the utilities owning CT .001 and CT .004 should be assessed.

Finally, we know little about the interactions of *C. flavula* with pollinators, herbivores, and seed dispersers. Changing interactions with these other species, especially at the edge of its range, could limit reproduction and survivorship of *C. flavula*. Critical unknowns related to its conservation biology include: the identity and importance of pollinators, herbivores, and seed dispersers; the level of reproductive output and success at each site; and the long-term threats presented by drought, climatic change, and other forms of disturbance.

**CURRENT CONSERVATION MEASURES IN NEW ENGLAND**

Two of the *Corydalis flavula* sites in New England receive explicit conservation protection. The Nature Conservancy owns the area where the known population of *C. flavula* occurs at CT .001 in Middletown. If other populations exist at CT .002, they most likely occur on Water Company land. The partners named in the Tri-Town land use plan have provided protection for the summit of CT .003. No management actions directed specifically toward conserving *C. flavula* are occurring at either of these sites, however (David Gumbart, personal communication). Sporadic monitoring of known populations has occurred since 1992, but no seed collection, propagation, or formal demographic analyses have been undertaken (Chris Mattrick, NEWFS, personal communication).

Public Act 89-224, "An Act Establishing a Program for the Protection of Endangered and Threatened Species," provides the primary legislative protection for this and other listed species in Connecticut and grants the Department of Environmental Protection the ability to conduct studies and determine actions to protect the taxon from extirpation in the state.
II. CONSERVATION

CONSERVATION OBJECTIVES FOR TAXON IN NEW ENGLAND

*Corydalis flavula* reaches the northeastern edge of its range in Connecticut. Because these populations are quite disjunct from the nearest known populations in eastern New York, they are likely to be genetically distinct due to founder effects, and should be protected to preserve genetic diversity in the species as a whole. Given its unique phenology and ecology, *C. flavula* has probably become an important spring ephemeral resource for pollinators and ants at the four mountain sites at which it occurs in Connecticut. Therefore, it is critical to maintain the vigor and viability of the existing populations. It is not clear if *C. flavula* has been more widespread in Connecticut in the past; certainly, herbarium collections show little evidence of this. Nevertheless, it should be looked for assiduously along other trap-rock ridges in Connecticut and at sites adjacent to New York with comparable habitat to the Hudson Highlands. Until other populations are located, the conservation objectives for this taxon in New England focus on:

- **maintaining the four known populations with an average of 500-1000 individuals each** in 3 years out of every 5, of which at least 75% of plants in each population are reproductive in a given year
- **maintaining at least three sub-populations per site** to insure against extirpation in the event a group of plants is destroyed
- **ensuring that these populations are stable**, by promoting fecundity and bolstering seedling establishment where necessary.

With respect to the first objective, the ideal of maintaining a population of 500 to 1000 stems derives from current population estimates of 500-1000 individuals at three of the four sites, and from generalized estimates of minimum viable population size for other comparable annual plants (Pavlik 1996 and references therein). Because *C. flavula* is an annual that may not form a large seedbank, it is vulnerable to extinction during years of a late spring or late frost (killing stems and limiting pollinator activity) or during periods of low resource availability (droughts, for example, that would kill mature stems or prevent germination of over-wintering seedlings). Such mortality has already been witnessed at CT .002. Moreover, because populations at three of four sites occur near popular human trails on exposed mountain summits, they are highly susceptible to disturbance. Environmental stochasticity can be particularly damaging to plants with a life history like *C. flavula* (Higgins et al. 2000), and findings from other studies of winter annuals indicates that the survivorship of seeds and over-wintering seedlings are the primary drivers of population persistence (Kalisz and McPeek 1992). Therefore, the first primary objective is to maintain as many reproductive individuals as possible to maximize seed output. Given that population numbers demonstrably fluctuate year to year, it is most realistic to seek to maintain high numbers during a majority of years (but not necessarily every year).
The most vigorous and apparently stable populations of *C. flavula* occur at CT .001 and CT .003 (see Table 4), where they are scattered across the summits in a series of clumped sub-populations. It is not surprising that individual stems are widely distributed, because safe sites for seed germination are patchy on these dry mountaintops. If ants are dispersing the seeds (which themselves can adhere together because of their sticky elaiosomes), dense stands of seedlings will most likely establish near ant nests. Far-flung plants can escape mortality, so maintaining several sub-populations of *C. flavula* at each site provides insurance against extinction. While there is no evidence as yet that *C. flavula* exhibits a meta-population structure (*sensu* Levins 1970), a patchy population distribution may be important to overall viability.

The third objective requires a much better understanding of the demography of *C. flavula* populations in Connecticut and the factors that influence juvenile survival. Are populations increasing or decreasing at each site? These trends must be assessed before we can develop projections for the future of the populations and arrive at a precise number of plants to aim for (Schemske et al. 1994). The physical characteristics of the micro-environments most favorable to seedling establishment should be precisely recorded. In addition, ecological studies should be designed to answer the general questions outlined in the "Threats to Taxon" section above.
III. LITERATURE CITED


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IV. APPENDICES


2. An explanation of conservation ranks used by The Nature Conservancy and the Association for Biodiversity Information

**Herbaceous species**

- Agrostis perennans
- Antennaria neglecta
- Anthoxanthum odoratum
- Aquilegia canadensis
- Arabis hirsuta var. pycnocarpa
- Arabis laevigata
- Asclepias quadrifolia
- Asplenium platyneuron
- Aster divaricatus
- Carex pensylvanica
- Carex communis
- Corydalis sempervirens
- Danthonia compressa
- Danthonia spicata
- Dryopteris marginalis
- Fragaria virginica
- Galeopsis tetrahit
- Geranium maculatum
- Geranium robertianum
- Hedeoma pulegoides
- Hepatica americana
- Hystrix patula
- Krigia virginica
- Linaria canadensis
- Muhlenbergia schreberi
- Muhlenbergia sobolifera
- Myosotis verna
- Panicum spp.
- Paronychia canadensis
- Poa compressa
- Poa annua
- Polypodium virginianum
- Rumex acetosella
- Saxifraga virginiensis
- Senecio obovatus
- Schizachyrium scoparium
- Solidago caesia
- Solidago bicolor
- Triodanis perfoliata

**Shrubs**

- Cornus racemosa
- Diervilla lonicera
- Euonymus alatus
- Prunus virginiana
- Rhus typhina
- Quercus ilicifolia
- Rosa multiflora
- Viburnum dentatum

**Trees**

- Acer saccharum
- Carya glabra
- Fraxinus americanus
- Juniperus virginiana
- Quercus prinus
Viola palmata
Woodsia ilvensis
2. An explanation of conservation ranks used by The Nature Conservancy and the Association for Biodiversity Information

The conservation rank of an element known or assumed to exist within a jurisdiction is designated by a whole number from 1 to 5, preceded by a G (Global), N (National), or S (Subnational) as appropriate. The numbers have the following meaning:

1 = critically imperiled
2 = imperiled
3 = vulnerable to extirpation or extinction
4 = apparently secure
5 = demonstrably widespread, abundant, and secure.

G1, for example, indicates critical imperilment on a range-wide basis—that is, a great risk of extinction. S1 indicates critical imperilment within a particular state, province, or other subnational jurisdiction—i.e., a great risk of extirpation of the element from that subnation, regardless of its status elsewhere. Species known in an area only from historical records are ranked as either H (possibly extirpated/presumed extinct) or X (presumed extirpated/presumed extinct). Certain other codes, rank variants, and qualifiers are also allowed in order to add information about the element or indicate uncertainty.

Elements that are imperiled or vulnerable everywhere they occur will have a global rank of G1, G2, or G3 and equally high or higher national and subnational ranks. (The lower the number, the “higher” the rank, and therefore the conservation priority.) On the other hand, it is possible for an element to be rarer or more vulnerable in a given nation or subnation than it is range-wide. In that case, it might be ranked N1, N2, or N3, or S1, S2, or S3 even though its global rank is G4 or G5. The three levels of the ranking system give a more complete picture of the conservation status of a species or community than either a range-wide or local rank by itself. They also make it easier to set appropriate conservation priorities in different places and at different geographic levels. In an effort to balance global and local conservation concerns, global as well as national and subnational (provincial or state) ranks are used to select the elements that should receive priority for research and conservation in a jurisdiction.

Use of standard ranking criteria and definitions makes Natural Heritage ranks comparable across element groups—thus, G1 has the same basic meaning whether applied to a salamander, a moss, or a forest community. Standardization also makes ranks comparable across jurisdictions, which in turn allows scientists to use the national and subnational ranks assigned by local data centers to determine and refine or reaffirm global ranks.

Ranking is a qualitative process: it takes into account several factors, including total number, range, and condition of element occurrences, population size, range extent and area of occupancy, short- and long-term trends in the foregoing factors, threats, environmental specificity, and fragility. These factors function as guidelines rather than arithmetic rules, and the relative weight given to the factors may differ among taxa. In some states, the taxon may receive a rank of SR (where the element is reported but has not yet been reviewed locally) or SRF (where a false, erroneous report exists and persists in the literature). A rank of S? denotes an uncertain or inexact numeric rank for the taxon at the state level.

Within states, individual occurrences of a taxon are sometimes assigned element occurrence ranks. Element occurrence (EO) ranks, which are an average of four separate evaluations of quality (size and productivity), condition, viability, and defensibility, are included in site descriptions to provide a general indication of site quality. Ranks range from: A (excellent) to D (poor); a rank of E is provided for element occurrences that are extant, but for which information is inadequate to provide a qualitative score. An EO rank of H is provided for sites for which no observations have made for more than 20 years. An X rank is utilized for sites that are known to be extirpated. Not all EO’s have received such ranks in all states, and ranks are not necessarily consistent among states as yet.