

## Status Update and Life History Studies on the Regal Fritillary (Lepidoptera: Nymphalidae)

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### Abstract

Eastern populations of the regal fritillary (*Speyeria idalia*) have been declining since at least the late 1940s. New England populations disappeared from north to south, with the last viable colonies occurring on island sandplain grasslands and heathlands off the coasts of Rhode Island and Massachusetts. Extensive field surveys in 1992 and subsequent efforts have failed to locate any colonies in New England. Females are perhaps the most fecund of all butterflies. In this study, eight captive females laid more than 1,300 eggs per female (range 227–2,494), and egg hatch ranged from 19 to 78 percent. The addition of less than 5 percent raw albumin to the honey-water diet of three adult females in 1993 coincided with an increase in daily egg output and hatch. One cohort of laboratory-bred larvae was almost entirely lost to a nuclear polyhedrosis virus. Young violet (*Viola*) leaves were suitable for the establishment of first instars, but mature foliage was not; the later resulted in 100 percent mortality of first instars.

We discuss reasons for the regal fritillary's decline and make management recommendations. Because females frequently oviposit away from the host plant, dense violet colonies should be especially advantageous for the establishment of the minute first-instar larvae. Given the long life of adults and their propensity for nectar, we think that the availability of late-summer nectar will be essential in efforts to maintain or reestablish this striking insect.

### Introduction

With its fiery orange forewings, iridescent blue-black hindwings, and 10-centimeter (cm) wingspan, the regal fritillary was one of New England's most magnificent grassland insects. Although always locally distributed, it formerly occurred in all six New England states (Scudder 1889, Denton 1900, Klots 1951, Opler 1983, 1992). Preferred habitats included marshes and swamp edges, wet meadows, fields, pastures, and native grasslands (Denton 1900, Weed 1926, Clark 1932, Clark and Clark 1951, Klots 1951, Schweitzer 1992, Glassberg 1993; see also Fig. 1). An examination of the numbers of specimens in collections and of accounts in the literature indicates that the species reached its greatest abundance in New England in Massachusetts on the sandplain grasslands of Martha's Vineyard, Nantucket Island, and other offshore islands (Scudder 1889, Jones and Kimball 1943). On the mainland and on Block Island, RI, the species was commonly associated with wet meadows and human-maintained grasslands created by mowing, grazing, and other agricultural practices. As in other *Speyeria*, the larvae are violet specialists. New England's regal fritillary colonies were associated with ovate-leaved violet (*Viola fimbriatula*), lance-leaved violet (*V. lanceolata*), common blue violet (*V. papilionacea*), and birdfoot violet (*V. pedata*) (Schweitzer 1987, Cassie et al. in press; D. Schweitzer pers. comm.).

Adult males begin emerging in mid- to late June, followed one to two weeks later by the first females (Scudder 1889, Clark and Clark 1951, Barton 1993, 1994). Adults are long-lived, with some individuals surviving up to 90 days in the wild (Barton 1993). Although females are believed to pair shortly after emerging from the chrysalis, few eggs are laid until the latter half of August or early September. Eggs hatch after two to three weeks, and the first instars immediately enter diapause, presumably without eating (Edwards 1879, Maynard 1886, Scudder 1889, Weed 1926, Mattoon et al. 1971). Feeding begins in spring, and larvae complete their development by late May or June; the pupal stage lasts an additional two-and-a-half to four weeks (Edwards 1879, Maynard 1886, DLW unpubl. data).

It is not known exactly when the regal fritillary began its decline in New England, but a letter from amateur lepidopterist John Bakeless in the correspondence of Alexander B. Klots (Homer Babbidge Library, Special Collections, Univ. of Connecticut) indicated that viable colonies in Connecticut were already disappearing by the late 1940s. The last known Connecticut colony, located on the Roxbury-Bridgewater town line, disappeared in 1971 (R. Muller pers. comm.). The species demise evidently proceeded from north to south, with the last mainland sightings occurring in the 1970s and early 1980s. By the mid-1980s only six populations remained, all on offshore islands: Block and

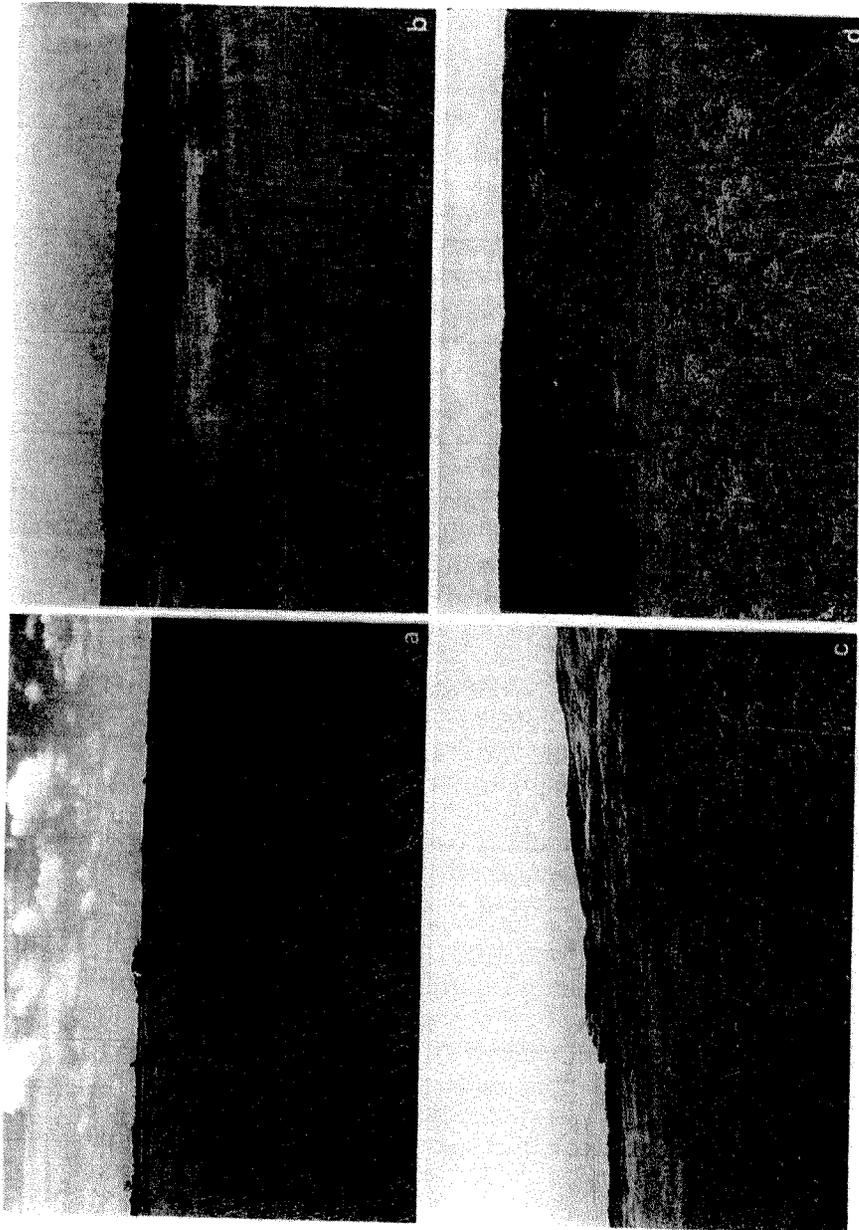


Figure 1. Regal fritillary habitats: (a) sandplain grassland, Katama Plain, Martha's Vineyard, MA; (b) heathland, Nantucket I., MA; (c) coastal pasture, Block Island, RI; and (d) upland grassy meadow, central Pennsylvania.

Conanicut islands in Rhode Island and Martha's Vineyard, Nantucket, Naushon Island, and No Mans Land in Massachusetts (Schweitzer 1987, D. Schweitzer unpubl. data). This pattern of disappearing from north to south was repeated in New York, where the last populations were recorded in the 1980s on Long Island. The last New England regal fritillary was seen by lepidopterist Larry Gall in 1991 on the north end of Block Island. Focused searches of the six aforementioned islands in July and August 1992 yielded no sightings, nor have any been reported since.

In December 1991 a meeting was organized by Scott Melvin, an endangered-species biologist with the Massachusetts Division of Fisheries and Wildlife, to review the status of the regal fritillary in New England and New York. The working group included staff from the U.S. Fish and Wildlife Service, Massachusetts Division of Fisheries and Wildlife, Natural Heritage Programs in Massachusetts, Rhode Island, and Connecticut, The Nature Conservancy, and Massachusetts Audubon Society; university entomologists; and other informed parties. The group recommended a two-step plan of action: first, to establish a captive breeding protocol (if any remaining butterflies were found, genetic stock from indigenous populations could be used to reestablish the species); and second, to study management issues. Only later did participants learn that the regal fritillary was already extirpated from New England and that breeding stock would have to be acquired from outside the region.

Below we discuss results from our efforts in 1992-1993 and 1993-1994 to establish rearing protocols for this butterfly and possible reasons for the species' decline. We discuss briefly two management issues: violet density and nectar availability.

### Methods

Females were obtained from colonies in Pennsylvania (1992;  $n = 3$ ), Missouri (1993;  $n = 2$ ), and Iowa (1993;  $n = 3$ ). Each female was individually housed in a 12-liter (l) cardboard ice-cream carton covered with netting and placed on a bench near a south- or east-facing window. Dried violet leaves and strips of crumpled toweling were provided as ovipositional substrates, and containers were misted with water two or three times a week to simulate rainfall. Females were removed and fed once a day with a sugar or honey solution using the feeding stations of Mattoon et al. (1971). Once a female had repeatedly retracted her proboscis or 15 minutes had passed, she was gently rinsed off with water and returned to her container. In 1992 a small portion of raw chicken-egg albumin (less than 5 percent by volume)

was added to the diet at the onset of egg-laying; in 1993 this was done 20 and 22 days after oviposition had commenced.

Newly deposited eggs were collected every day, placed in plastic vials, and misted once a week to elevate humidities. Eclosion was monitored daily; newly hatched first instars were transferred to sterilized, moistened wooden blocks, placed in a plastic bag, and held in a refrigerator at 2 to 5° C (Mattoon et al. 1971). Blocks were remoistened every six to eight weeks. Larvae in moldy blocks were transferred to blocks that had been autoclaved.

In the hope of establishing a laboratory colony that would produce multiple generations each year, we prevented first instars from entering diapause during the winter by exposing them to long day lengths and warm temperatures (Mattoon et al. 1971). Diapausing first instars were placed on new violet leaves in glass petri plates with moistened filter paper and held below an incandescent light to raise temperatures to 25 to 30° C for 14 hours each day. The filter paper was kept moist to ensure that the humidity remained high, and a new violet leaf was added daily. Larvae exposed to this regimen usually began feeding within a few hours to two days (a small percentage of stragglers took up to 20 days to begin feeding). Larvae fed on all four of the violets we offered: ovate-leaved violet, common blue violet, birdfoot violet (all of which grow wild in New England), and domestic cultivars of the three-colored violet (*V. tricolor*).

Adult offspring from midwestern stock obtained in 1993 were successfully paired in glass enclosures in January 1994. A second generation of larvae was obtained in February, and this cohort was immediately "forced" through to the adult stage.

Two species of violets associated with regal fritillary populations in New England, birdfoot and ovate-leaved violets, were used in a host and leaf preference study. Wild-collected plants of these two species and other violets were grown in the greenhouse at the University of Connecticut. Larval establishment and survivorship were followed for three size-age classes of leaves. For ovate-leaved violet, size-age classes were assigned as follows: young leaves were 1 to 3 cm long, pale green, and had the bases of the leaves curled over the midrib; intermediate leaves were 2 to 4 cm long, had begun to darken, and were mostly uncurled; and mature leaves were 2 to 6 cm long and were fully darkened and expanded. For birdfoot violet, leaf ages were assigned as follows: young leaves were less than 15 millimeters (mm) long and still had the lobes drawn together; intermediate leaves were 15 to 20 mm long, had begun to darken, and had edges that were partially uncurled and not touching the midrib; and mature leaves were fully darkened with the lobes separated. Rearing was done in glass petri plates to which

moistened filter paper had been added. Fresh leaves were provided daily, although a portion of the older leaves was always left as well.

## Results

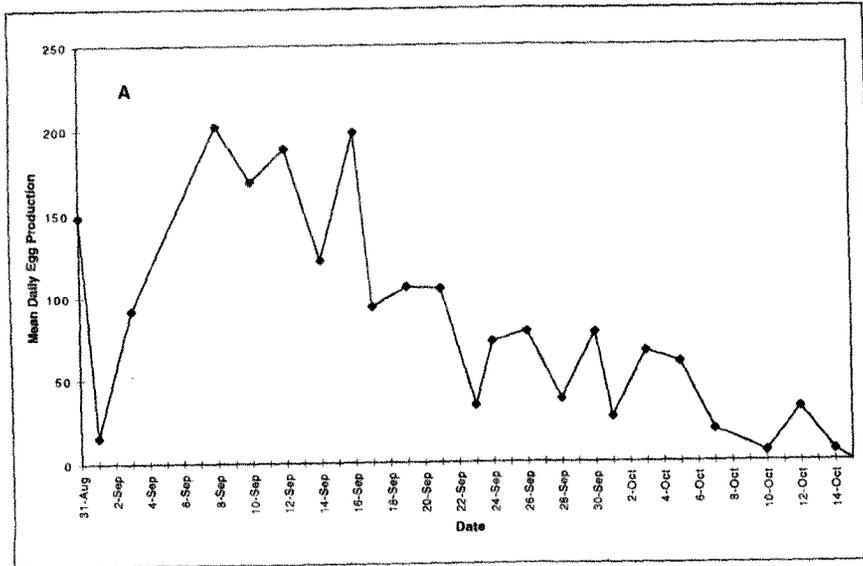
The three regal fritillary females collected 20 August 1992 in Pennsylvania laid an average of 1,447.6 eggs (range 906–1,849); the two females captured in Missouri in late August 1993 laid an average of 1,417.5 eggs (range 341–2,494); and the three females captured in Iowa in late August and early September 1993 laid an average of 1,159.3 eggs (range 227–2,240). The females laid eggs on the sides of the cardboard containers, nylon screening, crumpled paper, and dried violet leaves. They were especially apt to place ova in protected crevices and seams.

Captive females laid eggs over a four- to six-week period, with peak production occurring in the first four weeks of ovipositional activity (Fig. 2A). After the first week in October, egg production was modest. The last eggs were laid on 14 October (1992) and 28 October (1993). All females died within 10 days of their last ovipositional date.

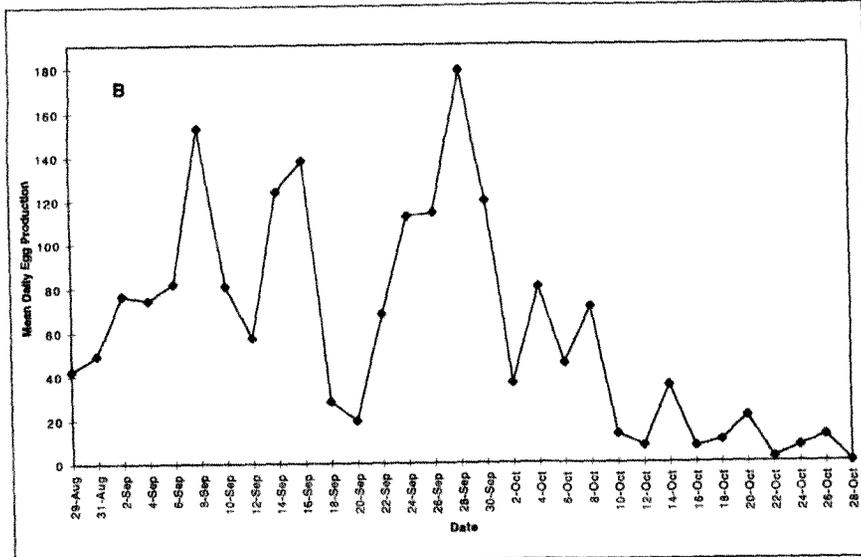
We noted marked fluctuations in daily egg production in both years of the study. In the second year of the study, albumin was added to the diet of one female on day 20 (18 September 1993) and to the diet of two other females on day 22 (20 September 1993). This addition was followed by an increase in fecundity (Fig. 2B). Egg hatch from our eight captive females ranged from 19 to 78 percent (summing across all ovipositional dates for a given female). Percentage egg hatch was similar for our three collections: Iowa 65 percent ( $n = 2$ ), Missouri 62 percent ( $n = 2$ ), and Pennsylvania 65 percent ( $n = 3$ ). Healthy eggs were white or cream colored when laid and darkened to a frosted gray as the caterpillars matured. Eggs that failed to hatch were often yellow and collapsed. The last eggs to be laid were often inviable. As in egg production, we noted considerable fluctuations in egg hatch. In 1993 an increase in hatch coincided with the addition of albumin to the female's honey-water diet, although this observation was largely due to the performance of a single female (Fig. 3).

In 1983, larval development and survivorship were followed for a single cohort of 86 larvae that were started on common blue violet shortly after the larvae emerged from eggs in October. The first five instars were of similar duration, lasting from an average of 3.6 days to 6.6 days. The sixth and final larval instar was much longer, lasting an average of 17.1 days.

After noting that early instars seemed to prefer leaves that were not yet fully expanded, we set up an experiment to examine larval establishment and survivorship on leaves representing three size-age classes

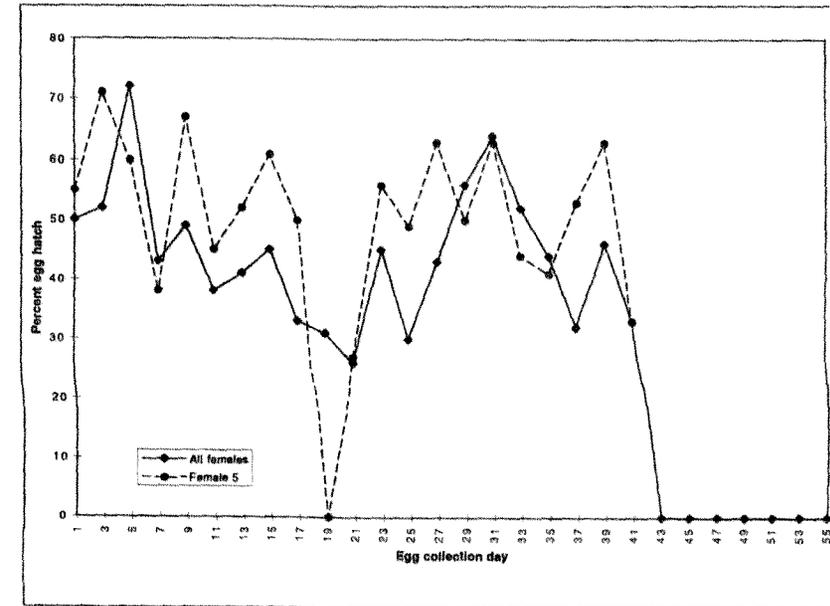


A.



B.

**Figure 2.** Regal fritillary oviposition. (A) Mean daily egg production for three Pennsylvania-captured females (1992); albumin was added to their diet from the first day of oviposition. Two females were laying through the first two dates; three females from 3 Sept. until 7 Oct.; two from 7 to 12 Oct.; and only one thereafter. (B) Mean daily egg production for three midwestern-captured females (1993); albumin was added to their diets on 18 and 20 Sept. One female was laying through the first two dates; three females from 2 Sept. until 6 Oct.; two from 6 to 14 Oct.; and only one thereafter.



**Figure 3.** Percentage egg hatch by date for five midwestern-captured regal fritillaries (1993); x axis gives number of days after a given female began depositing eggs. By day 9, one female had stopped laying; by day 19, two had stopped; albumin was added to the diet of the three surviving butterflies on days 20 and 22. By day 39, two females were still laying; by day 41 only a single female was laying (and all of her eggs failed to hatch).

from ovate-leaved and birdfoot violets. Both young and intermediate leaves proved suitable for larval establishment, but no larvae survived more than 13 days on mature leaves of either violet (Table 1). Larvae often remained and continued to feed on one- to three-day-old leaves even after they had wilted.

### Discussion

The 2,494 eggs laid by one of our captive regal fritillaries from Missouri were more than twice the previous number known to be laid by any butterfly species (1,200 by an Edith's checkerspot [*Euphydrya editha*]; Labine 1968). It is possible that even greater fecundities might have been realized had our captive females been given access to living flowers, soil exudates, and other natural substrates. Compared with other butterflies, the regal fritillary appears to be a "sweepstakes strategist" that has placed a premium on the number of eggs it can produce. However, not all eggs hatch. For the eight wild-caught

**Table 1.** Establishment of first-instar regal fritillary larvae on ovate-leaved violet and birdfoot violet. Stock from Pennsylvania (1992) females. Ten larvae were started on each of the three leaf-classes: young, intermediate, and mature.

Number Surviving	Day 1	Day 5	Day 9	Day 13
<b>ovate-leaved violet</b>				
young leaves	10	5	4	4
intermediate leaves	10	10	9	9
mature leaves	10	4	0	0
<b>birdfoot violet</b>				
young leaves	10	5	5	5
intermediate leaves	10	6	5	3
mature leaves	10	4	1	0

females in our study, the hatch rate was never more than 78 percent and was as low as 19 percent (mean = 64.3%). We cannot explain why females would invest in the production of such a high percentage of eggs that fail. Nor do we know if the unhatched eggs that we observed were infertile or failed to hatch for some other reason. Although adult nutrition of our captive females or improper incubation conditions may explain our low hatch, similar levels of egg failure have been observed in the Mormon fritillary (*Speyeria mormonia*; C. L. Boggs pers. comm.).

It is likely that most mortality occurs in the first instar, which must survive a six- to seven-month diapause having fed only on a portion of its egg chorion (Edwards 1879, Scudder 1889, Weed 1926, Mattoon et al. 1971). Our lab-reared larvae consumed only enough of the chorion to free themselves from the egg. Females are indiscriminate egg layers, ovipositing on grass, soil, and under pebbles, presumably in the vicinity of violets but only rarely placing eggs on violets (Scudder 1889, Clark 1932, Klots 1951, Scott 1986, Barton 1993, B. Barton pers. comm.); thus, the task of locating new violet leaves in the spring must be difficult for the tiny first instars. Flooding, mold, desiccation, predators, and starvation undoubtedly take high tolls, and the high fecundity of the regal fritillary helps compensate for the losses suffered in the first instar. Even when first-instar larvae were supplied with freshly picked foliage, losses were high (50%) in our lab colony (Table 2).

It was exceedingly difficult in our study to get captive-bred adults to pair in the winter. Adults housed in a flight cage (2 x 2 x 2 meters [m]) and provided with high temperatures and humidities, natural light

**Table 2.** Larval development of the regal fritillary. A cohort of 86 larvae was forced out of diapause in early October 1993 (see text). An incandescent lamp was used to raise rearing temperatures to approximately 25–27° C.

	N	Mean (d)	SD (d)	Stage Mort <sup>1</sup> (%)	Cumulative Survival (%)
1st instar	86	4.8	3.6	50	50
2d instar	43	5.9	1.6	0	50
3d instar	43	4.1	1.3	5	48
4th instar	41	3.6	1.2	0	48
5th instar	41	6.6	1.7	0	48
6th instar	41	17.1	2.7	37	32
Pupa	26	—	—	31	21
Adult <sup>2</sup>	18	—	—	—	21

<sup>1</sup>Percent succumbing in a given instar.

<sup>2</sup>Surviving at least to pharate adult.

supplemented with artificial lights, violets, honey water, nectar plants (buddleia [*Buddleia*] and heliotrope [*Heliotropium*]), animal dung, and salts showed little interest in coupling. Of the 50-plus adults bred in December (1993) and January (1994), only two pairings were obtained over the four weeks the adults were housed together. Our inability to achieve mating in the winter remains the principal hurdle to establishing a captive breeding program for this butterfly.

### Reasons for the Regal Fritillary's Decline

The regal fritillary's decline has been noted rangewide. There is only one viable eastern colony, in central Pennsylvania; the range of the midwestern populations also appears to be contracting along the species' western and northern boundaries (Schildknecht 1986, Nagel et al. 1991, Opler 1992, Schweitzer 1992, 1993, Glassberg 1993, Swengel 1993). Explanations for the decline include habitat fragmentation and conversion, fire, hurricane impact, pesticide drift, collecting, competition with other *Speyeria*, and the introduction and/or spread of a parasitoid or pathogen (Nagel et al. 1991, Schweitzer 1992, 1993, Swengel 1993). Perhaps all of these factors have contributed to the demise of one or more populations, yet only the first, and possibly the last, are apt to apply rangewide. The regal fritillary was a likely beneficiary of the extensive agriculture practiced across the eastern United States and southern Canada in the early twentieth century. Pastures,

for example, are favorable areas for violet growth and have often provided habitat for regal fritillaries, especially when bordering marshy lands or ponds. It is likely that this grassland butterfly peaked in abundance in the Northeast during Colonial times when much of the region had been cleared for crops and pasture (Clark 1914, Bell 1985). Conversely, as New England has reforested, suitable habitat for the butterfly has diminished and become increasingly fragmented.

Nagel et al. (1991) recorded an average daily movement of 0.07 kilometers (km) for 23 recaptured regal fritillaries on the Rowe Sanctuary in Nebraska. Barton (1993, 1994) found that males and females occasionally flew long distances: in 1993 the average distance moved by 22 marked adults identified as dispersers was 3.4 km. One male flew 15.8 km in a 12-hour period. In expansive tallgrass prairies, where the regal fritillary reaches its greatest abundance, such movements would not carry it away from suitable habitat as often as would be expected in the East where grasslands are usually small and isolated by forest. Perhaps the regal fritillary persisted longer on New England's offshore islands because dispersing adults were repeatedly turned back by open ocean.

In the spring of 1994 we lost more than 80 percent of a second-generation cohort of middle- to late-instar larvae to a nuclear polyhedrosis virus (NPV). Prior to this we had seen very low mortalities in second to fifth instars (Table 2). The role that this or other pathogens play in low egg hatch, the deformation of wings, or other aspects of the species' decline remains unknown, but certainly pathogens need to be considered since a natural enemy such as a parasitoid or pathogen could account for the observed pattern of decline. Because pathogens tend to act in a density-dependent fashion, a highly specific agent would be expected to occur at very low incidence or to disappear entirely as host populations dwindled (Anderson and May 1980). If regal fritillaries shared pathogens with other fritillaries or more distantly related Lepidoptera, however, the disease agent could remain abundant and cause continued high mortality, even as regal fritillary populations declined to extinction (see Holt and Lawton 1994).

#### **Reestablishment and Management Considerations: Violets and Nectar**

Compared with other butterflies, female regal fritillaries appear to be r-selection strategists with regard to their fecundity and ovipositional behavior. Because females only occasionally oviposit directly onto violets, dense violet growth should promote survivorship of the vulnerable first instars. Tree clearing, mowing, and thatch removal have been employed successfully to favor the proliferation of violets on the coastal prairies where the Oregon silverspot (*Speyeria zerene*

*hippolyta*) has recovered from near extinction (Hammond 1987, 1988, 1989, Hammond and McCorkle 1991). It is important to learn if larval establishment and survivorship are differentially affected by different violet species.

Males and females of all fritillaries are avid nectar feeders (Howe 1975, Dornfeld 1980, Ferris and Brown 1981). In the Mormon fritillary (Boggs and Ross 1993) and zerene fritillary (*Speyeria zerene*; Hammond and McCorkle 1991), adult diet is known to affect both longevity and fecundity. Regal fritillaries feed on nectar throughout their long flight season, from June through September (Barton 1993, 1994). Summer mowings that remove nectar sources such as thistle (*Cirsium*), milkweed and butterfly weed (*Asclepias*), ironweed (*Vernonia*), and others (Scudder 1889, Weed 1926, Nagel et al. 1991, Schweitzer 1992, Barton 1993, 1994) would force adults to move away from emergence sites. Iftner et al. (1992) noted that a colony of regal fritillaries in Ohio disappeared after milkweed was eliminated at the site. In Pennsylvania, an abundance of thistle seems to be especially important for the welfare of the regal fritillary (B. Barton pers. comm.).

Given the descriptive nature of our data, it is difficult to conclude with certainty that the addition of egg albumin to the daily "nectar" solution provided to our regal fritillary females increased fecundity and hatch (Figs. 2B and 3). Even if our results were coincidental, nectar quality and quantity must be essential to the reproductive success of such a long-lived butterfly. Management plans for the regal fritillary should include provisions to ensure the availability of nectar at or near those sites with highest violet densities. Access to nectar, especially in late summer when flowers can be very scarce in New England grasslands, may prove critical in efforts to reestablish or manage this species.

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