Regal Fritillary (*Speyeria idalia* Drury): A Technical Conservation Assessment

Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project

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Acknowledgments

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Author's Biography

Gerald Selby developed an interest in butterflies at an early age while growing up in Pakistan. He received a B.S. in Biology from Sterling College in Kansas in 1976, and an M.S. in Biology (Ecology and Systematics emphasis) from the University of Michigan in 1979. His interest in butterflies was rekindled through contact with Dr. W.H. Wagner (Pteridologist and butterfly enthusiast), and after completing his M.S. he had the opportunity to do additional butterfly collecting in Pakistan during an extended visit. From 1980-1987 he worked for the Clinton County Conservation Board in eastern Iowa, and during that time an exposure to prairie ecology and issues of prairie management gave purposeful direction to what had been a youthful hobby. A work accident left him with paralysis in his right arm, so he entered a Ph.D. program at Iowa State University in 1987, where his dissertation research was focused on the ecology and management of prairie butterflies in southwestern Minnesota. He worked as the Director of Science and Stewardship at The Nature Conservancy in Iowa from 1993-2002, and has been self-employed as an ecological consultant since 2002. Gerald has been actively involved in prairie butterfly surveys and research in Iowa and Minnesota since 1988.

Cover Photo Credit

Regal fritillary (*Speyeria idalia*) male on butterfly milkweed (*Asclepias tuberosa*). Adapted from photograph ©Joseph Hovis (used with permission).

Summary of Key Components for Conservation of the Regal Fritillary

Status

The regal fritillary (*Speyeria idalia*) has been documented from 33 states and five Canadian provinces. It has been assigned a Global Heritage Status Rank of G3 (vulnerable). The rationale for this species' G3 ranking is that despite the relatively large number of extant populations (>100) in the western portion of its range, the regal fritillary ". . . cannot be considered secure . . . because of its very recent large scale decline and range contraction, resulting in a recent loss of approximately thirty percent of historic range, and on-going decline in some or possibly all other parts of its range. . . . There is no convincing evidence the species is stable anywhere although westward it does not appear to be crashing as rapidly as happened eastward from about 1970-1991."

The National Heritage Status Rank for United States populations of regal fritillaries is the same as its global rank (N3), and for Canada this species is ranked NH (possibly extirpated) (NatureServe 2005). State Heritage Status Ranks are presumed extirpated (SX) in seven states, possibly extirpated (SH) in ten states and one province, critically imperiled (S1) in six states, imperiled (S2) in three states, vulnerable (S3) in four states, and apparently secure (S4) in one state. The regal fritillary is not ranked in the remaining two states and four provinces where it has been documented.

Currently there is no federal protection for the regal fritillary in the United States under the Endangered Species Act, but the USDA Forest Service (USFS) has designated it as a sensitive species in Regions 1, 2, 8 and 9. This species is listed as endangered in five states, threatened in one state, and of special concern in four states. Its decline in the East was so rapid that in many states the regal fritillary had disappeared before it could be listed. Still, the regal fritillary does not currently have any legal protection or special concern designation in any of the states comprising Region 2 of the USFS.

Primary Threats

Historic loss, fragmentation, and degradation of the prairie landscape have been the primary factors contributing to the decline and current vulnerability of regal fritillary populations, and continued habitat loss, fragmentation, and degradation are the greatest threats to future populations. Activities that threaten further habitat loss and fragmentation include row crop agriculture, urban development and housing construction, road construction and maintenance, gravel mining, and wind generators. Threats to habitat quality and the availability of critical resources (e.g., nectar plants, larval food plants) include indiscriminant use of herbicides, invasive exotic species, and encroachment by woody vegetation (native and exotic). Fire, grazing, and haying can play important roles in maintaining and shaping prairie ecosystems, so the complete absence of these influences can constitute a threat to the extent and quality of prairie remnants. However, they can also pose direct and indirect threats to regal fritillaries depending on their timing and intensity. Larvae in the leaf litter are extremely vulnerable to direct mortality from fires and indirect mortality from increased exposure after the fires remove the protective litter layer. Improperly timed fires, grazing, and haying can all impact the availability of nectar and larval food resources at critical times. Other more direct threats to regal fritillaries can include extreme weather (e.g., harsh winters, late frosts, unusually cool and wet growing seasons, and severe storms), indiscriminant use of insecticides, disease, and predation. A reduction in fitness resulting from genetic isolation may also pose a long-term threat.

Primary Conservation Elements, Management Implications and Considerations

Regal fritillaries require relatively non-degraded native mixed- and tallgrass prairie, and they cannot survive in the altered landscapes (e.g., row crops, non-native pasture, developed areas) surrounding prairie remnants. Because they do not migrate and have limited dispersal capability, isolated populations that are extirpated are unlikely to be repopulated. Each stage of the life cycle must be completed successfully each year at each site for local populations to persist through time. The small size and isolation of remnant regal fritillary populations make them more susceptible to events that they might have survived in the original prairie landscape. Therefore, management activities need

to be designed to mitigate, not exacerbate, these increased vulnerabilities. Activities that improve the size, quality, and connectivity of prairie remnants should help to ensure long-term survival by reducing the probability of local extinctions, and by increasing the probability of recolonization if local extinctions do occur. The timing, intensity, extent, and duration of management activities such as grazing and prescribed fires need to be adapted to ensure the availability of critical resources (e.g., nectar plants, larval food plants) when they are needed, and to mitigate any direct mortality that might result from those management activities.

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INTRODUCTION

This conservation assessment is one of many being produced for the Species Conservation Project being undertaken by the USDA Forest Service (USFS), Rocky Mountain Region (Region 2) (**Figure 1**). The regal fritillary (*Speyeria idalia*) is the focus of an assessment because the USFS in Region 2 lists it as a sensitive species. Within the USFS, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or in habitat capability that would reduce its distribution [FSM 2670.5 (19)]. A sensitive species may require special management, so knowledge of its biology and ecology is crucial. This assessment addresses the biology of the regal fritillary throughout its range, but emphasizes Region 2 as information permits.

Goal

Species conservation assessments produced for the Species Conservation Project are designed to provide land managers, biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment seeks to provide critical summaries of scientific knowledge, discussion of conservation implications of that knowledge, and an outline of information needs. The assessment does not seek to prescribe management; rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (e.g., management implications). It discusses management recommendations proposed or implemented elsewhere.

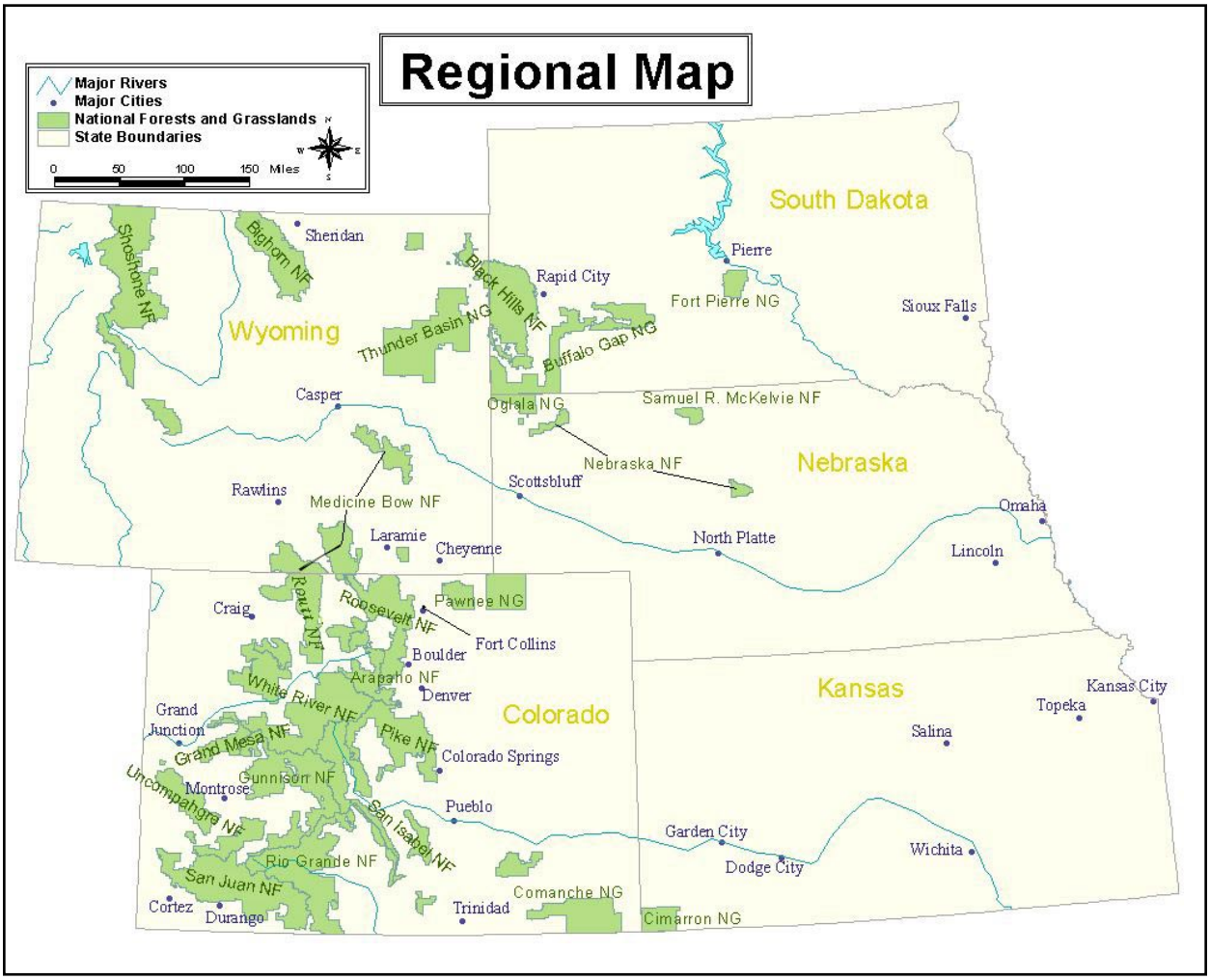

Figure 1. National Forest System lands within USDA Forest Service Region 2.

Scope

The regal fritillary conservation assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although some of the literature on this species originates from field investigations outside the region, this document places that literature in the ecological and social context of the central Rocky Mountain region.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies and butterfly experts. Not all publications on regal fritillaries are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were used when information was unavailable elsewhere, but were regarded with greater skepticism. Unpublished data (e.g., Natural Heritage Program records, research reports, reports from butterfly experts) were important in estimating the geographic distribution of this species. Natural Heritage Program records were fairly incomplete (Colorado, Nebraska, South Dakota) to nonexistent (Kansas, Wyoming) for states in Region 2 , so it was necessary to supplement those records with data from other sources (e.g., published distribution maps, research reports, state experts) to get a more complete picture of the distribution and status of the regal fritillary in the region. These data required special attention because of the diversity of persons and methods used in collection. Often regal fritillary data were only available as county records. More specific data (e.g., dates, locations, population trends) would have been helpful, and attempts were made to obtain additional documentation with some success. However, tracking down and evaluating the accuracy of individual records in raw data form was beyond the scope of this assessment.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct critical experiments that produce clean results in the ecological sciences. Often, we must rely on observations, inference, good thinking, and models to develop and test predictions, and to guide our understanding of ecological relationships. Confronting uncertainty, then, is not prescriptive. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described where appropriate.

Application and Interpretation Limits

Information used to complete this assessment includes studies from across the geographical range of the regal fritillary. Most information should apply broadly throughout the range of the species, but certain life history parameters may vary along environmental gradients. Inferences made from this information regarding threats to the species are understood to be limited in scope (see section above) and take into account the particular conditions present in Region 2. Therefore, information regarding the conservation status of this species pertains specifically to Region 2 and does not necessarily apply to other portions of the species' range.

Publication of Assessment on the World Wide Web

To facilitate use of these conservation assessments, they are being published on the Region 2 World Wide Web site (http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml). Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. In addition, it facilitates their update and revision, which will be accomplished according to protocols established by Region 2.

Peer Review

In keeping with the standards of scientific publication, assessments developed for the Species Conservation Project have been externally peer reviewed prior to their release on the Web. This assessment was reviewed through a process administered by the Society for Conservation Biology, which chose two recognized experts (on this or related taxa) to provide critical input on the manuscript.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

NatureServe (2005) has determined that the regal fritillary is globally "vulnerable" and has assigned it a Global Heritage Status Rank of G3. This ranking was last reviewed on 24 January 2005, and it has not been changed since 24 February 2000. The rational for the G3 ranking states that despite the relatively large number of extant populations (>100) in the western portion of its range, the regal fritillary ". . . cannot be considered secure . . . because of its very recent large scale decline and range contraction, resulting in a recent loss of approximately thirty percent of historic range, and on-going decline in some or possibly all other parts of its range. . . . There is no convincing evidence the species is stable anywhere although westward it does not appear to be crashing as rapidly as happened eastward from about 1970-1991" (NatureServe 2005). It goes on to state that there are probably very few strong metapopulations, and threats to the long-term survival of the isolated remnant populations include habitat fragmentation, extreme weather (e.g., drought or flood), pesticides, and excessive use of prescribed fire. Some of these threats can be mitigated by modifying management practices, with the possibility of reversing the declines. The World Conservation Union does not provide a global classification ranking for the regal fritillary (IUCN 2004).

The National Heritage Status Rank for regal fritillary populations in the United States is the same as its global rank (N3), but for Canada, this species is ranked NH (possibly extirpated). The scattered regal fritillary records from Canada are not thought to represent permanent populations (Layberry et al. 1998), and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assigned no national status designation. Separate western (*Speyeria idalia occidentalis*) and eastern (*S. i. idalia*) subspecies were recognized recently based on morphological and DNA analyses (Williams 2001b). The Global and National (United States) Heritage Status Ranks are critically imperiled (G3T1Q; N1) for the eastern subspecies and vulnerable (G3T3Q; N3) for the western subspecies. Federal protection under the Endangered Species Act may be warranted for the eastern subspecies, which may be reduced to a single viable population in Pennsylvania. All populations in USFS Region 2 are the western subspecies.

There are historic records for regal fritillaries from 33 states and five Canadian provinces. State Heritage Status Ranks are presumed extirpated (SX) in seven states (Connecticut, Delaware, District of Columbia, Maine, New Hampshire, Rhode Island, and Vermont), possibly extirpated (SH) in ten states (Kentucky, Maryland, Massachusetts, Michigan, New Jersey, New York, North Carolina, Ohio, Oklahoma, and West Virginia) and one province (Manitoba), critically imperiled (S1) in six states (Arkansas, Colorado, Indiana, Pennsylvania, Virginia, and Wisconsin), imperiled (S2) in three states (Illinois, Iowa, and North Dakota), vulnerable (S3) in four states (Minnesota, Missouri, Nebraska, and South Dakota), and apparently secure (S4) in one state (Kansas). A state rank has not been assigned (SNR) for Wyoming, and there is no state ranking information for several other states/provinces (Montana, New Brunswick, Nova Scotia, Ontario, and Saskatchewan) with historic records. These states/provinces are at the periphery of the regal fritillary's range, and it is possible that many of the records were simply "strays." The regal fritillary is listed as state endangered in five states (Indiana, Michigan, New York, Ohio, and Wisconsin), state threatened in one state (Illinois), and of special concern in four states (Connecticut, Iowa, Minnesota, and Vermont). The decline in the East was so rapid that in many states, it had disappeared before there was a chance to list it (Williams 1999). Global, national, and state/province status ranks and legal protection status for the regal fritillary are summarized in **Table 1**. State/province status ranks and historic county distribution records are illustrated in **Figure 2**.

The USFS has designated the regal fritillary as a sensitive species in Regions 1, 2, 8, and 9 (USDA Forest Service 2004). The Region 2 sensitive species listing rationale cites the "dramatic reduction in range and numbers" (e.g., extirpation in some fifteen states and declines in most other areas), and the insecurity of most populations due to "fragmentation and isolation of populations and suitable habitat, leading to apparent meta-population collapse" (USDA Forest Service 2001). Specific threats listed include habitat loss to agricultural conversion and development, fire, and grazing.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The regal fritillary was listed as a Category II species (possible candidate for listing) under the United

Table 1. Natural Heritage Program Global, National, and State/Province Status Ranks, and legal protection status (adapted from NatureServe 2005).

	State Rank	Protection Status
Global	G3	—
USA (National)	N3	—
USA (State)		
Connecticut	SX	SC
Delaware	SX	—
District of Columbia	SX	—
Maine	SX	—
New Hampshire	SX	—
Rhode Island	SX	—
Vermont	SX	SC
Kentucky	SH	H
Maryland	SH	X
Massachusetts	SH	—
Michigan	SH	E
New Jersey	SH	—
New York	SH	E
North Carolina	SH	SR
Ohio	SH	E
Oklahoma	SH	SS2
West Virginia	SH	—
Arkansas	S1	—
Colorado*	**S1**	—
Indiana	S1	E
Pennsylvania	S1	—
Virginia	S1	—
Wisconsin	S1	E
Illinois	S2	T
Iowa	S2	SC
North Dakota	S2	—
Minnesota	S3	SC
Missouri	S3	—
Nebraska*	**S3**	—
South Dakota*	**S3**	—
Kansas*	**S4**	—
Wyoming*	**SNR**	—
Montana	—	—
Canada (National)	NH	—
Canada (Province)		
Manitoba	SHB	—

Status Rank Definitions

G1/N1/S1 = Critically imperiled
G2/N2/S2 = Imperiled
G3/N3/S3 = Vulnerable
G4/N4/S4 = Apparently Secure
GX/NX/SX = Presumed extirpated
GH/NH/SH = Possibly extirpated
SNR = Not ranked

Protection Status Definitions

E = Endangered
T = Threatened
SC = Special Concern

State Specific Status Definitions

H = Historic
SR = Significantly rare
SS2 = Possibly threatened
X = Endangered extirpated

— No Status Rank/Protection Status

***USFS Region 2 States**

States Endangered Species Act until 1996 when this category was eliminated (U.S. Fish and Wildlife Service 1996). Currently, it has no federal protection in either the United States or Canada. It does have legal protection in several states outside of USFS Region 2 (**Table 1**), but no legal protection or special concern designations are afforded by any of the states comprising Region 2. Listing the regal fritillary as a sensitive species in USFS

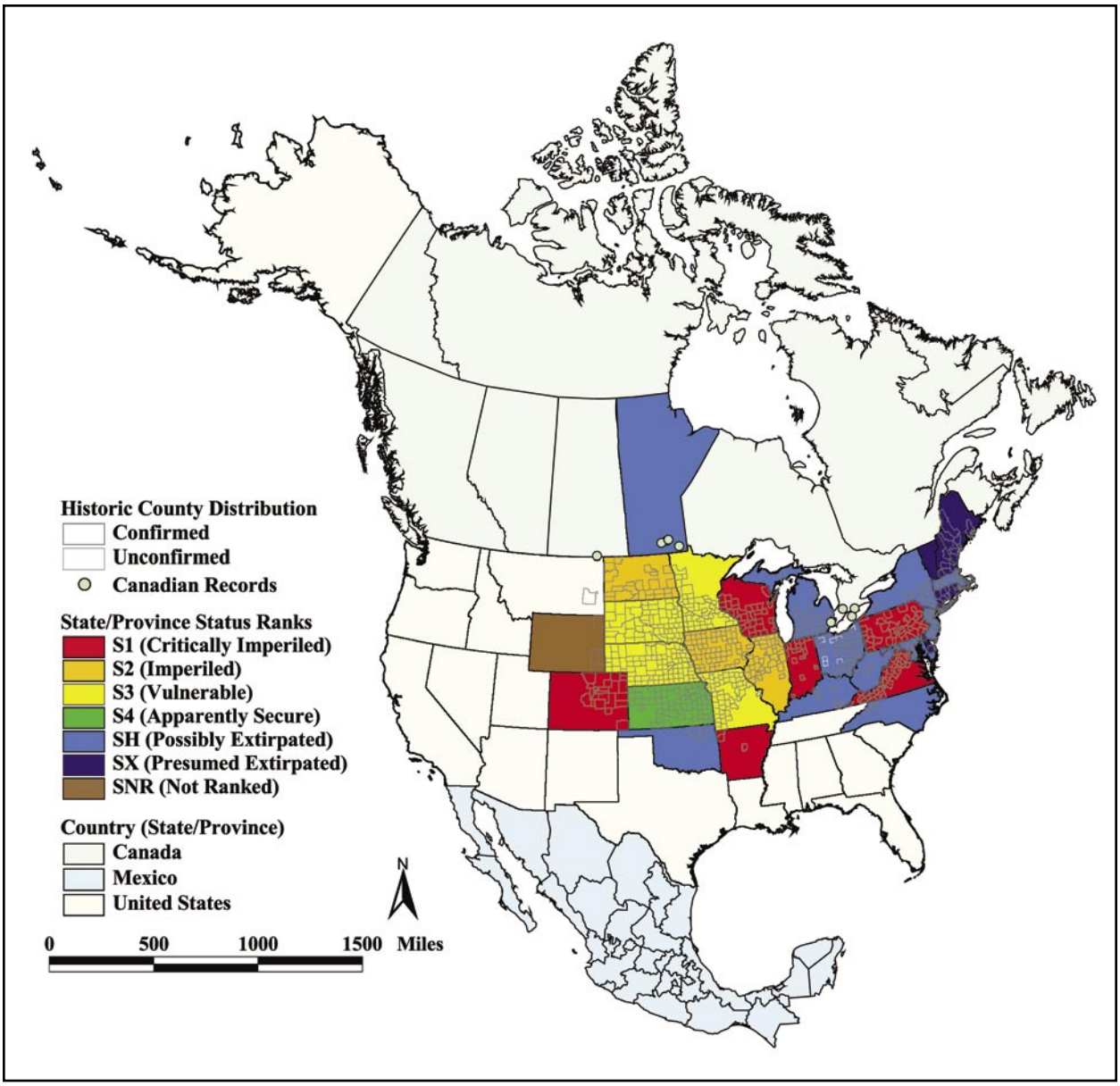

Figure 2. National Heritage Program State/Province Status Ranks and historic county distribution for regal fritillaries in North American (adapted from NatureServe 2005).

Regions 1, 2, 8, and 9 does not confer legal protection, but it does help to ensure that appropriate conservation/management objectives and practices are implemented on those National Forest System lands where it occurs.

A working group was formed in the fall of 1992 to look at the plight of regal fritillaries in New England (Wagner 1995). The working group included representation from the Natural Heritage Programs in Massachusetts and Rhode Island, Massachusetts Audubon, The Nature Conservancy, U.S. Fish and Wildlife Service, and other university scientists and concerned experts. They proposed a recovery program modeled after the 'Oregon' zerene fritillary (*Speyeria zerene*) recovery program (Hammond 1989). It included establishing a captive breeding program and developing habitat management plans to assist in re-establishing the regal fritillary in New England. Unfortunately, the last New England colony disappeared from Block Island coastal island in 1992, and early attempts at captive breeding met with only limited success (Wagner 1995, Wagner et al. 1997).

A five-year (2002-2006) habitat management plan has been developed for the last remaining Pennsylvania population of regal fritillaries at the Fort Indiantown

Gap (FTIG) National Guard Training Center (Zercher et al. 2002). It was prepared for the Pennsylvania Department of Military and Veterans Affairs, Fort Indiantown Gap Environmental Section by the Nature Conservancy of Pennsylvania and the Fort Indiantown Gap Office as part of the Integrated Natural Resources Management Plan for FTIG.

There are also numerous general conservation and management resources available to managers that are relevant to regal fritillary conservation. Opler (1981) and Panzer (1988) developed general guidelines for managing prairies for insect conservation, and Moffat and McPhillips (1993) provide managers with a literature review and general guidebook for managing butterflies in the northern Great Plains. Various research papers (Dana 1989, Dana 1991, Swengel 1996, Panzer 1998, Swengel 1998, Swengel and Swengel 1999, Swengel and Swengel 2001, Panzer 2002) also provide guidelines that can be applied to the management of prairie butterflies and invertebrates. Additional resources can be found in a fairly comprehensive review of literature dealing with prairie insect management issues by Swengel (2001a). The relevance of these resources to the conservation and management of regal fritillaries in the Great Plains prairies associated with National Forest System lands in Region 2 is covered in more detail in the Conservation section of this paper.

Biology and Ecology

Systematics and general species description

Systematics

Classification and Nomenclature

Scientific Name: *Speyeria idalia*
Common Name: Regal fritillary
Class: Insecta (Insects)
Order: Lepidoptera (Butterflies and Moths)
Superfamily: Papilionoidea (True Butterflies)
Family: Nymphalidae (Brush-footed Butterflies)
Subfamily: Heliconiinae (Heliconians and Fritillaries)
Genus: *Speyeria* Scudder, 1872
Specific Name: *idalia* (Drury, 1773)
Subspecies:
Speyeria idalia occidentalis Williams, 2001 (western subspecies)
Speyeria idalia idalia (Drury [1773]) (eastern subspecies)

Controversial or Unresolved Taxonomy: None at the species level; see discussion of subspecies designation (below)

The regal fritillary is the type species for the genus *Speyeria* (type location is New York City, New York) (dos Passos and Grey 1947). This genus is endemic to North America and includes the large fritillary butterflies (Williams 2001a). There are relatively few species in the genus (14 recognized by the North American Butterfly Association [2001], 16 recognized by Opler and Warren [2003]), but most are polytypic (having many forms or types), and there are more than 100 recognized subspecies (Williams 2001a). The regal fritillary is one of three species in the genus that is considered monotypic (having a single type; no subspecies); the other two monotypic species are Edwards' fritillary (*S. edwardsii*) and Diana fritillary (*S. diana*). However, because these species are morphologically distinct and relatively simple to identify, it is possible that variability within each species has simply been overlooked (Williams 2001a, 2001b). Williams (2001a, 2001b) took a closer look at morphological and genetic variability across the range of regal fritillaries, and determined that separate eastern (*Speyeria idalia idalia*) and western (*S. i. occidentalis*) subspecies should be recognized. Morphological analyses were based on museum specimens from three eastern states (New Jersey, New York, and Pennsylvania) and three Midwestern states (Illinois, Iowa, and Nebraska). DNA analyses were based on material obtained from live specimens from a single population in an eastern state (Pennsylvania) and from several populations in each of eight Midwestern states (Illinois, Iowa, Kansas, Minnesota, Missouri, Nebraska, South Dakota, and Wisconsin). Williams did not have access to genetic and morphological data for the only other extant eastern population in Virginia. That population was presumed to be the eastern subspecies, but he did not make a formal determination of its taxonomic status. More recent examination of morphological data suggests that the Virginia population is actually the western subspecies (Ferster personal communication 2005a, Hovis personal communication 2005). There is still uncertainty about the taxonomic status of some extant and historic populations at the interface between the eastern and western subspecies (NatureServe 2005). An updated genetic study by the Philadelphia Academy of Natural Science is in progress (Hovis personal communication 2005). Based on museum specimens from a more representative sample of populations from eastern states, this study should help to clarify those taxonomic issues. All populations in USFS Region 2 are the western subspecies.

For this manuscript, butterfly nomenclature follows Opler and Warren (2003) for scientific names, and the North American Butterfly Association (2001) for English names. Plant nomenclature follows the National Plant Data Center (USDA Natural Resources Conservation Service 2005).

General species description

Royer and Marrone (1992) described adult regal fritillaries as "unique and unmistakable." NatureServe (2005) states that no butterflies "anywhere in the world" resemble them and that the dorsal surface of their hindwings is "absolutely unique." They are large butterflies about the size of a monarch (*Danaus plexippus*). Their wingspan ranges from 6.8 to 9.3 cm (2.69 to 3.63 inches) in the West (Opler and Wright 1999), and from 7.9 to 10.5 cm (3.13 to 4.13 inches) in the East (Opler and Malikul 1992). Females are slightly larger than males. The dorsal surface of the forewings is predominantly tawny orange with black borders, and it has a submarginal row of inwardly pointing chevron-shaped spots that are creamy white in females and tawny orange in males (**Figure 3**, upper). The dorsal surface of the hindwings is "velvety, blue-black" with two bands of spots, and "cannot be mistaken for any other species" (Klots 1951). Both bands are creamy white in females, but in males the outer band is fulvous or tawny orange (**Figure 3**, upper). The ventral wing surfaces are olive brown to black with bold silvery white spots (**Figure 3**, lower). Other large orange butterflies (e.g., monarchs or other large fritillary species) might be confused with regal fritillaries at a distance, but usually the distinctive dark dorsal surface of their hindwings is easily observed when they are on the wing. The ventral wing surfaces are also unique but not as apparent when viewed from a distance. [This description was adapted from Klots (1951), Royer and Marrone (1992), NatureServe (2005).]

Regal fritillary eggs are similar to the eggs of other fritillaries such as the Diana and great spangled (*Speyeria cybele*) fritillaries (**Figure 4**, upper left; great spangled fritillary egg illustrated). Healthy eggs are "white or cream colored" when they are laid and then darken to a "frost gray" as the developing larvae mature, but non-viable eggs are "yellow and collapsed" (Wagner et al. 1997). Edwards (1879) provides the following technical description for the eggs: "Shaped like that of *Diane* and *Cybele*; conoidal, truncated, rounded at base, the sides well rounded; depressed at summit; marked vertically by about 18 vertical ribs, somewhat wavy, half extending from base to summit, the remainder ending irregularly at about three-fourths the distance from the base; between each pair of ribs are equi-distant, transverse, slightly raised striae."

Regal fritillary larvae are about 2.03 mm (0.08 inches) long when they hatch, and they reach a length of 44.45 mm (1.75 inches) when fully developed (Edwards 1879). Scott (1986) describes regal fritillary larvae as ". . . ochre-yellow to orangish, yellow on the rear, with a black middorsal line, black blotches in front of the dorsal and subdorsal spines, two black transverse lines on each segment behind the spines, and yellowish middorsal and lateral stripes, the dorsal spines silvery at the base, the subdorsal and lateral spines orange at the base; head black, orangish on top rear" (**Figure 4**, lower). The pupae (chrysalises) are about 27.94 mm (1.10 inches) long (Edwards 1879), and are described by Scott (1986) as ". . . light mottled brown tinged with pink, with small black spots on the wings and thorax, short dorsal cones, and yellow transverse bands on the abdomen" (**Figure 4**, upper right).

Distribution, abundance, and population trends

Global perspective

The historic range for the regal fritillary extended from southeastern Montana to Maine in the north, with scattered records just across the border in Canada, and from eastern Colorado to northwestern North Carolina in the south (**Figure 2**, **Figure 5**). Three major "regions" or "range components" can be recognized within this broad range (Williams 1999, Williams et al. 2003):

1) **Eastern –** Michigan and Indiana east to New England; historically isolated; two extant isolated populations in Pennsylvania and western Virginia.

2) **Midwest prairies –** Minnesota, Iowa, and Missouri east to Wisconsin, Illinois, and western Indiana; scattered isolated populations in a more recently (since 1860's) fragmented prairie landscape.

3) **Great Plains –** North Dakota south through Kansas and western Missouri, and west to eastern Colorado and Wyoming; more abundant and less isolated populations in relatively continuous habitat throughout most of this region; populations at the periphery of the region tend to be more isolated.

Figure 3. Regal fritillary male dorsal (top, left), male ventral (bottom, left), female dorsal (top, right), and female ventral (bottom, right). Photographs copyrighted Gerald Selby.

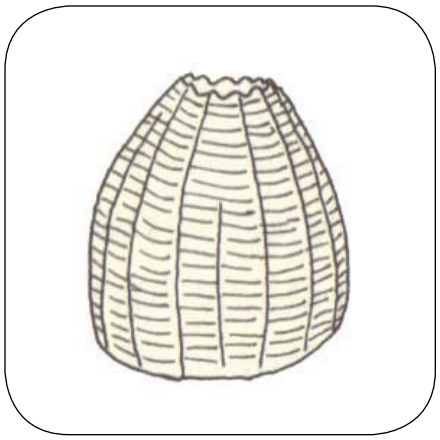

Figure 4A. Egg illustration from James A. Scott, The Butterflies of North America, C 1986 by the Board of Trustees of the Leland Stanford Jr. University. Used with permission of Stanford University Press, www.sup.org.

Figure 4B. Pupa photo from J. Richard and Joan E. Heitzman, Butterflies and Moths of Missouri, C1987 by the Conservation Commission of the State of Missouri. Used with permission.

Figure 4. Great spangled fritillary egg (top left; similar to regal fritillary), regal fritillary pupa (top right), and final instar larva (bottom). Egg illustration from Scott (1986); Pupa photo from Heitzman and Heitzman (1987); Larva photograph ©Nathan Brockman. Used with permission.

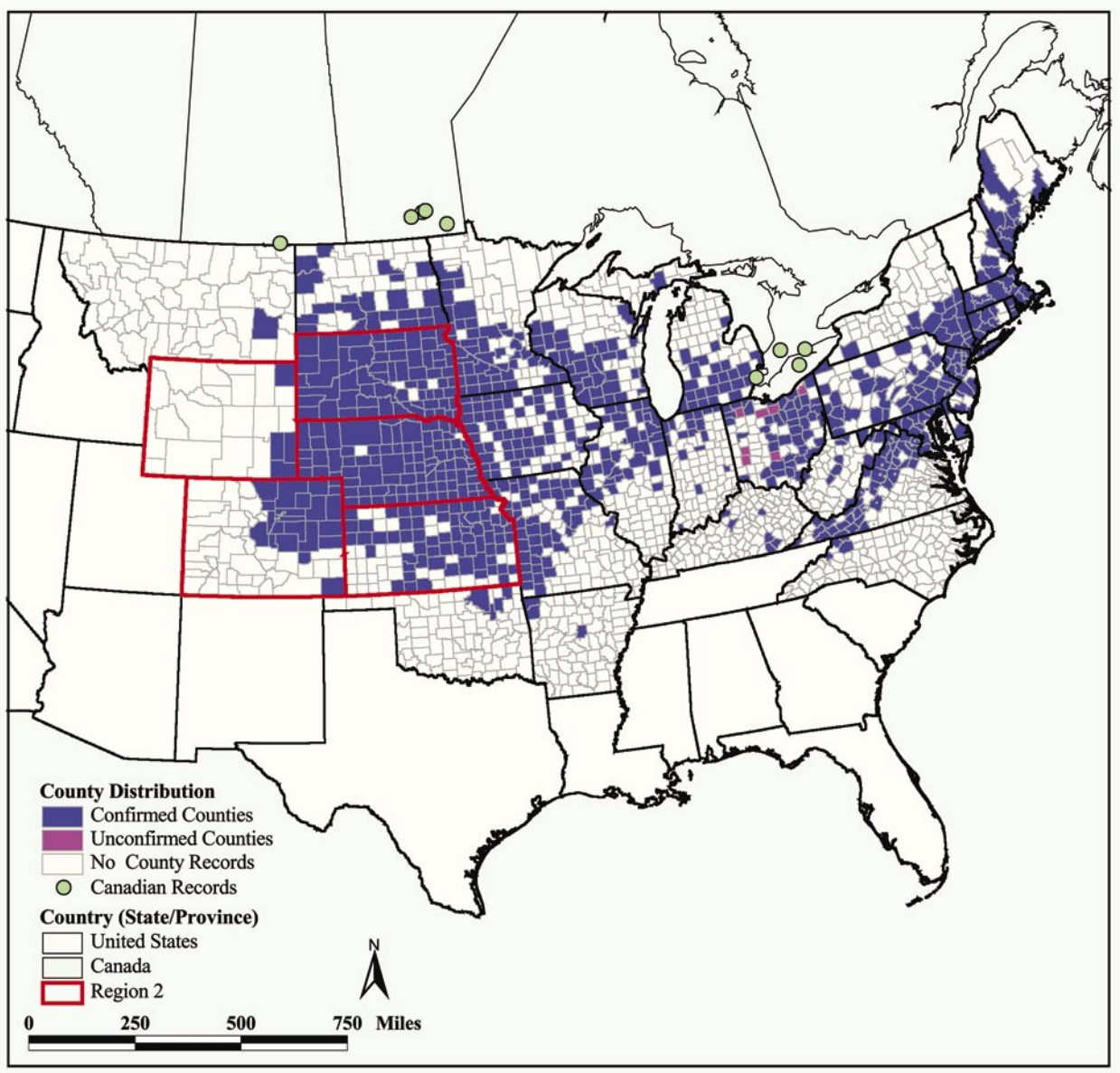

Figure 5. Historic county distribution for regal fritillaires throughout their range in North America.

Range-wide status and population trends

The historic range of regal fritillaries includes records from at least 760 counties in 33 states and five Canadian provinces (**Figure 5**). This range extended from eastern Colorado to Maine, but in recent years, regal fritillaries have experienced dramatic large-scale population declines and range contraction. These declines have achieved catastrophic levels in the East, and have raised concerns about the potential for similar declines in western populations. The range of regal fritillaries east of Illinois has been reduced from at least 270 counties in 18 states to three populations in three states (Indiana, Pennsylvania, and Virginia). These losses started at the northeastern extent of the range (New England states) and proceeded to the south and west.

Regal fritillaries may have never been abundant in the extreme northeastern portion of their range. As early as 1884, they were described as uncommon and restricted to the western portion of Maine (Fernald 1884). Viable colonies in Connecticut were starting to disappear by the late 1940's (Wagner et al. 1997), and the disappearance of populations in other New England states was apparent by the 1950's (Wagner 1995). The last Connecticut colony disappeared in 1971, and the last mainland sightings in New England were in the 1970's and early 1980's (Wagner et al. 1997). By the 1980's there were only six populations remaining on

offshore islands of Massachusetts and Rhode Island (Wagner 1995, Wagner et al. 1997). Several of these populations experienced severe population declines in the late 1980's to 1990 (Dunwiddie and Sferra 1991), and the last New England colony was seen on Block Island coastal island in 1991 (Wagner 1995, Wagner et al. 1997). Habitat fragmentation was probably the major factor responsible for the New England population declines on the mainland, but collecting and gypsy moth (*Compsilura concinnata*) spraying may have been the final factors in the loss of several extinction prone populations (Schweitzer 1993). Offshore island populations were also impacted by habitat loss due to development (e.g., summer homes) and succession resulting from fire suppression and the elimination of grazing. The final blows to those populations may have been the combined impacts of salt spray damage from hurricanes Gloria in 1985 and Bob in 1991, and cold, damp springs in 1989 and 1990 (Schweitzer 1993).

A similar north to south disappearance was repeated in New York (Wagner et al. 1997), and has extended as far west as Indiana. In Pennsylvania, there were 40 known historic populations, and all but one population was extirpated between 1930 and 1992 (Barton 1995, Zercher et al. 2002). This Pennsylvania population is the last confirmed extant and viable population of the eastern subspecies (Williams 1999, 2001a, 2001b), and it is the focus of considerable effort to monitor it and to implement conservation measures (Zercher et al. 2002, Ferster 2005b). The only other extant regal fritillary population east of Indiana is a small colony in western Virginia. It was too small to allow for sampling in the morphological and genetic analyses used for the original subspecies determination (Williams 2001b), so its formal taxonomic status remained undetermined. This population has been presumed to be the eastern subspecies (NatureServe 2005), but a more recent examination of morphological traits of specimens from this population suggest that it is actually the western subspecies (Ferster personal communication 2005a, Hovis personal communication 2005).

Similar declines have occurred as far west as Indiana. In Ohio, regal fritillaries were at one time "common throughout" the state (Iftner et al. 1992). Shuey et al. (1987a, 1987b) state that they were still relatively secure in the southeastern counties, but there were no recent records from the northwestern counties and only a few north-central records since 1970. They suggested the potential for continued general decline in the state, which was unfortunately realized much sooner than anticipated. Shuey (personal communication 2004) is unaware of any documented regal fritillary observations in Ohio since the 1980's, and the species has probably been extirpated from the state (NatureServe 2005). Although regal fritillaries have been documented from 25 counties concentrated in the southern portion of Michigan, they have always been scarce there (Nielson 1999) and have not been documented in the state since 1980 (Cuthrell personal communication 2005). Most historic regal fritillary records for Indiana are from the northern portion of the state. They have been described as "uncommon to rare in widely scattered counties" and absent in some years (Shull 1987). Currently, there is only one remaining metapopulation near Indiana's border with Illinois in the northwest corner of the state. This metapopulation was small in the early 1990's, but it has actually expanded in recent years to an approximately 25 square mile area (Shuey personal communication 2004).

Swengel (1993) describes states immediately to the west of Indiana and Michigan as the ". . . tension zone between the wave of extinction from the East and apparent but localized stability in populations westward." Regal fritillaries have also experienced declines throughout the western portion of their range, but these declines are progressively less dramatic from the eastern portion of the Midwest to the heart of the Great Plains. As one moves west through the Midwest and into the Great Plains, habitat fragmentation decreases, the size and number of prairie remnants increase, and regal fritillary populations experience a corresponding increase in their size, number, and long-term viability.

Regal fritillaries have been documented from 33 counties in the northern half of Illinois (Irwin and Downey 1973, Sedman and Hess 1985, Bouseman and Sternburg 2001, NatureServe 2005, Opler et al. 2006). Their distribution in west-central Illinois was described as "spotty", with populations that were relatively "common and widespread" in sand dune and floodplain areas of Mason and Cass counties, but small elsewhere (Sedman and Hess 1985). The statewide distribution and status of regal fritillaries are described as "locally common to scarce" in the northern third of the state (Bouseman and Sternburg 2001). They are primarily associated with sandy native prairie, where they occur as scattered populations that fluctuate dramatically between years of relative abundance and scarcity (Bouseman and Sternburg 2001). Regal fritillaries have state protection as a threatened species, and Sedman and Hess (1985) suggest the need for habitat preservation to ensure their survival in the state.

Regal fritillaries have been reported from 37 counties in southern and western portions of Wisconsin (Masters 1975, Hennessey and Celebreeze 1995, Swengel 2001b, Swengel 2001c, Swengel 2004, NatureServe 2005, Wisconsin Department of Natural Resources 2005b, Opler et al. 2006). They have been associated with dry prairie in the Central Plains, Southeastern Ridges and Lowlands, and Southwestern Upland natural divisions of the state (Ferge 2002). Good data on the historic distribution and status of regal fritillary populations are not available, so it is difficult to make inferences about historic trends (Swengel and Swengel 2001). However, regal fritillaries were already considered scarce and localized prior to 1970 (Ebner 1970), and they have apparently experienced even more serious declines in recent decades. During the 1970's and 1980's, regal fritillaries were still present in 33 counties, but in 1994 and 1995, they were found only at 11 sites in four counties during status surveys conducted at more than 70 sites in 23 counties (Hennessey and Celebreeze 1995). Based on those surveys, they recommended that the state protection status be changed from threatened (1989 listing) to endangered; the status was changed in 1997 (Swengel 2004, Wisconsin Department of Natural Resources 2005a). Several populations in Wisconsin have been monitored regularly since 1990 (Swengel 2001c, Swengel and Swengel 2001, Swengel 2004). Numbers have varied significantly from year-to-year and from site-to-site, but average numbers for all sites have been trending upwards from 1999 to 2003 (Swengel 2004). These positive trends may reflect the implementation of more favorable management practices (e.g., less aggressive fire regimes, "permanent non-fire refugia", alternate practices such as brush cutting and light grazing), and suggest the important role that proper management can play in slowing, perhaps even reversing, the current wave of regal fritillary extinctions (Swengel 2004).

Regal fritillary populations are still highly fragmented further west in southeastern Minnesota, eastern Iowa, and northeastern Missouri, but they are larger and less fragmented in the western portions of those states. In Minnesota, historic records are located southwest of a line from the southeast corner to just south of the northwest corner of the state, and there are Natural Heritage Program element occurrence records from 46 out 87 counties (Minnesota Natural Heritage Program 2003). Most records are concentrated in the southwest quarter and further north along the western edge of the state, but there are also more scattered records in the southeast quarter (**Figure 5**). Less than one percent of the original 20 million acres of tallgrass prairie remains in Minnesota, and regal fritillaries have only been recorded from 28 counties in the last 20 years (Mason 2001). Regal fritillaries can be locally abundant in southwestern Minnesota (Selby and Glenn-Lewin 1989, Selby 2006b), and populations can be found on many prairie remnants (Reiser 1997, Selby 2006b). In many areas, however, they tend to occur in low densities and are threatened by continued habitat destruction (Mason 2001).

Regal fritillaries have been documented from 60 of 99 counties in Iowa (**Figure 5**) (Nekola 1995, Debinski and Kelly 1998, Iowa Natural Heritage Program 2005, Schlicht personal communication 2005, Opler et al. 2006). Prior to settlement, about 85 percent of Iowa was covered with tallgrass prairie, and regal fritillaries were probably abundant throughout the state. Today, less than 0.1 percent of the original 30 million acres of prairie remains (Smith 1990), and most extant regal fritillary populations are restricted to small isolated prairie fragments where their long-term survival is uncertain. Recent surveys have suggested that regal fritillaries might be declining in the state. In the 1990's, the Iowa Department of Natural Resources failed to find regal fritillaries in several counties where they had occurred in the past (Schlicht and Orwig 1998), and in 1995 they were only found at 11 out of 52 prairie remnants surveyed in the southern two-thirds of the state (Debinski and Kelly 1998). Only five of those prairie remnants had population estimates of more than 50 individuals. In 2005, regal fritillaries appeared to have disappeared from Kalsow Prairie State Preserve (Selby 2006a), one of those five sites where Paul Hammond had estimated a population size of about 500 in 1995 (Debinski and Kelly 1998). Regal fritillaries appear to be more secure in northwest Iowa and along the western edge of the state in the Loess Hills. In recent surveys of about 16 sites in northwest Iowa, regal fritillaries were found at all but two of the sites surveyed (Selby 2000, 2004a, Selby 2006a). Populations in the Loess Hills are doing quite well in the north, but are progressively smaller with decreasing amounts of prairie towards the southern end of the Loess Hills, and are rare to absent in the southern counties (Selby 2003a, 2005).

Regal fritillaries have been documented from 50 of 105 counties in the northern and western portions of Missouri (**Figure 5**; Missouri Department of Conservation 2004, Koenig personal communication 2005, Opler et al. 2006). They are locally abundant on larger prairies in central and western portions of the state, but less common in the north, and mostly absent from the Ozarks and Mississippi lowlands (Heitzman and Heitzman 1987, Heitzman personal communication 2004). Regal fritillaries were doing "very well" on

many Missouri prairie remnants visited in 2004 by Koenig (personal communication 2005). He noted that they were the only prairie-specialist butterfly that was common, and they were frequently the most common butterfly on the prairie. The Missouri Department of Conservation (2000) provides the following assessment of the status of regal fritillaries in the state: "Although the regal fritillary is rare in Missouri, its population in the state is stable due to prairie conservation and management."

There are historic records for regal fritillaries in several other states at the periphery of the range in the West, but there are very few data documenting their status and it is unlikely that they represent breeding populations with long-term viability. The eastern Montana record at the northwestern edge of the regal fritillary range is based on a single specimen collected by Wiley in 1894 at Miles City in Custer County (Wiley 1894, Elrod 1906). Elrod (1906) assumed that regal fritillaries should be found in the eastern part of the state, but documentation for additional more recent records was not found. The Montana Natural Heritage Program lists regal fritillaries as "accidental/nonregular" in the state; consequently, they do not track them and there are no records in their database (Maxell personal communication 2005).

Immediately to the east in North Dakota, there are historic regal fritillary records from 22 of 53 counties, most of which are in the southern portion of the state (Royer and Marrone 1992, Stanford and Opler 1993, Royer 2004, Opler et al. 2006). Regal fritillaries historically occurred regularly in southwestern counties (Royer 1988), but all observations in the 10 years prior to 1992 were restricted to localized virgin prairies south of Interstate Highway 94 and east of the Missouri River Valley (Royer and Marrone 1992). They are still abundant within the Sheyenne National Grassland (Royer 1988, Orwig 1997, Swengel and Swengel 1999, Spomer 2001, Spomer 2002, Spomer 2004). It was assumed that there were no breeding populations of regal fritillaries north of Interstate Highway 94 or west of the Missouri River, but more recent observations at Cross Ranch in Oliver County (Orwig 1994) and at the Little Missouri National Grassland in McKenzie County (Royer 2003) suggest the possibility that there could be breeding populations in the west-central portion of the state. Royer and Marrone (1992) concluded that regal fritillaries were not in imminent danger of extinction in either North or South Dakota, but they could be in jeopardy within a few decades if trends continued.

At the southwestern extent of their range, regal fritillaries have been documented from four counties in northeastern Oklahoma and three counties in northwestern Arkansas (Opler et al. 2006). In Oklahoma, they are listed as possibly extirpated (SH) by NatureServe (2005) and as SS2 (special concern with the possibility of being threatened for extirpation, but needing additional information) by the Oklahoma Natural Heritage Inventory (Oklahoma Natural Heritage Inventory 2001, 2003). Regal fritillaries are listed as critically imperiled (S1) in Arkansas, but no county element occurrences are listed (NatureServe 2005), and they are not included in the Arkansas Natural Heritage Commission's list of "Animal Species of Special Concern in Arkansas" (Arkansas Natural Heritage Commission 2005).

There are historic regal fritillary records from five Canadian provinces across the northern portion of their range, but there are probably no permanent extant populations in Canada (Gregory 1975, Gregory 1983, Layberry et al. 1998, Canadian Biodiversity Information Facility 2003). Fresh (e.g., recently emerged) specimens caught near Culross, Manitoba in 1986 and 1987 suggested the possibility of a temporary colony, but this species has not been documented from that area since then. The most recent documentation for regal fritillaries in Canada was a worn specimen collected from Saskatchewan in 1998; it was assumed to be a stray blown in by very strong southwesterly winds (Canadian Biodiversity Information Facility 2003).

Regional distribution, abundance, and population trends

Region 2 is included in the "Great Plains" portion of the regal fritillary's range. Status ranks for states in Region 2 are apparently secure (S4) in Kansas, vulnerable (S3) in Nebraska and South Dakota, critically imperiled (S1) in Colorado, and not ranked (SNR) in Wyoming. Kansas, Nebraska, and South Dakota make up the heart of the Great Plains portion of the regal fritillary range, where their habitat tends to be less fragmented and populations are more abundant and less isolated. Regal fritillaries can be abundant in those areas (mostly the eastern two-thirds of these states) where adequate amounts of quality native prairie remain (Johnson 1973, Ely et al. 1986, Marrone 2002). Still, in many areas (especially in the West), this species is declining due to the loss and fragmentation of its grassland habitat and associated larval food sources (Wright et al. 2003, South Dakota Natural Heritage

Program 2005b). Regal fritillaries continue to do well in the area in and around Fort Pierre National Grassland in central South Dakota. Although there is good potential for healthy populations of this species on other units of the Nebraska National Forest in Nebraska and South Dakota, most National Forest System lands in Region 2 are at the western periphery of the regal fritillary range, and there are very few documented records from them (**Figure 6**). Populations tend to be smaller and more isolated at these distributional limits, and surveys are needed to determine their status in these areas. An overview of the distribution and abundance of regal fritillaries in each state in Region 2, and their likely occurrence on National Forest System lands follows.

Kansas (S4): Regal fritillaries remain relatively abundant in Kansas (Delisle personal communication 2005), where they have been documented from 66 of the 105 counties (Ely et al. 1986, Dole et al. 2004, Opler et al. 2006). The species is not tracked by the Kansas Natural Heritage Program due to its relative abundance. They have completed the State Ranking Form but not the Characterization Abstract (Delisle personal communication 2005). Ely et al. (1986) stated that regal fritillaries can be locally abundant, but they are generally uncommon in the eastern two-thirds of the state and rare westward. More recently, Dole et al. (2004) described regal fritillary abundance in the state as rare to locally common. They can be relatively abundant at larger prairie remnants, but they are among several Kansas prairie butterflies that are experiencing contracting ranges and becoming threatened or endangered in portions of the state because of continued loss and degradation of their habitat, and pesticide use (Wright et al. 2003). Their numbers fluctuate dramatically from year to year, and in 1997 they were so abundant at Konza Prairie (Geary, Pottawatomie, and Riley counties) that Wright et al. (2003) describe being able to ". . . stand in one spot and look out across the prairie at hundreds of individuals floating among the milkweeds (*Asclepias* spp.) and coneflowers (*Echinacea* and *Ratibida* spp.)."

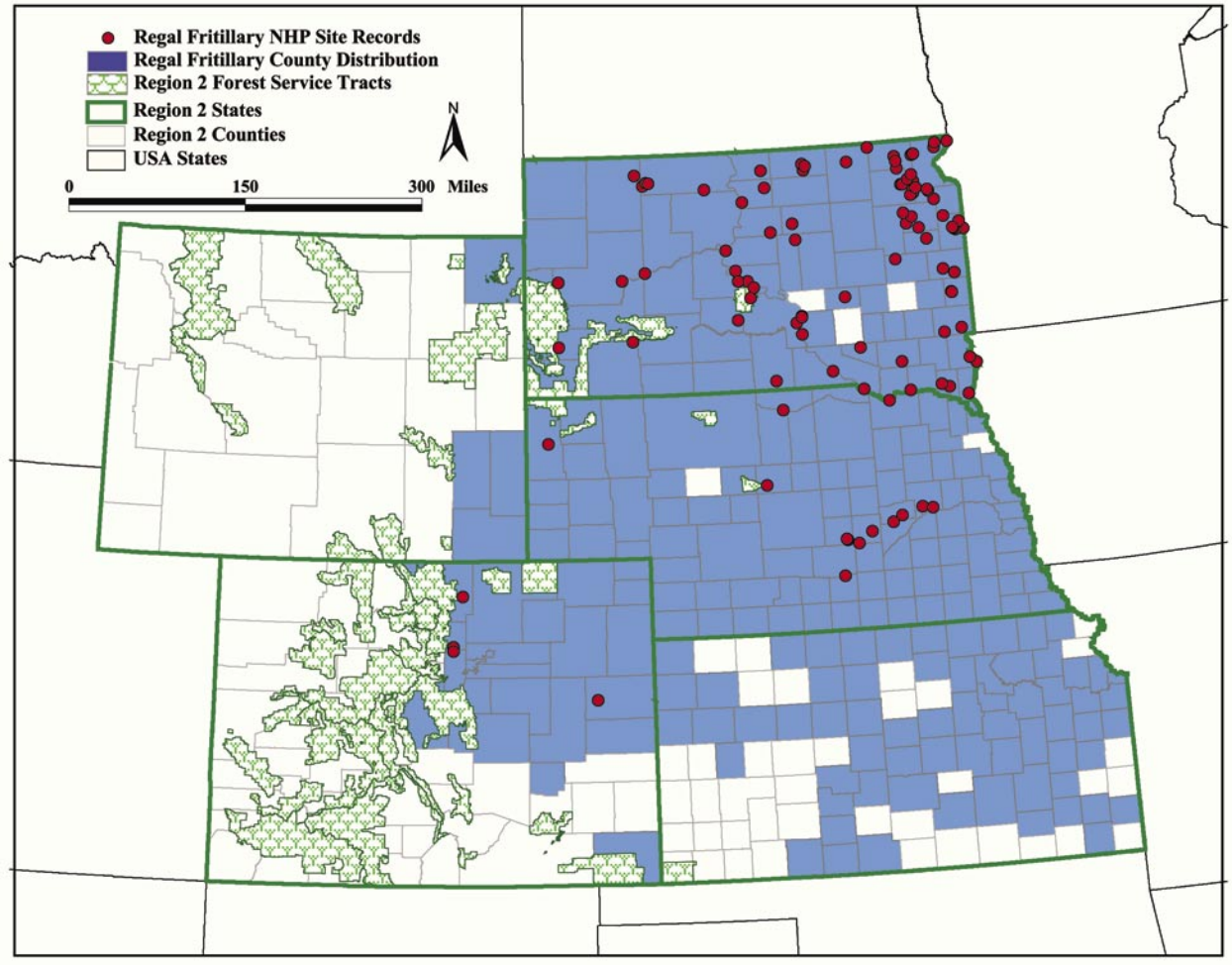

Figure 6. Historic county distribution and Natural Heritage Program site records for regal fritillaries, and National Forest System lands within Region 2.

Located in the southwestern corner of the state in Morton County, the Cimarron National Grassland unit of the Pike/San Isabel National Forest and Cimarron/Comanche National Grassland is the only National Forest System land in Kansas (**Figure 1**, **Figure 6**). There are no documented regal fritillary records from this or adjacent counties in southwestern Kansas, and the Cimarron National Grassland is about 130 to 160 km (81 to 100 mi.) south and west of the next closest county record in Kansas. Opler et al. (2006) show a confirmed county record immediately to the west in Baca County, Colorado, but this county is about 80 to 110 km (50 to 69 mi.) south of the next closest county record in Colorado, and may not represent a permanent breeding colony. Extensive areas of shortgrass prairie and scattered areas of "mixed-grass – disturbed land" are mapped within the Cimarron National Grassland (U.S. Geologic Survey Great Plains GAP Landcover Web site: http://gapanalysis.nbii.gov/portal/server.pt). These community types are not optimal habitat for regal fritillaries, and this National Forest System unit is disjunct from the main regal fritillary range by well over 100 km (63 mi.). USFS staff are unaware of any records from Colorado or Kansas units of the Pike/San Isabel National Forest and Cimarron/Comanche National Grassland (Cox personal communication 2005). If regal fritillaries are documented from the area, it would be important to determine whether they are merely strays, or an actual permanent breeding colony.

Nebraska (S3): Regal fritillaries have been documented from 91 of the 93 counties in Nebraska (Johnson 1973, Rosche 1986, Spomer 2004, Opler et al. 2006), but they are generally more abundant in the eastern part of the state (Johnson 1973). The Nebraska Natural Heritage Program has not actively tracked this species and has only 12 element occurrence records from eight counties on record (**Figure 6**; Nebraska Natural Heritage Program 2005). In Nebraska, regal fritillaries are associated with native tallgrass prairie in the east, wet meadows in the Sandhills, and subirrigated meadows associated with stream drainages throughout the state (Fritz 1997). They are generally considered rare or uncommon in the state, but high density populations can still be found, and are especially prevalent in wet meadows along the Platte River in central Nebraska (Nagel et al. 1991). The Rowe Sanctuary in Buffalo County has produced the highest regal fritillary counts in the nation every year that they have participated in the Xerces Society's Fourth of July butterfly counts since 1970 (Xerces Society Butterfly Counts; cited in Nagle et al. 1991).

National forest and grassland units within the Nebraska National Forest are in northwestern Nebraska and southwestern South Dakota, and all occur in counties with regal fritillary records. They likely are the most important National Forest System lands in Region 2 for regal fritillaries. In Nebraska, these units include the Ogalla National Grassland and Nebraska National Forest (Pine Ridge District) units in Sioux and Dawes counties, Nebraska National Forest (Bessey District) unit in Thomas and Blaine counties, and Samuel R. McKelvie National Forest unit in Cherry County (**Figure 1**, **Figure 6**). Johnson (1973) describes Pine Ridge as an area of distributional overlap between "eastern" and "western" butterflies, with many species reaching their eastern and western limits in the area. He cites several regal fritillary records from Pine Ridge, where they would be at or near their western limits. In 1995, Stephen Spomer and James Reiser conducted butterfly surveys on Nebraska National Forest units in the state of Nebraska (Fritz 1997). Surveys targeted the tawny crescent (*Phycoides batesii*) and the regal fritillary. Tawny crescent surveys were focused in the Pine Ridge District (ten sites), and regal fritillary surveys were focused in the Drinkwater Enclosure of the McKelvie National Forest and the Bessey District (three sites). The only documented regal fritillary records were from the Bessey District units at Whitetail Campground in Thomas and Blain counties (three individuals) and at Whitetail Campground Road in Thomas County (one individual). Larval food plants (*Viola* spp.) were present at the Whitetail Campground site, but in very low numbers. No regal fritillaries were observed at the Drinkwater Enclosure of the McKelvie National Forest, and while the site is well within the range of breeding regal fritillaries, the community types were not well suited for them (Fritz 1997). Comprehensive surveys of National Forest System lands in Nebraska are needed to determine if breeding populations of regal fritillaries are present, and if they are, to determine their distribution and abundance within those lands.

South Dakota (S3): Regal fritillaries have been documented from 63 of the 66 counties in South Dakota (Marrone 2002, NatureServe 2005, Opler et al. 2006), and appear to be common where sufficient quantities of quality native prairie remain (Marrone 2002). They are declining elsewhere due to the loss of those grasslands and associated larval food sources (South Dakota Natural Heritage Program 2005b). Areas in the state where regal fritillaries are doing well include tallgrass prairie associated with marshes in the northeast, non-degraded mixed-grass prairie along Missouri River

breaks, and the Fort Pierre National Grassland (Marrone 2002). Regal fritillaries are tracked by the South Dakota Natural Heritage Program. They have 92 element occurrence records from 41 counties (South Dakota Natural Heritage Program 2005a, 2005b), but only a few of those records are near National Forest System lands (**Figure 6**).

The Buffalo Gap National Grassland units of the Nebraska National Forest include parts of Custer, Fall River, Jackson, and Pennington counties in the southwest corner of South Dakota, where there are documented regal fritillary occurrences from each of these counties (Opler et al. 2006). Western portions of the Buffalo Gap National Grassland are near the western extent of the regal fritillary range. Historic records from western portions of the grassland might not represent breeding colonies, but eastern portions are well within the range and are more likely to contain breeding colonies. The closest Natural Heritage Program element occurrence record is just south of the eastern unit in Shannon County, and it was based on 11 males that were observed patrolling for females in 1998 (South Dakota Natural Heritage Program 2005a).

The Fort Pierre National Grassland unit of the Nebraska National Forest includes parts of Jones, Lyman, and Stanley counties in central South Dakota. It is located in the heart of the Great Plains portion of the regal fritillary's range, and the species has been documented from each of those counties. There are two regal fritillary element occurrence records from the Lyman and Stanley County portions of the Fort Pierre National Grassland, and in 2001, this species was reported as present throughout those portions of the grassland (South Dakota Natural Heritage Program 2005a). The Fort Pierre National Grassland contains extensive areas of grassland mapped as "low, moderate and high cover grassland" (U.S. Geologic Survey Great Plains GAP Landcover), and this unit is identified as one of the areas where regal fritillaries are abundant in the state (Marrone 2002).

The Black Hills National Forest unit in South Dakota includes parts of Custer, Fall River, Lawrence, Meade, and Pennington counties, all of which have regal fritillary records. This unit is dominated by forest vegetation, but scattered areas of "low, moderate and high cover grassland" are mapped throughout the area (U.S. Geologic Survey Great Plains GAP Landcover). Good examples of dry mixed-grass, mesic mixed-grass, and mesic tallgrass prairie were identified during 1996-1998 plant community inventories (Marriot et al. 1999). No documented regal fritillary occurrences were found for the Black Hills National Forest, but there are element occurrence records immediately to the northeast in Meade County, and to the east of the southern portion in Custer County (South Dakota Natural Heritage Program 2005a). Both records included July observations, which are more likely to represent breeding colonies, and it is possible that the scattered prairie remnants in this National Forest System unit could support regal fritillaries.

Healthy populations of regal fritillaries have been documented at the Fort Pierre National Grassland, and these populations should be monitored as part of an adaptive management program to ensure their long-term survival at the site. At the other National Forest System lands in South Dakota, surveys focused on regal fritillary habitat need to be completed to determine if the species occurs there, and if it does, to determine its distribution and abundance within those lands, and whether the occurrences represent viable breeding populations.

Wyoming (SNR): The range of the regal fritillary barely extends into eastern Wyoming, where it has only been recorded from four counties near the eastern border of the state (Ferris 1971, Ferris and Brown 1981, Stanford and Opler 1993, Opler et al. 2006). The Wyoming Natural Heritage Program does not currently track any invertebrates, so there are no regal fritillary element occurrence records for the state (Beauvais personal communication 2005), and no documentation was found for occurrences on National Forest System lands in Wyoming. The Black Hills National Forest unit in Wyoming falls entirely within Crook County, one of the counties where regal fritillaries have been documented. This unit of the Black Hills National Forest is dominated by forest vegetation, but it does have areas of mixed-grass prairie (U.S. Geologic Survey Great Plains GAP Landcover) that could provide habitat for regal fritillaries. The Medicine Bow/Routt National Forest and Thunder Basin National Grassland occur adjacent to counties with regal fritillary records, and they have significant areas of mixed-grass prairie (U.S. Geologic Survey Great Plains GAP Landcover) where regal fritillaries could occur. Although there are historic records from counties near National Forest System units in Wyoming, it is possible that those records are from wandering individuals and do not represent breeding colonies. If regal fritillaries are documented from National Forest System lands in Wyoming, efforts should be focused on determining whether they represent breeding colonies, and if they do, monitoring the populations and adapting management practices to ensure their long-term survival.

Colorado (S1): Regal fritillaries have been documented from 22 counties in the northeast quarter of Colorado, and one disjunct county in the southeast corner of the state (Ferris and Brown 1981, Stanford and Opler 1993, Opler et al. 2006). Despite the apparent contiguous distribution of regal fritillaries in the northeast quarter of the state (**Figure 6**), most of the observations are late season strays (e.g., worn specimens observed in September), and probably do not represent breeding colonies (Colorado Natural Heritage Program 2005b, Drummond personal communication 2005). There are only four regal fritillary element occurrence records for Colorado (**Figure 6**), and only one of those (Kit Carson County in east-central Colorado) is thought to represent a confirmed viable and reproducing colony (Colorado Natural Heritage Program 2005a, Colorado Natural Heritage Program 2005b, Drummond personal communication 2005). Two of the records (Boulder and Jefferson counties) are from surveys for the city of Boulder Open Space and Mountain Parks (Pineda 1998, Pineda and Ellingson 1998). These observations were made during the breeding season in July, but additional surveys are needed to confirm their status as breeding colonies. The fourth record (Larimer County) is based on observations in early September and may simply represent late season strays. In Colorado, regal fritillaries are associated with wet meadows and non-degraded prairie near marshes and, possibly, moist areas associated with irrigation projects (Colorado Natural Heritage Program 2005b). Northern sandhill prairies (*Artemisia filifolia*/*Andropogon hallii*) in eastern Colorado may also contain regal fritillaries, and surveys are warranted in those areas (Colorado Natural Heritage Program 2005b).

Recent records for unconfirmed breeding colonies of regal fritillaries are in a north/south line that runs east of the Roosevelt National Forest unit of the Arapaho/Roosevelt National Forest and Pawnee National Grassland from just south of Boulder to Fort Collins (**Figure 6**). These locales are associated with "foothills zone mixed-grass prairie" immediately east of the Colorado Front Range foothills (Colorado Natural Heritage Program 2005a). Suitable prairie types for regal fritillaries are east of the Roosevelt National Forest unit (U.S. Geologic Survey Great Plains GAP Landcover), and there does not appear to be adequate regal fritillary habitat within that National Forest System unit to support breeding colonies. The Arapaho National Forest unit is even further from recent regal fritillary records and habitat, and it is even less likely that there would be regal fritillaries in that unit.

The Pawnee National Grassland units of the Arapaho/Roosevelt National Forest and Pawnee National Grassland are east of Larimer County near the northern Colorado border in Weld County. Regal fritillaries have been documented from this and the surrounding counties, but no documentation was found for extant breeding colonies on the grassland. There is an abundance of shortgrass prairie and some mixed-grass prairie within the boundaries of these units and more limited amounts of tallgrass prairie between them (U.S. Geologic Survey Great Plains GAP Landcover), so it is possible that regal fritillaries could occur there.

The Pike National Forest unit of the Pike/San Isabel National Forest and Comanche/ Cimarron National Grassland is located in counties with historic records for regal fritillaries (Douglas, El Paso, Jefferson, Park, and Teller counties), but no recent records in or near those National Forest System units were found. The only confirmed viable population of regal fritillaries in Colorado is over 160 km (100 mi.) to the east. There do not appear to be any suitable prairie community types within the Pike National Forest (U.S. Geologic Survey Great Plains GAP Landcover), so it is unlikely that breeding colonies of regal fritillaries would occur here.

The Comanche National Grassland units of the Pike/San Isabel National Forest and Comanche/ Cimarron National Grassland are located in southeastern Colorado (Baca, Las Animas, and Otero counties). Shortgrass prairie is the dominant vegetation in these units, but there is also some mixed-grass prairie in the southwest corner of the Baca County unit (U.S. Geologic Survey Great Plains GAP Landcover). The only documented historic regal fritillary records are from Baca County (Opler et al. 2006), 80 to 110 km (50 to 69 mi.) south of the next closest county record in Colorado. Community types in these units are only marginally suited for regal fritillaries, and given the distance from the main range of the regal fritillary, it is unlikely that there would be breeding colonies in any of these National Forest System units.

No regal fritillaries have been documented from any of the Arapaho/Roosevelt National Forest and Pawnee National Grassland units (Lowry personal communication 2005), or from the Pike/San Isabel National Forest and Comanche/Cimarron National Grassland units (Cox personal communication 2005), but this could simply be the result of inadequate survey effort. Regal fritillary habitat (e.g., especially

wet meadows and non-degraded prairie near marshes) in the units should be surveyed to determine whether regal fritillaries are present as breeding colonies, and if they are, to determine their distribution and abundance within those units.

Activity pattern and movements

Activity pattern

A generalized timeline summarizing the seasonal phenology of the principal stages of the regal fritillary life cycle is presented in **Figure 7**. The primary source for immature stage length data is Edwards (1879). The date ranges for immature life stages are estimates based on those data and the flight period, and they should only be used as a very general guideline.

Regal fritillaries are univoltine (having a single generation per year) with an adult flight from about the middle of June through the middle of September (Klots 1951, Tilden and Smith 1986, Wagner et al. 1997). The actual flight period varies somewhat across their range, and it can vary significantly from year-to-year depending on weather patterns. In the Great Plains and Midwest, the emergence of males coincides with the blooming of coneflowers (e.g., *Echinacea angustifolia* and *E. pallida*) and the emergence of several other prairie butterflies (e.g., Dakota skipper [*Hesperia dacotae*], Ottoe skipper [*H. ottoe*], and Poweshiek skipperling [*Oarisma poweshiek*]) where they co-occur (Selby and Glenn-Lewin 1990, Selby 1992, 2000, 2003a, 2004a, 2006b). The emergence of males in the eastern Pennsylvania population coincides with the blooming of common milkweed (*Asclepias syriaca*) (Ferster 2005b). Females have a longer larval development period and emerge about one to two weeks after the males (Wagner et al. 1997, NatureServe 2005). Regal fritillaries usually mate soon after they emerge (Wagner et al. 1997, NatureServe 2005), but oviposition is delayed until late August to early September (Wagner et al. 1997, Kopper et al. 2001b).

First instar larvae consume the chorion (outer covering of the egg) after hatching and enter diapause immediately, presumably without any additional feeding (Wagner et al. 1997). This is the most precarious stage for regal fritillaries and other *Speyeria* species (Mattoon et al. 1971). Challenges they face include harsh winter conditions, fires that burn through the leaf litter where they are sheltered, disease, parasitoids, and locating freshly emerged violet leaves in the spring. Larval development begins again in the spring with the emergence of young violet leaves, and is completed by late May to June (Wagner et al. 1997). The pupal stage lasts from two and one half to four weeks (Wagner et al. 1997).

Mobility and migration

Regal fritillaries are a patrolling species, and when males are not taking nectar or basking, they patrol continuously throughout the day in search of females (Scott 1986, Swengel 1993, Royer 2004). They tend to remain close to the emergence area where violets are more abundant; this could be an adaptation

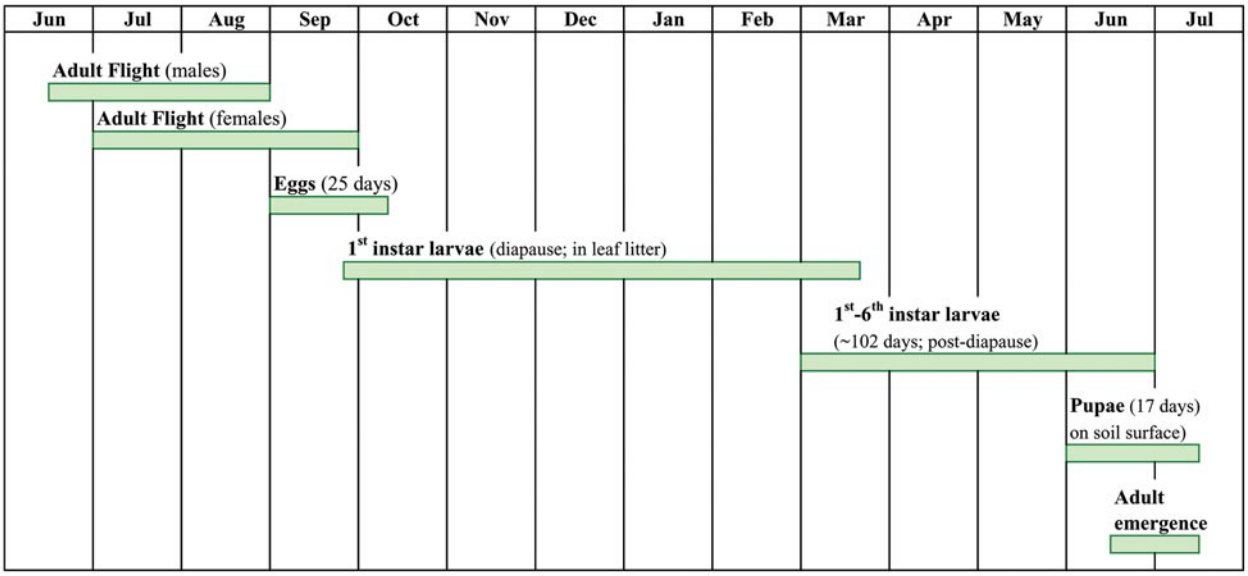

Figure 7. Regal fritillary life history stages and their approximate seasonal phenology (adapted from Edwards 1879).

to be in the "right place" when the females emerge one to two weeks later (Nagel et al. 1991). Females mate soon after emerging, and then enter a period of postmating reproductive diapause until late August or early September (Kopper et al. 2001b). During this time, they continue to feed on nectar but become less active and spend more time resting in the shade of vegetation (Kopper et al. 2001b). In late August to early September, the females become more active, wandering extensively in search of suitable oviposition sites, and then landing in the grass and walking around to deposit eggs (Opler and Krizek 1984, Allen 1997). Females have a propensity for late-season wandering, and many specimens have been captured long distances from breeding colonies.

Regal fritillaries do not migrate, and they are not likely to disperse long distances between isolated prairie fragments. However, they are more mobile than most prairie specialist butterflies and can be expected to move throughout a prairie remnant, and even between remnants that are relatively close together. An eastern population of regal fritillaries on New England's Nantucket Island responded to local changes in nectar availability over the course of the summer by ranging over several thousand acres (Bliss and Schweitzer 1987, Schweitzer 1989). In mark-recapture studies by Nagle et al. (1991) at Rowe Sanctuary in Nebraska, most movements were local (daily average = 68.6 m [225 ft.]), but several movements were 1,600 m [5,249 ft.], the maximum distance possible at the site. Selby (1992) obtained similar results in a study of regal fritillaries and Ottoe skippers in the northern Loess Hills of western Iowa, where wooded valleys separated linear prairie ridges from each other. Most regal fritillary movements were local moves within prairie ridges (modal distance range was 0-200 m [0-656 ft.]), but there were also numerous longer moves along and between the prairie ridges (maximum distance was 1,515 m [4,970 ft.] across several valleys). That study only included the first part of the regal fritillary flight, so the sample size was small (38 captures, 16 recaptures), and movement patterns associated with the latter portion of the flight were not documented. Zercher et al. (2002) provide a preliminary summary of movement data collected at the FTIG National Guard Training Center in Pennsylvania over a 14-day period in July 2001. Sixty-one movements between units were recorded for 41 males. Based on the minimum linear distance between units, 14 movements were at least 7.6 km (4.8 mi.), 27 were 4.3 km (2.7 mi.), 13 were 2.1 km (1.3 mi.), and the remaining seven movements were less than 2.1 km. In studies by Barton (1993, 1994), the average distance traveled for 22 late season dispersers was 3.4 km (2.1 mi.), and the maximum distance traveled was 15.8 km (9.9 mi.). It is generally assumed that late season dispersing females do not play a role in establishing new colonies, but more data are needed to determine if this is true. To recolonize habitat at a new site successfully, dispersal would need to occur before the females finish laying eggs, and the eggs laid would need to survive to the adult stage.

Ries and Debinski (2001) tracked the response of regal fritillaries to four prairie edge types (row crop, road, non-prairie grassland, treeline), and found that they had a tendency to turn away from prairie borders, avoided exiting the prairies, and if they did exit, were likely to return to the prairie. They responded strongly to all edge types, but for some edge types, their response was density dependent. Their response to low contrast non-prairie grassland edge was only strong when conspecific densities were high. This suggests that regal fritillaries are more likely to emigrate from prairie remnants where population densities are low, which could exacerbate the impact of other factors causing a population decline, or make it more difficult to re-establish populations due to the initial low population levels (Ries and Debinski 2001). Mark-recapture data from a 73-ha (180-acre) prairie in Nebraska showed very little movement from the interior to the margins, and no regal fritillaries were found in adjacent overgrazed pastures, suggesting that there was very little emigration from that prairie (Nagel et al. 1991).

These results suggest that where regal fritillaries occur in complexes of closely associated prairie fragments, dispersal between fragments could occur. They are capable of strong and rapid flight, and sometimes wander extensively late in the season, but population recovery will take longer if it depends on recolonization between fragments, and the probability of successfully repopulating distant isolated habitat fragments is low. Therefore, where regal fritillaries occur in an isolated prairie fragment, it should be assumed that recolonization will need to occur from within that fragment, and management should be planned accordingly (e.g., burning, grazing or mowing only a portion of the fragment at any one time).

Habitat

The regal fritillary is associated with the Upper Austral and Transition Life Zones of the eastern United States, and the Prairie Grassland Zone of the Great Plains (Hammond 1974, Scott 1986). Habitats are generally described as tallgrass prairie, wet meadows, and marshy areas (Klots 1951, Scott 1986, Tilden and Smith 1986, Opler and Malikul 1992, Opler and Wright

1999, Brock and Kaufman 2003). Eastern populations tend to be associated with more mesic habitats while western populations are generally associated with more xeric habitats (Williams 1999, 2001a).

Preferred habitats of Eastern populations have been described as "almost entirely artificial" (Schweitzer 1993), and Glassberg (1993, 1999) states that they included ". . . a variety of largely unnatural open situations, such as pastures and hayfields, usually wet." General habitat types listed for New England populations have included marshes and swamp edges, wet meadows, fields, pastures, and native grasslands; more specific mainland and coastal island habitats included sandplain grasslands, heathlands, and coastal pasture (Wagner et al. 1997). Early twentieth century agricultural practices in the eastern United States and southern Canada may have actually benefited populations of regal fritillaries. Eastern populations appear to have peaked in abundance during colonial times, when most of that region had been cleared for crops and pasture (Wagner et al. 1997). Violets were often more abundant in the grazed pastures (Mello 1989), and as agricultural practices changed and New England became reforested, those pasture habitats declined and became increasingly fragmented (Wagner et al. 1997).

The last remaining Pennsylvania population of regal fritillaries is associated with grasslands in an old field successional stage dominated by broomsedge (*Andropogon virginicus*), little bluestem (*Schizachyrium scoparium*), and a variety of other warm-season and cool-season grasses (Zercher et al. 2002). There are also healthy populations of the preferred larval foodplant (arrowleaf violet [*Viola sagittata*]) and a variety of nectar sources (Zercher et al. 2002). These successional grassland habitats require active management to maintain their open nature and to prevent reforestation. Management activities include manual tree and shrub removal, mowing, haying, and prescribed fire (Zercher et al. 2002). Some National Guard training activities (e.g., soil disturbance by tracked vehicles) may actually benefit regal fritillaries by maintaining open areas and promoting violet growth, but the amounts and types of activities that are beneficial or detrimental to regal fritillaries are unknown (Zercher et al. 2002).

In West Virginia, regal fritillary habitat has been described as "grasslands adjacent to boggy or marshy areas or containing damp meadows," and populations are typically associated with higher elevations or hilltops where wind currents were stronger (Allen 1997). Farther west, eastern populations are associated with native prairie and other grassland habitats. Regal fritillary populations in Ohio were associated with a variety of mesic grassland habitats. In the southeastern part of the state, habitats included pastures, recently abandoned fields, and hay fields that were usually near a woodland border; in the north, habitats included mesic prairies that graded into wetlands (Shuey et al. 1987b, Iftner et al. 1992). Michigan populations were associated with prairies, meadows, old fields, and floodplain forest openings and edges (Nielson 1999), and Indiana habitats included prairie remnants along railroad tracks, virgin grasslands, and occasionally wet meadows in woodlands (Shull 1987).

In the Midwest and Great Plains, regal fritillary habitat is described as relatively non-degraded native tallgrass prairie, wet fields, meadows, and, to a lesser extent, shortgrass prairie (Hammond and McCorkle 1983[84], Glassberg 2001). Habitats in Illinois and Wisconsin include dry upland prairie hillsides, dry sand prairie and wetland complexes associated with river terraces, and marshy areas along stream margins (Ebner 1970, Sedman and Hess 1985, Bouseman and Sternburg 2001, Ferge 2002). Swengel (2001b) also reported a rather unusual occurrence of a large regal fritillary population from a site in Wisconsin that had been drained, plowed, abandoned, and regrown as old field. In Iowa and Minnesota, regal fritillaries are found on a variety of mixed- and tallgrass prairie types associated with sand, limestone, glacial till, dry loess, and black soil substrates. Missouri habitat includes high quality tallgrass prairie (Missouri Department of Conservation 2004) and prairie meadows (Heitzman 1987).

Habitat in the Great Plains states is generally described as pristine tallgrass prairie in Kansas, Oklahoma, and north Texas (Dole et al. 2004), and virgin prairie in North and South Dakota (Royer and Marrone 1992). More specific habitat descriptions for South Dakota include tallgrass prairie near marshes in the northeast, and non-degraded mixed-grass prairie along the Missouri River breaks and Fort Pierre National Grassland (Marrone 2002). Regal fritillary habitat in Nebraska includes native tallgrass prairie in the east, wet meadows in the Sandhills, and subirrigated meadows associated with stream drainages throughout the state (Fritz 1997). Dispersing individuals can also be associated with drier grasslands (Fritz 1997). The highest density populations are associated with wet meadows along the Platte River in central Nebraska (Nagel et al. 1991). In Colorado, regal fritillaries are associated with wet meadows and non-degraded prairie near marshes, and possibly moist areas associated with irrigation projects (Colorado Natural Heritage

Program 2005b). Recent records immediately east of the Colorado Front Range foothills are associated with "foothills zone mixedgrass prairie," and northern sandhill prairies (*Artemisia filifolia*/*Andropogon hallii*) in eastern Colorado have potential to support regal fritillaries (Colorado Natural Heritage Program 2005b).

There are no documented permanent regal fritillary populations in Canada, but habitats in Canada where regal fritillaries might be found include tallgrass prairie and "wet prairie-like clearings in woodlands" that have violets growing in them (Layberry et al. 1998, Canadian Biodiversity Information Facility 2003).

Food habits

Nectar plants

The availability of suitable adult food resources throughout the adult flight period can be as important as the presence of larval host plants in determining whether an area can support populations of particular butterfly species (Opler and Krizek 1984). This is especially true for long-lived butterflies such as regal fritillaries. Most butterflies use nectar resources primarily to meet energy needs, but many long-lived butterflies also use food resources for egg production (Opler and Krizek 1984). Boggs and Ross (1993) found that for the Mormon fritillary (*Speyeria mormonia*), adult food limitation did not have an impact on the lifespan or the mean mass of individual eggs, but fecundity did decrease dramatically. Individual females have a fixed number of oocytes at the time they emerge, and these oocytes are laid, resorbed by the female, or retained in the ovaries at the time of death (Boggs 1986, Boggs and Ross 1993). In the Mormon fritillary, adult food limitation resulted in re-allocation of resources away from reproduction through the resorption of the oocytes (Boggs and Ross 1993), and similar results might be expected for regal fritillaries. Adding protein to the diet of female regal fritillaries increased both their fecundity (number eggs laid) and fertility (number eggs hatching), suggesting the importance of late-summer nectar sources to the species' long-term survival (Wagner 1995). A diverse assemblage of nectar sources may be needed to ensure the continuous supply of nectar needed throughout the regal fritillary flight, and it has been suggested that the loss of large contiguous tracts of habitat where those diverse nectar resources are most likely to occur could have been a primary factor in the species' decline (Ferge 1990). Huebschman (1998) found that regal fritillary population density was positively correlated with both site size and the diversity of known nectar resources, but there was some annual variability in the relationship with nectar plants.

Regal fritillaries use a variety of plant species as nectar sources to meet the demanding nutritional requirements of their extended adult lifespan. Some of the most important nectar sources include milkweeds (*Asclepias*), thistles (*Cirsium*), coneflowers (*Echinacea*), blazing-stars (*Liatris*), bergamots (*Monarda*), goldenrods (*Solidago*), clovers (*Trifolium*), and ironweeds (*Vernonia*). Milkweeds and thistles are the preferred nectar plants for the extant Pennsylvania population (Zercher et al. 2002, Ferster 2005b). The staggered phenology of two milkweed and two thistle species at the site provide a constant supply of nectar, and they are used almost exclusively (Ferster 2005b). Common milkweed starts blooming when male regal fritillaries are emerging and is an important nectar source early, followed by butterfly milkweed (*A. tuberosa*), which blooms for a more extended time period. Later in the season, important nectar sources include pasture thistle (*C. pumilium*), followed shortly by field thistle (*C. discolor*). Nectar sources that have been reported for other eastern regal fritillary populations include swamp milkweed (*A. incarnata*) and wild bergamot (*M. fistulosa*).

Milkweeds and thistles are also important nectar sources for regal fritillaries in the Midwest and Great Plains. Preferred nectar sources include butterfly weed, common milkweed, and pale-purple coneflower (*Echinacea pallida*) in Missouri (Heitzman and Heitzman 1987); milkweeds and purple coneflower (*E. angustifolia*) in Nebraska (Fritz 1997); milkweeds, thistles, and blazing-stars in North Dakota (Royer 2004); and purple coneflower, thistles, milkweeds, wild bergamot, blazing-star, hoary vervain (*Verbena stricta*), and alfalfa (*Medicago*) in South Dakota (Marrone 2002). Pink flowers were used 85 percent of the time, and thistles were "strongly preferred" in 1,058 observations compiled from several states by Swengel (1993). During a study at 10 sites in eastern Nebraska, regal butterflies used 21 different plant species, but milkweeds accounted for 50 percent of nectar plants used (Huebschman 1998). Common milkweed received the most visits and was the most important nectar source during the first part of the flight (before 18 July), and wild bergamot received the second most visits and was more important later in the flight (after 18 July). In another Nebraska study, milkweeds accounted for 67 percent of nectar plant use (Nagle et al. 1991).

Larval food plants

Violets (*Viola*) are the larval food plants for all members of the genus *Speyeria* (Klots 1951, Hammond 1974, Ferris and Brown 1981). Regal fritillaries use a variety of species throughout their range, including bog white violet (*V. lanceolata*), Nuttall's violet (*V. nuttallii*), birdfoot violet (*V. pedata*), prairie violet (*V. pedatifida*), arrowleaf violet, common blue violet (*V. sororia*), and Johnny jumpup (*V. tricolor*). While they are able to use a variety of species, regal fritillaries tend to be associated with specific violet species in different parts of their range. Larvae of New England populations preferred arrowleaf violet, birdfoot violet, and bog white violet (Wagner et al. 1997), and arrowleaf violets are the preferred, perhaps exclusive, larval food plant at the last extant Pennsylvania population (Zercher et al. 2002, Ferster 2005b). In Ohio, regal butterfly larvae used birdfoot violet as a food plant, but this plant species was considered too rare in the state to be the primary food source (Shuey et al. 1987a, Shuey et al. 1987b, Iftner et al. 1992). Birdfoot violet and prairie violet are listed as preferred larval food plants throughout the Midwest and Great Plains (Swengel 1997, Kelly and Debinski 1998, Dole et al. 2004), and arrowleaf violet is used in several Midwestern states (Swengel 1997). Other species listed include Nuttall's violet in South Dakota (Marrone 2002), common blue and lanceleaf violets in Kansas, Oklahoma, and northern Texas (Dole et al. 2004), and Johnny jumpup in the Rocky Mountain states (Ferris and Brown 1981).

Violets are an important component of habitat suitability for regal fritillaries, and studies have demonstrated a positive correlation between the abundance of certain violet species (e.g., prairie violet and arrowleaf violet) and regal fritillaries (Swengel 1997, Debinski and Kelly 1998). Still, the decline or absence of regal fritillaries in an area cannot always be explained by the absence of violets (Bliss and Schweitzer 1987, Ferge 1990, Huebschman 1998, Ferster 2005b). At the FTIG National Guard Training Center in Pennsylvania, the density of arrowleaf violets in areas where regal fritillaries were abundant was not significantly different from the density in areas where regal fritillaries had disappeared or were much less abundant (Zercher et al. 2002, Ferster 2005b). Birdfoot violet was the most abundant and widespread violet species at sites in a survey of Midwest prairies, but there was no significant correlation between that species and regal fritillaries (Swengel 1997). The hypothesis that larval food limitation could be a factor in the decline of Iowa regal fritillary populations was examined (Kelly 1997, Kelly and Debinski 1998). The weight of individual regal fritillaries and the density of violet populations were both significantly smaller in Iowa than in neighboring states, but the relationship between host plant density and regal fritillary population size was not as clear.

Breeding biology

Courtship and mating

Regal fritillaries are a "patrolling" species, exhibiting fast, steady flight close to the grass in the large open fields where they are found (Allen 1997). Patrolling is the primary mate-seeking behavior, and when they are not taking nectar or basking, males patrol continuously throughout the day in search of females (Scott 1986, Swengel 1993, Royer 2004). Nagel et al. (1991) noted that males tend to remain in the emergence area where violets are more abundant, irrespective of nectar plant distribution, and suggested that this could be an adaptation to be in the "right place" when the females emerge one to two weeks later. Females mate shortly after emergence (Mattoon et al. 1971, Allen 1997, Wagner et al. 1997, Zercher et al. 2002), and most males die about two weeks after mating (Kopper 1997, Kopper et al. 2001b). Following mating, females enter a prolonged period of postmating "reproductive diapause," during which there is no further fat body depletion or maturation of the oocytes (cells that undergo meiosis to produce an egg) (Kopper et al. 2001b). During this time, the females continue to feed on nectar, but they become less active and spend more time resting in the shade of vegetation (Kopper et al. 2001b).

Reproductive diapause is a characteristic life history trait for members of the genus *Speyeria* (Edwards 1874, Edwards 1897, Sims 1984). Factors leading to the onset of reproductive diapause are poorly understood (Sims 1984), but they may include long days and, to a lesser extent, high summer temperatures (Kopper et al. 2001b). Termination of reproductive diapause and the initiation of oogenesis (meiotic division and maturation of the oocytes) coincide with shorter photoperiods and rapid increases in the levels of juvenile hormone (Sims 1984, Kopper et al. 2001b). In regal fritillaries, this occurs from late August to early September, and it is followed shortly by oviposition (Kopper et al. 2001b). This reproductive strategy may be an adaptation to the seasonal phenology of the larval food plants (Kopper et al. 2001b). Most violet species are senesced during the adult flight period for regal fritillaries, and the fresh young leaves required by first instar larvae are not available until the following spring (Wagner et al.

1997, Kopper et al. 2001b). Delaying oviposition until early fall reduces the exposure of first instar larvae to the desiccating effects of the hot, dry summer, and the overall time that overwintering larvae are exposed to the elements (Sims 1984).

Oviposition behavior

Regal fritillaries delay oviposition until late August to early September (Scott 1986, Wagner et al. 1997, Zercher et al. 2002). Females become more active at this time, wandering extensively in search of suitable oviposition sites, and then landing in the grass and walking around, depositing eggs (Opler and Krizek 1984, Allen 1997). Oviposition behavior appears to be somewhat haphazard, with eggs laid singly near, but not necessarily on the violet host plants (Scott 1986, Swengel and Swengel 2001). Kopper et al. (2000) examined oviposition site selection in a Kansas population of regal fritillaries and found that females tended to lay eggs on the underside of dead vegetation near the ground in shaded microsites, rather than orienting towards or ovipositing on their larval host plants. Violet species used as larval host plants are senesced at the time females lay the eggs, so the larvae overwinter as first instars without feeding (Wagner et al. 1997, Kopper et al. 2001b). Kopper et al. (2000) speculate that oviposition site-selection behavior may be influenced more by the need to survive the impact of environmental stresses (e.g., high temperatures and intense solar radiation during the egg stage; harsh winter conditions for overwintering first instar larvae) than by the advantages of orienting to larval host plants. Regal fritillaries have extraordinarily high potential fecundity per female. One captive female laid more than 1,440 eggs over a 3-week period (Allen 1997), and another captive female laid more than 2,450 eggs over a 12-week adult life, which is more than twice the previous maximum documented for any butterfly species (Wagner 1995)! This high fecundity may enable regal fritillaries to use a "sweepstakes" strategy, placing a premium on the number of eggs produced, rather than maximizing the survival of individual eggs (Wagner 1995, Wagner et al. 1997, Kopper et al. 2000).

Larval stages

Regal fritillary eggs hatch after about 25 days (Edwards 1979). The hatching larvae immediately consume the chorion (outer covering of the egg), seek shelter in the leaf litter, and enter winter diapause as first instars (Hammond 1974, Wagner et al. 1997). Mortality is very high during this life stage for most *Speyeria* species (Mattoon et al. 1971), and this stage is the most precarious for regal fritillaries. The tiny (2 mm), unfed larvae must survive the harsh conditions of winter, and then locate freshly emerging violet leaves before exhausting their limited reserves. This challenge is compounded by the tendency for the violets to be uncommon and clumped in distribution, the inability of larvae to detect violets from a distance of more than 1 to 2 cm, and the formidable challenge that the uneven microterrain poses for the tiny larvae (Kopper et al. 2000). Larvae are also extremely susceptible to disease, parasitoids, and direct and indirect mortality from fires that consume the vegetation where they are sheltered. Larval development begins again in the spring when the young violet leaves are just starting to expand, and it is completed by late May to June (Wagner et al. 1997). The young larvae require this fresh growth and will die if they are fed more mature leaves, but the older larvae are able to use any violets (Wagner 1995). There are six larval instars, followed by the pupal stage, which lasts from 2.5 to 4.0 weeks (**Table 2**; Edwards 1879, Wagner et al. 1997).

Larvae of members of the genus *Speyeria* are generally thought to be nocturnal, feeding at night and resting during the day in a hidden location, usually away from the host plant (Klots 1951, Hammond 1974, Ferris and Brown 1981, Royer 1988). It has been assumed that regal fritillary larvae are also nocturnal (Royer and Marrone 1992), but in field and laboratory studies of a Kansas population, all documented activity suggested that they are actually diurnal foragers (Kopper et al. 2001a). Categories of larval behavior observed in that study included feeding, walking, and resting. During the day, larvae would walk in a curved path, feeding on plants that were directly in their path; they did not appear to perceive plants as close as 1 cm away. Towards sunset, walking and feeding behavior declined progressively until the larvae became inactive for the remainder of the night. Early instars (1st to early 3rd) rested in the curls of young violet leaves, and late instars (3rd to 6th) rested at the base of violet plants or perhaps other plant species. This study provided consistent evidence for diurnal foraging behavior in regal fritillaries, but it was based on limited observations from a single site. More data are needed from a larger geographic area to determine how widespread this behavior is for regal fritillaries, and perhaps for other *Speyeria* species (Kopper et al. 2001a).

Table 2. The size (length) and duration (days) of immature regal fritillary stages (adapted from Edwards 1879).

Stage	Length (inches)	Length (mm)	Duration (days)	Cummulative Duration (days)
1st instar	0.08-0.15	2.03-3.81	diapause + 23	23
2nd instar	0.15-0.30	3.81-7.62	12	35
3rd instar	0.30-0.70	7.62-17.78	15	50
4th instar	0.70-1.00	17.78-25.40	17	67
5th instar	1.00-1.20	25.40-30.48	20	87
6th instar	1.20-1.75	30.48-44.45	15	102
Chrysalis	1.1	27.94	17	119

Demography

Genetic characteristics and concerns

Genetic isolation resulting from habitat fragmentation can lead to reduced fitness due to genetic drift, which can in turn lead to decreases in heterozygosity and elevated inbreeding coefficients (Britten and Glasford 2002). Until recently, regal fritillaries were one of only three *Speyeria* species for which there were no recognized subspecies (Williams 1999). Regal fritillaries are strong flyers, capable of moving between fragmented populations, and the resulting gene flow could account for their apparent lack of genetic variability (Hammond 1991, Williams 1999). However, as regal fritillary populations become more isolated because of increasing habitat fragmentation, their ability to move between populations may be significantly reduced (Williams 1999). In the initial examination of genetic variation in regal fritillaries, Williams (1999, 2001a, 2001b) found very few genetic differences among Great Plains and Midwestern populations, but the Pennsylvania population had several genetic differences at slowly mutating segments of the DNA. These data suggested the Pennsylvania population had been separated from the other populations for as much as 400,000 years, but that there was "high gene flow" among Great Plains and Midwestern populations.

Williams (2003) used different genetic markers to examine the genetic impacts of fragmentation more closely. Genetic differentiation and diversity were compared among non-fragmented (Great Plains), fragmented (Midwest), and historically isolated (eastern) populations. The analyses reinforced conclusions from the previous genetic study suggesting significant differentiation of the eastern Pennsylvania population resulting from long-term isolation, and the results also supported predicted genetic effects of more recent (at most since the 1860's) habitat fragmentation. Fragmented Midwestern populations showed increased differentiation and decreased genetic diversity when compared to unfragmented Great Plains populations (Williams 2003). Allelic diversity and expected levels of heterozygosity were lower for Midwestern than Great Plains populations and lowest for Pennsylvania, but observed levels of heterozygosity were not always consistent with expected patterns, had higher variance, and were typically lower than expected levels based on Hardy-Weinberg equilibrium (Williams 2003).

Similar results were obtained in a study of Dakota skipper populations from Manitoba to northeastern South Dakota and southwestern Minnesota (Britten and Glasford 2002). Results indicated that the studied populations were genetically isolated from each other, but that they had been more connected in recent history. Genetic variability was similar to that of other lepidopterans from highly fragmented habitats, but less variable than variability of lepidopterans from more continuous habitats. Populations also had significant heterozygote deficiencies relative to Hardy-Weinberg expectations and high inbreeding coefficients. These studies suggested that isolated populations will experience genetic drift and an erosion of genetic variability over time, and that the fairly small, genetically effective population sizes could accelerate this process. Most National Forest System lands in Region 2 are at the western extent of the regal fritillary range, where the effects of genetic isolation are likely to be most pronounced. Maintaining or augmenting connectivity between regal fritillary populations should be a top conservation priority to help mitigate genetic drift and an erosion of genetic variability over time.

Life history characteristics

The facts that regal fritillaries do not migrate and are unable to survive in the altered landscapes that surround the fragmented prairie remnants have important conservation implications. Although they have greater dispersal capability than most other prairie butterflies, the odds of successfully repopulating distant prairie fragments are low. If an isolated population in the highly fragmented prairie landscape is extirpated,

it is unlikely that it will be repopulated. Therefore, the entire life cycle must be completed successfully each year at each site for local populations to persist through time at those sites.

Mating occurs soon after the females emerge in late June to early July, but females do not begin laying eggs until late August or early September. Diverse nectar resources are required to provide adequate nutritional resources throughout the extended flight of females. Regal fritillaries have extraordinarily high potential fecundity per female (Wagner 1995, Allen 1997), and they appear to place a premium on the number of eggs produced, rather than maximizing the survival of individual eggs. The larvae hatch after two to three weeks, but since their larval food plants are senesced at this time, they immediately enter winter diapause as first instars. In the spring, they end diapause and begin feeding on freshly emerged violet leaves. They complete their development by late May to June and enter the pupal stage, which lasts from 2.5 to 4.0 weeks (Wagner et al. 1997). They are in the leaf litter during these immature stages and vulnerable to extreme weather, disease, and fire.

Ecological influences on survival and reproduction

During the adult flight, severe storms can cause direct adult mortality, and prolonged periods of cool temperatures, overcast skies, and rain can limit reproduction by limiting adult activity. The availability of diverse nectar sources throughout the flight may be a critical factor limiting fecundity. Unfed first instar larvae are extremely vulnerable to extreme conditions during the winter and during their initial search for suitable food plants in the spring. Extremely harsh winters, late hard frosts following a spring thaw, severe storms, or cool damp conditions can all negatively affect their survival. The impacts of extreme weather can be significant because they are often expressed over a large geographic area. Disease, parasitism, and predation can also influence the survival of each stage in the life cycle. Disease has been demonstrated to have a major impact in captive breeding programs (e.g., 80 percent mortality from the polyhedrosis virus (NPV)). This virus can be transmitted from females to their offspring in eggs, or between individual larvae through their frass (excreta) (Wagner et al. 1997). Parasitism of the larvae by Hymenoptera has also been shown to be a mortality factor (Kopper et al. 2001a).

Factors limiting population growth

The size and quality of suitable prairie fragments are likely the most important factors limiting population size in a given area. The size and reproductive potential of populations associated with small sites are limited, and it is more likely that a catastrophic event will affect an entire population. Litter buildup can limit population growth by making it more difficult for first instar larvae to locate food plants, lowering the abundance and nutritional quality of the food plants, and reducing flowering of nectar sources (Dana 1991). Larval development rates are proportional to temperature, so unusually cool conditions could slow growth rates and prolong exposure to mortality factors (Dana 1991). During the adult flight, prolonged periods of cool temperatures or overcast skies and rain will limit adult activity, potentially limiting reproduction. Long-lived butterflies like regal fritillaries use food resources for egg production (Opler and Krizek 1984), so a constant supply of nectar is necessary to maintain maximum fecundity. Regal fritillaries only have a single generation per year; therefore, they are expected to recover more slowly than species with several generations per year (Swengel 1996, Panzer 2002). Larval food plants are not available at the time the larvae hatch, and they overwinter without feeding as first instars. These tiny larvae must contend with surviving harsh winter conditions, disease, parasitoids, and direct and indirect mortality from fires that consume the vegetation where they are sheltered. Those larvae that survive the winter must contend with locating freshly emerging violet leaves in the spring before exhausting their limited reserves. The extraordinarily high female fecundity may be an adaptation to compensate for high mortality during this stage.

Community ecology

Disease, parasitism, and predation

Royer and Marrone (1992) state that there are no known diseases or predators that are specific to regal fritillaries. Parasitism, predation, and viral or fungal pathogens are likely mortality factors, and the spread of a parasitoid or pathogen has the potential for rangewide impacts (Wagner et al. 1997). Parasitoids or pathogens may have played a part in the decline of eastern regal fritillary populations, but there is little or no direct field evidence for this (Zercher et al. 2002, NatureServe 2005). Disease has proven to be

an important mortality factor in attempts to rear regal fritillaries in the lab. NPV can be transmitted from females to offspring in eggs or between individuals through frass (excreta), and in one captive group, this virus caused 80 percent loss (Wagner et al. 1997). If reintroduction programs are to be successful, it will be necessary to culture virus-free lines (Wagner et al. 1997). Mortality rates were also high (50 percent) for 12 field-collected larvae observed in a feeding behavior study in Kansas (Kopper et al. 2001a). Three of those larvae were parasitized by Hymenoptera, and three others died from unknown causes. Predation by birds or predacious invertebrates is a likely mortality factor, but no documentation of the impacts of predation on regal fritillary populations was found in the literature. During 15 days of fieldwork at Rowe Sanctuary in Nebraska, no evidence of bird predation of regal fritillaries was noted (Nagle et al. 1991).

Competition

Competition with other *Speyeria* (e.g. Aphrodite fritillary [*S. aphrodite*]) is included among the explanations that have been postulated for the decline of regal fritillaries in the East (Wagner et al. 1997, Mason 2001), but there is very little field evidence to confirm this (Zercher et al. 2002). The impact of competitive interactions on the dynamics of regal fritillary populations is poorly understood and requires further study.

Envirogram

Andrewartha and Birch (1984) define the environment of an animal as ". . . everything that might influence its chance to survive and reproduce." The important ecological relationships that affect regal fritillaries are depicted graphically as an envirogram in **Figure 8**. The "centrum" includes direct influences that are the proximate causes of the regal fritillary's condition; these are grouped into positive (e.g., resources and mates) and negative (e.g., malentities and predators) influences. The "web" includes distal causes of the regal fritillary's condition. They act indirectly by modifying the centrum and can be one to several steps removed from it (e.g., 1st to nth order modifiers) (Andrewartha and Birch 1984).

Important resources for the regal fritillary are larval food plants and adult nectar sources. Adults also require an adequate moisture supply, which can come from nectar plants or wet soil (e.g., pond margins). High quality native prairie or other suitable grassland communities are required to provide these resources. Suitable soil types, rainfall amounts, grazing, and fire combine to influence the type and quality of prairie remnants. Prairie also supports species that are parasites or predators, so conditions that favor those species will have an indirect, negative impact on regal fritillaries. Malentities include habitat loss or degradation resulting from agriculture, development, woody succession, exotic invaders, and overgrazing, and direct mortality of larvae resulting from prescribed fires, overgrazing, or extreme weather events. It is important to note that activities such as fire and grazing can have both positive and negative effects, and they must be used with caution to maximize positive impacts and minimize negative impacts.

CONSERVATION

Threats

Grassland conversion

Habitat loss and fragmentation are the greatest historical factors contributing to the decline and current status of the regal fritillary, and continued elimination or degradation of the native prairie and grassland habitats they require are the greatest future threats to this butterfly. Populations in the East were primarily associated with wet meadows and "human-maintained" grasslands (Schweitzer 1993, Wagner et al. 1997). The elimination of livestock grazing, reforestation of abandoned farmland, row crop agriculture, and urban growth are all factors that contributed to the loss and degradation of the open habitats regal fritillaries required (Dunwiddie and Sferra 1991, Zercher et al. 2002). In the Midwest and Great Plains, regal fritillaries are primarily associated with native tallgrass prairie and wet meadows. Conversion of native prairie to row crop agriculture has had the greatest historical impact in this area, and activities that continue to eliminate remnant prairie habitats include row crop agriculture, urban development and housing construction, road construction and maintenance, gravel mining, and wind generators. In the absence of fire and grazing, some prairies will eventually be lost to encroachment by woody vegetation. While this can include native woody species, it has been exacerbated by the introduction of many aggressive exotic woody species that are very difficult to control. Other invasive exotic species can also threaten to degrade and eventually eliminate prairie habitat.

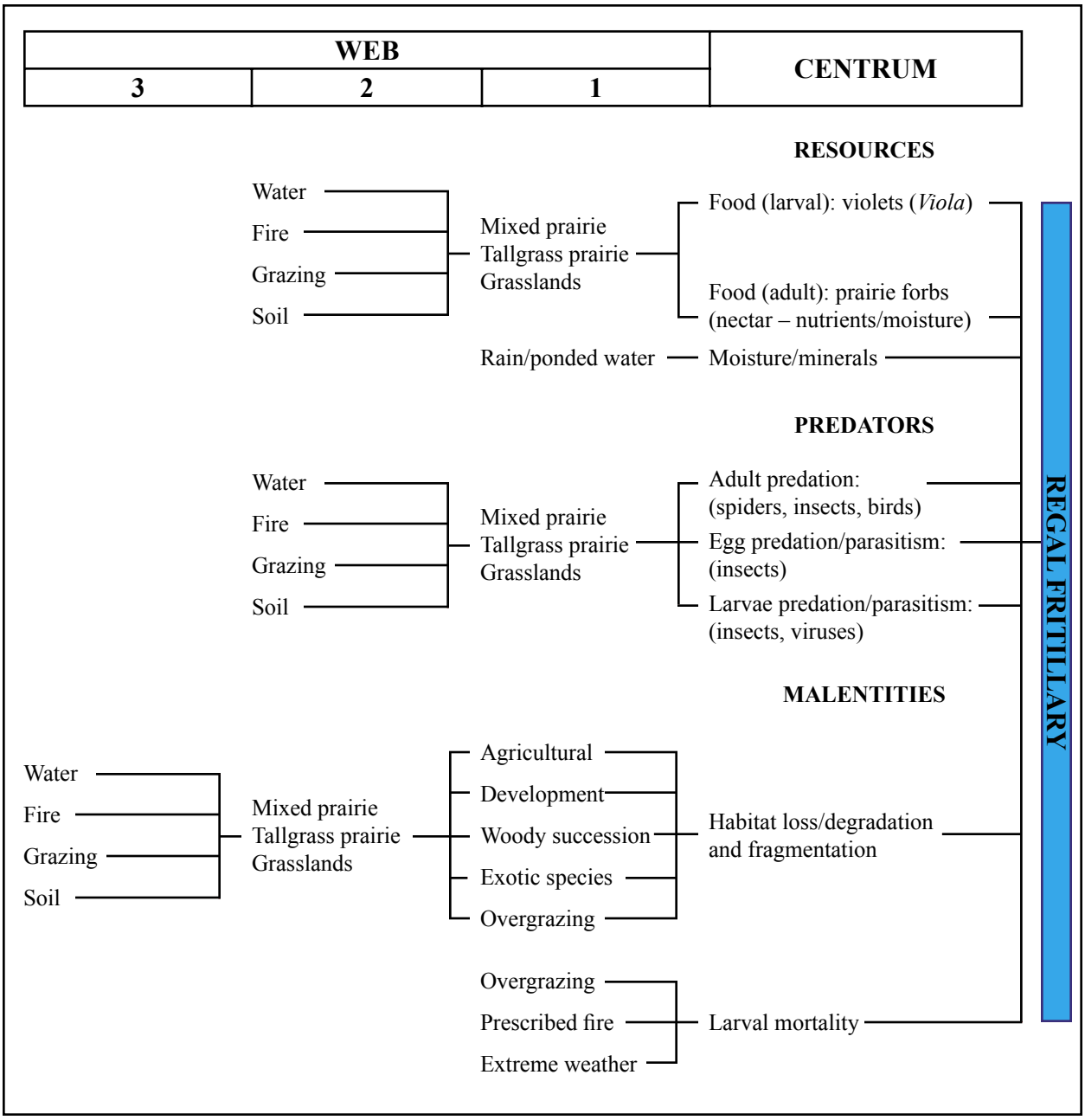

Figure 8. Envirogram for the regal fritillary.

Prescribed burning and wildfires

Prescribed fire benefits prairie specialist butterflies, such as the regal fritillary, by helping to control habitat loss to cool-season exotics and woody vegetation, increasing the vigor of native species (including larval food plants), and increasing flowering rates of important nectar sources. However, to reap these benefits, the butterflies must either survive the fire or recolonize burned areas from an adjacent source. Negative effects of fire can include direct mortality of larvae in the litter layer during dormant season burns (Dana 1985, 1991), and indirect mortality of larvae resulting from exposure to extreme winter conditions after fall burns remove the insulating litter layer. Improperly timed burns can also temporarily limit the availability of critical resources (e.g., larval food plants, nectar sources) immediately following the burn or by altering their phenology (e.g., delayed blooming due to a late burn). Given these factors, it should be assumed that overly extensive (e.g., burning all or most of the regal fritillary habitat at one time) or excessively frequent (e.g., every one to two years) fires will negatively affect regal fritillary populations (NatureServe 2005).

Studies in Kansas and Nebraska have suggested that regal fritillaries can persist with a moderate fire management regime. At Konza Prairie in Kansas, burning and grazing occur in a shifting mosaic, and Ottoe skippers, byssus skippers (*Problema byssus*), and regal fritillaries are abundant (Wright et al. 2003). Huebschman and Bragg (2000) examined the impact of a late spring burn on a regal fritillary population at Nine-mile Prairie in Nebraska. Regal fritillaries were observed throughout the study area in the pre-burn year, declined significantly in the burn unit during the first part of the post-burn flight, and then recovered to the same numbers as the unburned unit later in the season. Regal fritillaries have persisted at the site with a 3- to 4-year burn frequency since 1979. Other studies have consistently shown that aggressive fire management programs tend to depress prairie-specialist butterfly populations (Swengel 1996, Swengel 2001c, Swengel and Swengel 2001, Swengel 2004). Recent (1999-2003) upward trends for regal fritillary populations at monitored sites in Wisconsin suggest that those populations are benefiting from more moderate burn regimes and permanent non-fire refugia (Swengel 2004).

Grazing effects

Heavy grazing is a threat to regal fritillary populations (Hammond and McCorkle 1983[84], Royer and Marrone 1992, Dana 1997, Selby 2003c, 2004b, 2006b), but light to moderate grazing may actually be "highly favorable" to regal fritillaries and their larval food plants (NatureServe 2005). Eastern populations were often associated with artificial grassland habitats that were created and/or maintained by various agricultural practices, including mowing and grazing (Schweitzer 1993, Wagner et al. 1997). The elimination of grazing throughout the New England states may have contributed to the loss and/or degradation of the habitat (Dunwiddie and Sferra 1991). By the early 1980's, regal fritillaries had been eliminated from all but four island sites, and Dunwiddie and Sferra (1991) suggest that continued grazing at three of those four sites may have been a factor in their survival. On Rhode Island's Block Island, ovipositing females may have actually favored areas that were currently grazed or grazed the previous month (observations by Schweitzer; cited in NatureServe 2005). Cattle removed most of the overstory but did not severely graze the violets, which were more abundant in grazed areas (Mello 1989).

Grazing also appears to be an important component of regal fritillary habitat management further west. In studies of regal fritillaries in several Midwestern states, light to moderate grazing and haying were among the habitat factors that favored regal fritillary populations (Swengel 1997, 2001b, 2001c, Swengel and Swengel 2001). Wright et al. (2003) also found that regal fritillaries, Ottoe skippers, and byssus skippers were abundant at Konza Prairie in Kansas, where grazing and burning occurred in a shifting mosaic. Debinski and Kelly (1998) found that violet densities were significantly higher in moderately grazed prairies.

While light to moderate grazing appears to benefit regal fritillary populations, especially if there is some contiguous ungrazed habitat, heavy grazing is a threat (Royer and Marrone 1992, Dana 1997, Selby 2003c, 2004b, 2006b). In a study at Rowe Sanctuary in Nebraska, regal fritillaries were abundant on the 73-ha (180-acre) prairie, but none were found on adjacent overgrazed pastures (Nagel et al. 1991). Reduced availability of nectar resources is likely the primary factor, but changes to vegetative structure, removal of larval host plants, and trampling eggs and larvae may also be factors (Dana 1997, Fritz 1997).

Grazing allotments are a common practice on National Forest System lands, so it is important to understand the impact of grazing on the flora and fauna. There might be unique impacts of grazing on community structure (e.g., favoring mixed grasses over tall grasses; favoring certain forbs) that are not replicated by other management methods (Dana 1997), and properly managed grazing could be an alternative to other forms of management (Royer and Marrone 1992). Royer (2002, 2003) recently conducted surveys for five butterfly species, including the regal fritillary, in the Little Missouri and Blue Buttes National Grasslands in North Dakota. He noted that grazing is the "primary if not the sole" disturbance in the study area, and that it was important to manage grazing to minimize its impact on the abundance of larval food plants or adult nectar sources.

Exotic species

Prairie remnants survive in the context of a hostile environment. They are often surrounded by row crop agriculture and face a constant influx of eroded soil complete with annual weed seeds. Cool season exotics (e.g., smooth brome [*Bromus inermis*], Kentucky bluegrass [*Poa pratensis*]) have been introduced into many prairie pastures, and grazing practices often favor these species. Other threats include aggressive perennial species (e.g., leafy spurge [*Euphorbia esula*]) that can replace the diverse native

communities with dense monocultures. Aggressive non-native woody species have exacerbated the tendency of native grasslands to be lost to encroachment by woody vegetation. These invaders are difficult to control and may require a combination of mechanical removal and chemical treatment.

Pesticides

The control agent used in gypsy moth control programs is *Bacillus thuringiensis* (Bt), a bacterial pathogen that is lethal to all Lepidoptera larvae (Williams 1999). Gypsy moths are forest species, so most control programs target forested areas and should not impact regal fritillaries (NatureServe 2005). However, in the East where populations occurred in grasslands associated with woodland edges, gypsy moth spray programs may have been a final factor in the loss of some populations (Schweitzer 1993, Williams 1999). These programs were also considered a threat in Ohio (Shuey et al. 1987a). In recent years, concerns have been raised about possible contamination of milkweeds, the larval food plants for monarch butterflies, by pollen from Bt corn. In a laboratory setting, high levels of Bt corn pollen on milkweed leaves negatively affected larval development and survival; but under natural conditions, the levels of Bt pollen adhering to milkweed leaves within or close to a field with Bt corn was too low to impact larval development (Dively et al. 2000, Hellmich et al. 2000, Sears et al. 2000). Those results suggest that it is unlikely that Bt corn will affect regal fritillaries, but additional studies focused on regal fritillary populations found on prairies adjacent to Bt cornfields may be warranted. Indiscriminant use of insecticides for pest control on rangeland or adjacent cropland can be a major direct threat to regal fritillaries and other prairie-specialist butterflies. Royer and Marrone (1992) cite the combination of drought and grasshopper control programs along the Red River Valley in North Dakota as having serious impacts on Poweshiek skipperling populations. Broadcast spraying of herbicides, which usually targets dicots, can also affect regal fritillary populations indirectly by eliminating larval food plants and important nectar sources.

Over utilization for commercial, recreational, scientific, or educational purposes

Due to the high reproductive capabilities of insects, collecting rarely has an impact on insect populations and should not generally be a problem for most butterflies (Pyle et al. 1981, Hammond and McCorkle 1983[84]). Destruction of habitat and/or food resources is usually the primary factor responsible for population declines (McCorkle 1983[84]). However, populations that are already depressed or concentrated in small habitat fragments can be more sensitive to overcollecting (NatureServe 2005). One regal fritillary population in Maryland disappeared shortly after over 50 adults were collected on 4 and 6 July 1978, and a second population was rumored to have suffered the same fate in the 1980's (NatureServe 2005). The prolonged period of reproductive diapause in regal fritillary females might make them more sensitive to collecting than other butterfly species, since females removed from the population during this time have not had a chance to reproduce (NatureServe 2005). Regal fritillaries are also more attractive to collectors and have more potential commercial value than most prairie-specialist butterflies. In Colorado, overcollecting is listed as a possible threat due to the species' attractiveness to collectors and their colonial habit (Colorado Natural Heritage Program 2005b). Collecting for commercial or recreational purposes can pose a threat to small, isolated populations, but limited collecting for scientific documentation will not usually affect a population unless it is already severely depressed. Scientific collector permits are required in states where regal fritillaries have legal protection, and it is usually necessary to get permission to collect on protected areas.

Environmental factors

Extreme weather conditions can pose a threat to prairie specialist butterflies, such as the regal fritillary, and the impact can be expressed over a large geographic area. The tiny first instar larvae are susceptible to extreme winter weather, late spring hard frost, severe storms, or cool damp conditions. Humid conditions have been associated with increased susceptibility to bacterial septicaemia in some skipper species (MacNeill 1964), but evidence for this was not found for regal fritillaries. Cooler than normal temperatures could prolong exposure to mortality factors by slowing larval development rates (Dana 1991). During the adult flight, severe storms could cause direct adult mortality, and prolonged periods of cool temperatures, overcast skies, and rain could limit reproduction by limiting adult activity.

Conservation Status of the Regal Fritillary in Region 2

Kansas, Nebraska, and South Dakota are at the heart of the Great Plains portion of the regal fritillary's range where it is the most secure, so conservation

efforts in these states are critically important to the long-term survival of the species. Regal fritillaries are most abundant in the eastern two-thirds of those states, and tend to be more local and uncommon further west. Most regal fritillary observations in Colorado are considered late-season strays, and there are only three recent records that might represent breeding colonies. No documentation was found for extant breeding colonies of regal fritillaries in Wyoming.

Regal fritillaries are abundant in and around Fort Pierre National Grassland in central South Dakota (Marrone 2002), and this unit is probably the most important National Forest System land in Region 2 for regal fritillary conservation. Other National Forest System lands in southwestern South Dakota and northwestern Nebraska are in areas where regal fritillaries are likely to occur, and those units could play an important role in conserving regal fritillary populations at the western extent of their range. However, there are no recent records for confirmed breeding colonies in those units, and surveys are needed to determine the status of regal fritillaries in those lands. The regal fritillary has not been documented from National Forest System lands in Colorado, Kansas, and Wyoming, and most units in those states are not in areas where permanent regal fritillaries populations are likely to occur.

Potential Management of the Regal Fritillary in Region 2

Implications and potential conservation elements

Regal fritillaries in Region 2 require relatively non-degraded native mixed- and tallgrass prairie; they cannot survive in the surrounding altered landscape. These butterflies do not migrate and have limited dispersal capability, so if isolated populations are extirpated, it is unlikely that they will be repopulated. Each stage of this species' life cycle must be completed successfully each year at each site for local populations to persist through time at those sites. Historic loss, degradation, and fragmentation of the prairie landscape have contributed to the decline and current vulnerability of regal fritillary populations.

To prevent further losses, critical habitat areas (e.g., prairie ecosystems) need to be identified, protected, and managed to maintain or improve their size, quality, and connectivity. Land management on National Forest System lands should be directed toward maintaining intact native prairie remnants, preventing encroachment by woody vegetation and exotic species, maintaining adequate nectar sources, and increasing the vigor of larval food plants. Small, isolated regal fritillary populations are more vulnerable to events that might have been survived in the original prairie landscape, so management activities need to be designed carefully to avoid exacerbating those vulnerabilities. The timing, intensity, extent, and duration of management activities such as prescribed burning, grazing, and haying need to be adapted to ensure the availability of critical resources (e.g., nectar plants; larval food plants) when they are needed, and to mitigate any direct mortality that might result from them.

The status of regal fritillary populations on National Forest System lands in Region 2 is not well documented. One of the top priorities should be to inventory units with suitable habitat, determine the status and distribution of populations within those units, implement appropriate conservation practices (see below), and monitor the results so that management plans can be adapted as needed to maintain and/or enhance the size and health of the populations.

Tools and practices

Habitat management

Management for prairie invertebrates is often incidental to management focused on restoring or maintaining healthy native prairie vegetation. Prairie invertebrates, such as the regal fritillary, should benefit indirectly from the improved habitat, but it is important to make sure that they are not harmed directly by the management, or indirectly through shifts in community composition or structure. Standard habitat management methods are discussed below in the context of their impact on regal fritillaries and other prairie specialist butterflies.

Prescribed burning: Prescribed fire is one of the principal tools used to manage native prairies. It benefits prairie specialist butterflies, such as the regal fritillary, by helping to control habitat loss to cool season exotics and woody vegetation, increasing the vigor of native species (including larval food plants), and increasing flowering rates of important nectar sources. However, to reap these benefits, the butterflies must either survive those fires, or recolonize the area from an adjacent source. The combined results from numerous research projects (Dana 1991, Swengel 1996, Panzer 1998, Swengel 1998, Swengel and Swengel 1999, Huebschman and Bragg 2000, Swengel and Swengel 2001, Panzer 2002, Wright et al. 2003)

have been helpful in developing guidelines for the use of prescribed fire as a management tool for regal fritillaries. Moffat and McPhillips (1993) present a general summary of management guidelines developed from the earlier studies.

When developing prescribed burn plans for National Forest System lands with regal fritillary populations, it is important to understand the interactions between positive and negative effects of fire, and their combined effect on long-term survival. Royer (personal communication, cited in Moffat and McPhillips 1993) has suggested that when burning occurs, it is best to assume that there will be 100 percent butterfly mortality in the burned area. Therefore, only a portion of the regal fritillary habitat at a site should be burned in a given year, and the return interval between burns should be long enough to allow populations in the burn unit to recover to pre-burn levels. Based on the results of his comprehensive study of prairie insects in Illinois, northwestern Indiana, and southwestern Wisconsin, Panzer (1998, 2002) has suggested that three-year burn rotations are appropriate for insect conservation. Swengel (1996) has recommended that no more than 20 percent of the habitat for prairie specialist butterflies should be burned each year, and that burn rotations should be at least five years. Panzer's study did not include regal fritillaries or other prairie specialist species that can still be found on prairies west of his study area (e.g., Dakota skipper, Ottoe skipper, Poweshiek skipperling). Recommended burn rotations for regal fritillary habitat on National Forest System lands in Region 2 could range from three to six years depending on the size and context of the prairie remnants, and the size of the regal fritillary populations. In a large and well-connected prairie landscape with healthy regal fritillary populations, the size and frequency of burns could be increased, but on small isolated remnants with smaller populations, a more conservative approach would be recommended. In either case, it would be important to monitor the impacts of the prescribed burn program on the regal fritillary populations, and to adjust the size and frequency of the burns as needed to ensure full recovery between burns. To maximize recovery rates, it is best to avoid burning adjacent units on consecutive years. Specific management objectives will usually determine the timing of burns (e.g., early vs. late spring, summer, and fall). In each case, the positive and negative effects on regal fritillaries will vary, but if managers follow the guidelines for the size and frequency of burns, the overall impacts should be positive. Swengel (2004) has suggested that permanent non-fire refugia may play an important role in maintaining healthy regal fritillary populations, but those areas would require other forms of management to prevent degradation and/or loss of the native prairie habitat.

Grazing: Grazing by wide-ranging herds of bison (*Bison bison*) and fire were likely the dominant forces that shaped the pre-settlement prairie landscape. It is therefore important to consider the role that grazing should play in managing the remaining fragmented prairie remnants. Currently, most grazing is accomplished by domestic cattle confined to small prairie fragments that are vulnerable to invasive exotic species such as smooth brome and leafy spurge. While the typical manner in which cattle are grazed differs drastically from the historical free-range grazing of bison herds, it may still play an important role in maintaining habitat structure.

The spatial and temporal distribution of grazing intensity can be managed by adjusting stocking rates, modifying grazing regimes (e.g., season-long vs. rotational), and managing water resources to avoid concentrating activity in critical habitat areas (Royer 2002, 2003). Different grazing regimes can have significantly different impacts, and recent research suggests that the combined effects of integrated fire and grazing systems (e.g., patch-burn grazing) may be significant (Fuhlendorf and Engle 2001, Helzer and Steuter 2005). Butterfly numbers tend to be reduced in direct proportion to increasing grazing intensity (Dana 1997, Selby 2006b). Therefore, as a rule, grazing intensity should be lighter than might be typical. Definitions for measures of grazing intensity will vary depending on the type of prairie. For tallgrass prairie, leaving 6 inches or less of stubble might be considered heavy grazing, while for mixed-grass prairie, heavy grazing intensity might be defined by leaving less than 4 inches of stubble. Measures of intensity for regal fritillary conservation will need to take into account both stubble height and the impact on the flowering of nectar sources during the adult flight (June – September). Season-long grazing will tend to spread the impacts throughout the growing season, whereas for rotational grazing, the impacts will be concentrated both spatially and temporally. No matter what grazing regime is used, it will be important to make sure that only a portion of a site is grazed at any given time so that areas with an adequate supply of nectar sources will always be available.

Because very little rigorous research examining grazing impacts on prairie butterflies has been done, any grazing regime should be implemented with caution. Populations of regal fritillaries and other prairie specialist butterflies should be monitored, so

that managers can adjust the intensity, timing, duration, and extent of grazing in response to observed effects on the butterflies. Where possible, bison grazing may be preferable to domestic cattle grazing, since bison feed selectively on grasses while cattle tend to select forbs (Plumb and Dodd 1993), and when free to do so bison graze nomadically, as opposed to the concentrated grazing patterns of cattle.

Haying or mowing: The tradition of cutting prairie hay has helped to preserve many prairie remnants by providing an alternative to row crop agriculture, and in many cases, it has also helped to maintain the quality of those prairies by preventing the accumulation of excessive litter and succession to woody species. The practice also appears to favor prairie-specialist butterflies. McCabe (1981) noted that Dakota skippers have survived on sites with long histories of haying, and Swengel (1996) found that regal fritillaries and other prairie-specialist butterflies were more abundant in hayed than burned prairies.

Haying or mowing can be an effective alternative to prescribed fire, or it can be used to enhance the effectiveness of prescribed fire programs. Advantages of mowing are that it can be done when woody vegetation is already stressed (e.g., late summer when it is hot and dry, and when woody plants have most of their resources above ground), and it can be focused on problem areas. Prescribed fires are usually done in the spring and fall, when woody plants are dormant and have most of their resources stored below ground. Fires also tend to burn least effectively in those areas where woody vegetation problems are the worst, and even when successful in top-killing woody vegetation, vigorous suckers are produced following a burn. Late summer burns can be effective, but it is often difficult to burn hot enough in areas with established woody vegetation. Mowing and other forms of mechanical woody vegetation control can be used to enhance the effectiveness of prescribed fires by opening up areas to be burned so that fine fuels can both develop and burn more effectively.

As with any management practice, the effect of haying or mowing on regal fritillaries will depend on its frequency, timing, intensity, and extent. Many Missouri prairies have a long history of mid-July haying at a frequency of every two to three years, and this practice has been effective in maintaining a high diversity of prairie plants and controlling invasive woody vegetation (Solecki and Toney 1987). However, mid-July haying is likely to eliminate essential nectar sources when they are needed by adult regal fritillaries, so only a portion of a site (e.g., no more than one-third to one-half) should be hayed or mowed in a given year. Delaying haying until later in the season (e.g., September to October) is less likely to affect the availability of nectar sources, and McCabe (1981) has recommended this strategy as a preferred management practice for the Dakota skipper. If an area is mowed too short, the effects on developing eggs or larvae could be negative, so if possible, at least 6 inches of stubble should be left.

Chemical control of exotic species and woody vegetation: Selective applications of herbicides can be an effective way to control exotic species and woody vegetation. Cutting and treating stumps of woody vegetation with a systemic herbicide can effectively prevent suckering, and since treatment is localized, damage to the surrounding vegetation is kept to a minimum. Spot spraying of perennial exotic species might be necessary, but it should always be done as a last resort and with extreme caution to avoid damaging the surrounding vegetation. Non-persistent herbicides (e.g., glyphosphates) are preferable to more persistent herbicides (e.g., picloram), but they may not be as effective. While broadcast spraying with broadleaf herbicides is a common practice in range management, this is not recommended for prairie systems since native forbs are killed along with the targeted exotics. In extreme cases, where native vegetation is almost entirely replaced by non-natives, broadcast applications of non-persistent herbicides (e.g., glyphosphates), followed by reseeding to native vegetation might be necessary. Very late season applications of glyphosphates can be effective in killing non-native cool-season grasses without affecting native species that might be mixed in with them.

Biological control of exotic species: Biological control provides an alternative to the use of non-selective persistent herbicides for treating aggressive perennial exotic weeds. The control agents are tested rigorously to make sure they are "safe" for native species, but it is still a good idea to research any biological control options thoroughly before approving them for use on native prairies. Leafy spurge is one of the prime candidates for biological control. The most effective control agents include several species of flea beetle (*Aphthona* spp.), and they have proven to be much more cost-effective than chemical control methods.

Inventory and monitoring

Pollard transect surveys (Pollard et al. 1975, Pollard 1977, Pollard 1982, Pollard and Yates 1993) are the standard butterfly monitoring methodology adopted by many lepidopterists. They involve

surveying fixed routes (transects) using standardized protocols (e.g., survey speed, time of day, weather), and have the advantages of being fairly simple and easily replicated. The results are relative abundance values for each species that can be used to track trends in relative abundance over time. Absolute population estimates can be useful, but they involve much more labor-intensive mark-recapture methods (Ehrlich and Davidson 1960, Brussard 1970). The "checklist" survey is an alternate methodology in which the survey route is not fixed (Royer et al. 1998). It involves an unrestricted comprehensive search and has the advantages of being fairly simple and focusing the effort in habitat for the target species. Royer et al. (1998) compared the "checklist" and "transect" methods to determine which would be the most efficacious. The number of individuals counted per unit time was significantly higher for the checklist method, but there was no significant difference between the methods for the number of species observed per unit time. However, the checklist method was better at capturing sedentary, habitat-specialist species (e.g., many lycaenids and hesperiids). Royer et al. (1998) concluded that the checklist method was better for obtaining an initial site-specific butterfly species list, but that the transect method was better for long-term monitoring.

Since so little is known about the distribution and abundance of regal fritillaries on National Forest System lands in Region 2, checklist surveys, focused in regal fritillary habitat, are needed first. Once regal fritillary populations are identified, then their habitat requirements and distribution can be defined more clearly, and transect surveys can be designed to monitor those populations. Current Global Positioning System (GPS) technology makes it fairly simple to navigate defined survey routes, and to map the distribution of the butterflies and their preferred habitat areas.

Information Needs

Inventory and monitoring

There is very little information available regarding the occurrence and distribution of regal fritillaries on National Forest System lands within Region 2. USFS personnel were unaware of any regal fritillary records from most units in the region, despite the fact that many of them are in counties where regal fritillaries have been documented. Several National Forest System units are identified in this assessment as having historic regal fritillary occurrences or the potential for them. These units should be evaluated first to determine if they have regal fritillary habitat (e.g., mixed- and tallgrass prairie), and then areas with regal fritillary habitat should be surveyed. At those sites where regal fritillaries are found, it is important to determine whether they represent breeding colonies, to document their distribution and abundance within the sites, and to attempt to define their habitat requirements more precisely for that geographic area. This will make it possible to predict their potential distribution more precisely, and the actual and predicted distribution can be used to make more informed management decisions. Healthy populations of regal fritillaries have been identified at the Fort Pierre National Grassland unit of the Nebraska National Forest, and these should to be monitored as part of an adaptive management program to ensure their long-term survival.

Grazing impacts

Light to moderate grazing is generally thought to benefit regal fritillaries and their larval food plants while heavy grazing is considered a threat, but there is a need for more rigorous research examining the impacts of grazing on regal fritillaries and other prairie-specialist butterflies. This is especially relevant to National Forest System lands since so many of them contain grazing allotments. A study examining the impact of grazing on Dakota skippers was conducted in Minnesota (Selby 2003b, 2003c, 2004b, 2006b). The goal of the study was to examine the effects of grazing on each of the life stages of the Dakota skipper (e.g., adults, eggs, larvae), as well as the adult stage for other concurrent prairie-specialist butterflies. Unfortunately, the study coincided with a dramatic population crash for the Dakota skipper and several of the secondary target species. Populations were too low during the study to collect data adequate to test hypotheses on the adults, much less the other stages. Similar studies are needed to examine the effect of cattle grazing on the regal fritillary. In Region 2, there would also be opportunities to conduct studies comparing the impacts of bison vs. cattle grazing and perhaps even interactions with prairie dogs.

Fire management impacts

Various studies examining fire impacts on prairie butterflies and invertebrates (Dana 1991, Swengel 1996, Panzer 1998, Swengel 1998, Swengel and Swengel 1999, Swengel and Swengel 2001, Panzer 2002) provide general principles that can be applied to fire management. However, there is still a need to conduct additional research examining short- and long-term effects of prescribed burn programs on regal fritillaries and the interaction between prescribed burning and other management options (e.g., grazing

and haying). Specific questions that need to be addressed are the appropriate size (relative to the total area), frequency, and timing of burns, and the value of "permanent non-fire refugia" (Swengel 2004). Patch-burn grazing (Fuhlendorf and Engle 2001, Helzer and Steuter 2005) is a relatively new concept in prairie management, and its effect on prairie-specialist butterflies needs to be examined.

DEFINITIONS

Chorion – outer covering of an insect egg.

Diapause – a period of suspended growth and development.

Disjunct – separated; disconnected; as used here, populations that are disconnected from the main population.

Diurnal – active during the daytime, rather than at night.

Extant – populations that are still in existence; not lost, destroyed, or extinct.

Extirpate – to destroy completely or exterminate a population.

Glyphosphate – a general use, non-persistent systemic herbicide.

Habitat capability – the overall capacity of the habitat to support populations of the target species, including habitat components such as size, quality, fragmentation, isolation.

Instar – insect stages between molts; larval stages in this paper.

Larva – immature stage between egg and pupa in insects with complete metamorphosis.

Metapopulation – localized group of smaller populations living in separate habitat patches (Levins 1970, Mason 2001)

Oocyte – cell that will undergo meiosis to produce an egg.

Oviposition – laying eggs; especially in insects with an ovipositor (egg laying structure).

Picloram – a persistent systemic herbicide in the pyridine family of compounds, which is used to control woody vegetation.

Suckers – a secondary shoot arising from the base of a tree or shrub; multiple suckers are often produced after cutting or top-killing a tree or shrub.

Transition Zone – includes ponderosa pine in the west, grassland-forest mixture in the Midwest, and numerous deciduous trees, white pine, hemlock, etc. in the east (Scott 1986).

Univoltine – having a single generation per year.

Upper Austral Zone – relatively pure deciduous woodland in the East transitioning to grassland in the West (Scott 1986).

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