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Comparison of prairie sites and classification of their habitat attributes in relation to abundance of the Regal Fritillary Butterfly (*Speyeria idalia*)

by

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Abstract

Habitat and landscape attributes of eighteen prairie fragments in western Minnesota were considered in relationship to abundance of the regal fritillary butterfly, *Speyeria idalia*, in 1997 and 1998. Regal fritillary butterflies, their larval host plants (*Viola* spp.), and adult nectar sources were counted at each site. Environmental factors affecting variability in abundance (temperature, sunshine, wind speed, cloud cover, and site moisture) were also recorded. The objective was to determine whether regal fritillary abundance at these sites was related to patch size and proximity to other potential regal fritillary habitat. Analysis of the data, using stepwise linear regression, showed that the area of contiguous, road-free habitat available at each site accounted for more than 60% of the variance in regal fritillaries observed. An additional 11% of the variance was attributable to moisture conditions at the sites. Proximity of the sites to suitable but non-contiguous habitat did not show a significant effect.

Introduction

Among North America's largest and most beautiful butterflies, the regal fritillary (*Speyeria idalia*) is probably the least well known. Once common from the Atlantic coast to the Rocky Mountains, the regal fritillary has been extirpated in about 40% of its range (Schweitzer 1989). Historically, regal fritillaries were found in at least thirty states and provinces, from New Brunswick south to northwestern North Carolina, and west to southeastern Montana and northeastern Colorado. In its eastern range, the butterfly inhabited wet meadows and boggy pastures; tallgrass prairies are its habitat in the Midwest and Great Plains states. The regal fritillary has declined sharply in much of its range, and has disappeared from New Brunswick, Ontario, Manitoba, Maine, New Hampshire, Vermont, Rhode Island, Connecticut, New York, New Jersey, Maryland, Delaware, North Carolina, Tennessee, Georgia, West Virginia, Kentucky, Ohio, Indiana, Michigan, Wyoming, Montana and Arkansas (Schweitzer 1989, Opler and Malikul 1992, Williams 1999). Many causes have been postulated for the widespread extirpation of eastern populations, including development or reforestation of much of the land in New England, competition with *Speyeria aphrodite*, pesticide drift, and over-collecting (Bliss & Schweitzer 1987). However, the sharp decline of this species cannot be reliably attributed to any single cause.

Currently, regal fritillaries may be found in three general areas. There are several populations in the great plains states (North Dakota, South Dakota, Nebraska, Colorado, Kansas, and western Missouri); there are relatively few, fragmented populations in the Midwest (Minnesota, Iowa, Wisconsin, Illinois, and northeastern Missouri); and there are two isolated populations in the east, one in Pennsylvania and one in Virginia (Williams

1999). The number of populations in the Midwest has declined due to loss of regal fritillary habitat (prairies, hayfields, and grazing lands) to cultivation (Bliss & Schweitzer 1987).

Minnesota's tallgrass prairies extended over almost 20 million acres before European settlement; less than one percent of the state's native prairie remains today (Tester 1995). In Minnesota, the regal fritillary is a species of special concern, existing in small populations on fragmented prairie sites. Although regal fritillaries have been sighted in at least 28 Minnesota counties at some time within the last 20 years, they exist in low densities and continue to be threatened with habitat destruction (Dana 1987).

Prior to European settlement, regal fritillaries lived in continuous populations on Midwestern grasslands, probably since long before the last Ice Age (Opler & Krizek 1984). In a large expanse of unbroken prairie, the ability to disperse widely in search of nectar sources or prime oviposition sites could be highly advantageous. Conversion of most native prairie to cropland within the last 150 years has relegated such specialists to isolated prairie fragments. Small, isolated populations are vulnerable to local extinction and loss of genetic diversity unless ovipositing females are successful in locating other suitable sites.

Regal fritillaries are known to be strong and rapid fliers, and it is generally assumed that small populations found on prairie fragments are members of local metapopulations, connected by adult movement between fragments. A metapopulation is a localized group of smaller populations living in separate habitat patches (Levins 1970). Most individuals remain in their natal patch, but there is interaction through small-scale movement between patches, which are separated by unsuitable habitat. Within a cluster of these habitat patches, a metapopulation may survive for many years, provided that individuals are able to move across unsuitable habitat from one patch to another. Extinction of one colony, due to small-scale disturbance, will be offset by recolonization from another, as long as there is a sufficient total area of habitat fragments.

The size of habitat patches and their degree of isolation from occupied habitat have been shown to be important in metapopulation dynamics. Small habitat patches are less likely to be occupied than large patches (Hanski et al. 1994, Gutierrez et al. 1999), and local populations in small, isolated patches are more likely to go extinct (Hill et al. 1996, Wahlberg et al. 1996.) Isolated habitat is less likely to be occupied by butterflies (Gutierrez et al. 1999) and is occupied at decreasing density with increasing isolation from other populations (Hanski & Thomas 1994). Distance and unsuitable vegetation may form barriers to dispersal (Thomas 1982, Thomas & Harrison 1992, Sutcliffe and Thomas 1996, Kuussaari et al. 1996, Haddad 1999)

A knowledge of the dispersal ability and levels of migration of a threatened species is vital to understanding how the species operates within a spatially structured population system. Thus, information about mobility is crucial to conservation and management decisions (Hill et al. 1996, Sutcliffe et al. 1997, Mousson et al. 1999). Although many authors have noted the strong, rapid flight of the regal fritillary, quantitative, empirical data on regal fritillary movement has been almost nonexistent in published literature. In an unpublished mark-release-recapture study done on New England islands, a population of about 95 pairs ranged over several thousand acres on Nantucket Island, in response to local changes in nectar availability, over the course of a summer (Bliss and Schweitzer 1987, Schweitzer 1989). There are no additional studies to support the widely-held theory that regal fritillary populations interact within a metapopulation structure.

Two recent studies suggest that regal fritillary dispersal may be more constrained than previously believed. In a mark-release-recapture study on a 73 acre prairie in Nebraska, Nagel et al. (1991) found that recaptured butterflies had moved an average of 68.6 meters per day and a maximum of 228.6 m per day. Few regals moved from interior plots to the margins, and no regals were found in the overgrazed pastures which border the prairie to the east and the west. This suggests that regals in this population seldom emigrate from this prairie. A behavioral study by Ries and Debinski (in press) showed that regal fritillaries turn away from prairie borders, avoid exiting prairie plots, and are likely to return after exiting prairies that are bordered by row crops, tree lines, or non-prairie grassland.

In this study, I characterized eighteen prairie sites in western Minnesota according to regal fritillary abundance, host and nectar plant abundance, site moisture, patch size, and proximity to other potential regal fritillary habitat. I chose sites of varied sizes and degrees of isolation; my objective was to determine whether regal fritillary abundance at these eighteen sites could be related to site size and to degree of site isolation, as would be expected if this species functions within a metapopulation structure. I hypothesized that regal fritillary abundance would be greatest on the largest prairie fragments and on the sites that were part of a complex of neighboring prairie fragments, and that relatively fewer regals would be recorded on small and isolated sites.

Methods

Study sites

I conducted my research on eighteen prairie fragments in Norman and Clay counties, in northwestern Minnesota, on the North Dakota border. This area is characterized by warm summers (average temperature 20 degrees C) and very cold winters (average temperature -12 degrees C). Average annual precipitation is 56 cm; about 75% falls during the period from April to September. The soils in this region are primarily Mollisols, with occasional Entisols, Histosols, and Alfisols (Jacobson 1974, Jacobson 1982). The study area is in the southern tip of the glacial Lake Agassiz basin, a region characterized by level soils prone to wetness, interspersed with the well-drained sand and gravel ridges of ancient glacial beaches.

All of my study sites were publicly owned and included six sites in Norman County and thirteen in Clay County (Table 1). I subsequently eliminated one of the Clay County sites (Buffalo River State Park 16) because it was primarily wetland and woodland. Many of these survey sites were located within a contiguous network of prairies, the largest of which had an area of 26.75 square kilometers (or 17.85 square kilometers if intervening roads are considered to make adjacent areas discontinuous).

Surveys for nectar plants and larval host plants

In June and July of 1999, I did vegetation surveys to determine host plant and nectar plant abundance. I sampled the vegetation by walking four parallel, equidistant transect lines through each square or rectangular site. On each transect at these sites, I sampled an equal number of one-square-meter plots. On irregularly shaped sites, I used a map and compass to plan and walk transect routes of comparable extent to those in rectangular sites. Transect surveys covered areas ranging from 8 hectares to approximately 300 hectares in size. The number of plots sampled at each site was proportional to the square root of the area of the site, multiplied by a factor chosen to yield a minimum of 20 plots to be sampled at the smallest sites.

I counted and recorded host plants (*Viola* spp.) and nectar plants (*Liatris punctata* Hook, *Cirsium* spp., *Monarda fistulosa* L., *Asclepias* spp., and *Echinacea angustifolia* DC.) using a 1 m x 0.5 m plot frame at predetermined intervals on the transect lines. Because the larval host plants, *Viola* species, are patchily distributed, I was concerned that I might miss or under-count the host plants by sampling only at regular intervals. Therefore, I made two additions to my sampling protocol. As I walked the transects, I inspected the vegetation directly before me and stopped to count *Viola* plants (only) whenever I saw them. Secondly, each time I observed a *Viola* plant, within or between the regular plots, I surveyed an area of six square meters (contiguous with the position of the plant) for *Viola* spp.

Surveys for butterflies and nectar plants in bloom

I surveyed each site once during the 1998 flight period and once or twice during the 1999 flight period, counting regal fritillaries and blooming nectar plants. I confined my observations to July and early August, the time period when both sexes had emerged and before males had begun to die out. Before each survey of butterflies, I recorded the date, starting time, temperature, wind speed (measured using a Dwyer wind meter), and percent cloud cover. At most sites, I walked the same route I had used for the vegetation surveys. As I walked through each prairie site, I continuously recorded the species and number of all butterflies I saw within a radius of 5 meters in front of me and to both sides. I also continuously recorded the number of blooming nectar plants within the same 5 meter radius. When I observed a regal fritillary nectaring, I noted this and recorded which plant was used. At the end of each survey, I recorded the ending time, the percentage of the total time during which the sun was shining, and the approximate route length. I classified each site as dry, wet, or mesic, based on my observations at the time of the first survey at each site. Sites on which I observed exposed sand and gravel, no saturated soils, and no wetland plants, I classified as dry; sites on which I observed standing water, saturated soils, and wetland plants I classified as wet. The mesic classification includes sites where neither extreme was observed, as well as those in which occasional dry or wet areas occurred.

Landscape analysis

Standard measures of the effects of patch isolation on butterfly populations (Hanski & Thomas 1994) require that one know the area, distance between occupied patches, and population size for every occupied patch in the study area. Since the study area included hundreds of patches of potential regal fritillary habitat, it was impractical to visit all of them to survey for either the presence or the number of regal fritillaries. However, patch models of metapopulation dynamics predict that increasing patch area will decrease the extinction rate, and increasing patch isolation will decrease the colonization rate (Hanski & Thomas 1994). I used a simple regression model that incorporated the patch area and a population index for each of the eighteen sites that I surveyed, as well as the amount of potential regal fritillary habitat that might be accessible from each site, to separate the effects of patch size from those of patch isolation.

Working in ArcView GIS Version 3.1, and using data sets provided by the Minnesota Department of Natural Resources, I constructed maps of Clay and Norman counties and delineated my study site locations. In the DNR data, actual and potential regal fritillary habitat was classified as either "grassland" or "transitional agricultural land" (land previously used for grazing or growing crops). Because I could not reliably separate the two categories (and occupied sites that I visited were mapped in both categories), I treated them as one category (potential regal fritillary habitat) in my analysis.

I used three different approaches to investigate the possible relationships between regal fritillary abundance and available habitat area. I first considered the possibility that the amount of habitat available to regal fritillaries at any particular site might be limited only by their physical ability to fly to that site. Since estimates vary concerning the distance that regal fritillaries will fly to move from one suitable habitat area to another (Nagel et al. 1991, Debinski & Drobney 2000), I used four different scales to estimate the amount of habitat available. Using the circle tool from the Arc View drawing tool palette, I drew circles that extended beyond the boundary of each of my sites to a distance of 50 m, 500 m, 1000 m, and 5000 m., to determine the area (square kilometers) of habitat available to butterflies on these sites if they were to fly this distance from the site. I used Arc View's "select features using shape" function to highlight all "grassland" and "transitional agricultural land" parcels that were partially or entirely within these circles.

Potential available habitat accessible from each site, at each of the four distance scales, was calculated by adding the area of all parcels that were highlighted.

I also considered the possibility that landscape features such as agricultural fields and roads might represent barriers to regal fritillary movement. For each site, I used Arc View to calculate the area of potential regal fritillary habitat contiguous with the site (square kilometers of "contiguous habitat area"), considering cultivated land as a barrier to movement. Similarly, my final habitat category ("contiguous habitat area, roads as barriers") considers both cultivated land and roads as barriers to movement at each site.

Statistical methods

I used Statistix 7.0 to perform a stepwise linear regression, using mean regal fritillaries observed per hour as the response variable. The model considered the following predictor variables: host plant abundance, blooming nectar plant abundance, environmental variables (temperature at the time of the survey, the percentage of the total time during which the sun was shining, wind speed), length of survey time, site moisture classification made at time of first sampling, area of non-contiguous habitat available at four distance scales, area of contiguous habitat disregarding roads, and area of contiguous habitat regarding roads as barriers to movement (Table 2). Values for two or three observations at each site were averaged ($n=18$) so that each site corresponds to a single observation in the model. I created indicator variables for site moisture classification (dry, mesic and wet); the others were included as continuous variables. The threshold for significance was $P < 0.07$.

Results

In 1998, I saw no regal fritillaries on four of the study sites (Table 3). For surveys during which I saw regal fritillaries in 1998, abundance ranged from 0.6 regal fritillaries per hour (at Buffalo River State Park, # 15) to 40.7 regal fritillaries per hour (at Felton, #8). The average abundance of regal fritillaries for all surveys during which I observed them in 1998 was 12.5 regal fritillaries per hour.

In 1999, I saw no regal fritillaries on four of the study sites (Table 3). For surveys during which I saw regal fritillaries in 1999, abundance ranged from 0.3 regal fritillaries per hour (at Bluestem, #17) to 34.3 regal fritillaries per hour (at Bicentennial #9). The average abundance of regal fritillaries for all surveys during which I observed them in 1999 was 11.2 regal fritillaries per hour. At two of the sites (Dalby WMA, #1, and Ulen WMA, # 7), I saw no regal fritillaries in 1998 or 1999.

Larval host plant abundance, blooming nectar plant abundance, the environmental variables at the time of sampling, and the length of survey time had no significant relationship to regal fritillary abundance. Moisture conditions at the time of the first (1998) sampling accounted for 11% of the variance in regal fritillary abundance; specifically, dry sites are related to higher numbers of regal fritillaries observed per hour. When observations were grouped by soil moisture classification, dry sites had the highest regal fritillary abundance, mesic sites had intermediate abundance, and wet sites had the lowest regal fritillary abundance. The number of regal fritillaries observed per hour was most strongly predicted by the area of contiguous, road-free habitat available at each site. This predictor accounted for more than 60% of the variation in the response variable (Table 4). No significant relationship was found between regal fritillary abundance and the area of potential habitat that was adjacent to surveyed fragments but separated from them by roads. There was also no significant relationship between regal fritillary abundance and the area of non-contiguous potential habitat that was available at four scales of distance from surveyed fragments.

Discussion

Numerous studies (Hanski 1994, Hanski et al. 1994, Wahlberg et al. 1996, Sutcliffe et al. 1997) have shown that patch size is an important predictor of butterfly abundance. While it is clear that cultivated land provides no habitat for regal fritillaries, their patterns of habitat use in the isolated prairie and grassland fragments scattered over the cultivated Midwestern landscape are not well understood. By relating regal fritillary abundance to the area of contiguous, road-free potential habitat, this study is the first to suggest that roads may function as a barrier to regal fritillary dispersal.

The failure to show a connection between regal fritillary abundance and the proximity to suitable but non-contiguous habitat suggests that the degree of site isolation has no affect on these butterflies, and that there is very little dispersal between non-contiguous sites. However, other possibilities should also be considered. The approach that I used may not provide an accurate measure of site isolation. Although ArcView enables precise area calculations, many of the land-use classifications in the data I used were based on interpretation of aerial photographs taken in 1990. Some areas that I considered as potential regal fritillary habitat may be unsuitable, while the data set may have failed to identify other suitable areas. In addition, I did not survey all of the habitat within the study area to identify all areas that are actually used by regal fritillaries, a critical element in assessing habitat isolation (Hanski 1994). A more intensive study, in which all potential habitat patches in the study area are surveyed for regal fritillary abundance, might show a relationship between isolation from other occupied (as opposed to simply suitable) habitat and abundance.

However, if these butterflies are, as has been predicted, highly mobile, they could be expected to be abundant at different sites at different times, a situation that would complicate the estimation of population abundance at any particular site. Abundance at the beginning of the flight period indicates that the site (or contiguous habitat) was available and attractive to ovipositing females and was suitable for successful overwintering, early larval growth, and pupation. If regal fritillaries do, indeed, move freely between habitat patches, sites with greater availability of nectar sources and high conspecific density might be attractive in the middle of the flight period; late in the season, females will seek out appropriate sites for oviposition.

If the isolation of prairie fragments were shown, after all, to have no relationship to the size of regal fritillary populations on those fragments, the implication would be that these butterflies do not exist within a metapopulation structure. If that were the case, either prairie fragments harbor separate, closed populations of regal fritillaries, or the movement of regal fritillaries between patches is essentially unrestricted. Given the impermeability of prairie edges observed by Ries and Debinski (in press), the second possibility seems unlikely, but an extensive mark-release-recapture study may be necessary to define the mobility of this species. This is especially important because isolated butterfly populations rarely persist for more than 100 years unless they have an equilibrium size of more than 500 individuals; they must consist of many thousands of individuals in order to survive indefinitely (Hanski and Thomas 1994). Few local populations of butterflies meet this criterion, and clearly migration between habitat fragments did not save Eastern regal fritillary populations.

The concept of mobility classes (Pollard & Yates 1993, Thomas 2000) provides another way to think about regal fritillary movement. The decline or disappearance of the regal fritillary throughout its former range, and some observations of movements of the species, suggest that it may be in the intermediate mobility category, in which small local populations and migration failure (failure to locate new habitat) combine to increase local extinctions when habitat becomes highly fragmented. The characterization of regal fritillaries as highly mobile is based on Bliss and Schweitzer's 1987 study on Nantucket, a 124 square km island; this is a very different environment from the prairies of the Midwest or the Great Plains. Evidently, regal fritillaries failed to adapt to changing conditions in their eastern range, as all but two isolated populations are now extinct, and these two may not be large enough to survive for long (Williams 1999). Individuals that attempt to migrate out of one of the eastern populations have little chance of survival and almost no chance of encountering others of their species. When environmental conditions change and butterfly habitat fragments become more isolated, the survival of sedentary individuals may be strongly favored, and the evolution of characteristics leading to more limited mobility may be extremely rapid (Thomas 1991, Dempster et al. 1976). Perhaps the tendency of regals to remain within patches of high conspecific density and the relative impermeability of prairie edges that were observed by Ries and Debinski (in press) reflect adaptations to habitat fragmentation.

The relationship that I found between dry prairie sites and increased regal fritillary abundance could be connected to the topography of the area and the unusually high level of precipitation in the spring of 1998, the first year that I surveyed. Soils of the Red River Valley and glacial Lake Agassiz basin tend to be level and prone to wetness, except for those found on the dry sand and gravel ridges of the glacial lake shorelines. Native prairie fragments (and sites that have been allowed to return to prairie) are likely to fall into either extreme, because they are usually on land that is less profitable for cultivation. In the years 1992 through 1997, average total precipitation in May and June (when regal fritillary larvae feed and pupate) was 6.65 inches (16.89 cm) per month at the Moorhead, MN station (National Climactic Data Center 2001). The range of total May and June precipitation in these years was from 4.48 inches (11.38 cm) in 1995 to 9.34 inches (23.72 cm) in 1992. In 1998, the first year in which I surveyed, precipitation in May and June totaled 14.14 inches (35.92 cm).

Between July 5 to July 10 of 1998, when I first attempted to visit my research sites, the “mesic” sites were impassible due to wetness, and the “wet” sites were covered in standing water. Drainage ditches in the region were filled with water nearly to the level of the roadway. Drowning of immature stages, due to localized flooding in 1998, would explain my finding that regal fritillary abundance was highest on dry prairies, somewhat lower on mesic prairies, and lowest on wet prairies in 1998. This pattern of relative abundance continued in 1999, although rainfall in May and June of that year (as recorded at the Moorhead station) totaled only 7.67 inches (19.48cm). This result would be expected if adult movement between sites is limited; sites that experienced diminished adult populations due to flooding in 1998 would give rise to fewer regal fritillary offspring in 1999.

I found no relationship between regal fritillary abundance and either larval host plant abundance or blooming nectar plant abundance. This may simply indicate that all of the sites surveyed in this study had adequate larval and adult food supplies, and food availability was not a limiting factor here. Also, I was forced to discard my 1998 data on blooming nectar plants because a faulty pedometer resulted in inaccurate estimates of route length. My analysis used the average blooming nectar plant abundance in 1999 as an approximation, but this solution is problematic, especially given the large degree of variation observed at each site in 1999.

Studies by other researchers suggest that limitations in larval and adult food supplies may have adverse effects on regal fritillary individuals and populations, though results appear ambiguous. Observing that individual regal fritillaries in Iowa weigh less than regal fritillaries in neighboring states, and that states with higher-weight regal fritillaries also had larger violet populations, Kelly (1996) examined the relationship between regal fritillary biomass and violet density on prairies in southwestern Iowa. She found that regal fritillary weights were significantly lower in areas of low host plant density. However, she acknowledged that her use of "locally greatest" violet densities as estimates of host plant abundance, necessitated by the plants' patchy distribution, was inaccurate, since actual violet density varies across the habitat. In addition, some Iowa prairies surveyed by Kelly had substantial violet populations, either in terms of estimated number of plants per site (424,000) or in terms of density (9.7 plants per meter square), yet no regal fritillaries were observed on these sites during the 1995 surveys. She concluded that violet and insect data from sixteen sites was insufficient to predict regal fritillary population size from an estimate of total violet biomass. Williams (1999) gives an example of a tiny Illinois preserve where regal fritillaries number in the hundreds each year, although researchers have discovered only three violet plants on the site.

Wagner et al. (1997) proposed that, given the large size and long flight season of regal fritillary adults, nectar quality and quantity will be essential to the reproductive success of this species. In a study of ten native tallgrass prairies in eastern Nebraska, Huebschman (1998) found a significant, positive correlation between regal fritillary population density and nectar source diversity in 1996, but also found a significant, negative correlation between regal fritillary population density and nectar source blossom density in 1997. He found no significant correlation between regal fritillary population density and either violet density or violet abundance.

Management Considerations

Prescribed burns are widely used as a management tool on Minnesota prairie reserves. Such burns have been shown to benefit native plants and control some invasive species, including cool-season grasses. For this reason, early spring burning is a common practice. Because burning often stimulates lush regrowth and increased flowering in prairie plants, adult regal fritillaries are commonly observed nectaring on recently burned prairies. However, it is not known whether butterflies observed on these sites have survived spring burning or have moved in from unburned areas.

Opinions differ concerning whether eggs and larvae of the regal fritillary can survive fire. Bliss and Schweitzer (1987) cite both Ron Panzer's report of the fireinduced extirpation of a population of *S. idalia* on an Illinois prairie and Richard Arnold's contrasting observation of a congener, *S. calliope,* surviving as larvae after grassland fires. Kelly (1996) hypothesized that recent or frequent burning on two of the Iowa prairies she studied, on which host plant resources seemed adequate, may explain the low regal fritillary populations at these sites. Until it can be shown that regal fritillary larvae survive controlled burns, it should be assumed that all larvae are eliminated from the burned portion of a prairie. Given that assumption, the focus should be on assuring that the remaining habitat at each site is adequate to allow some larvae to survive on that preserve. Burning only one portion of a particular preserve at a time, on a rotating schedule, may be only a first step toward maintaining regal fritillaries at that site.

It is well known that the eastern habitat of regal fritillary populations, damp meadows and marshy pastures, is different from the tall grass prairies they inhabit in the Great Plains and Midwest (Opler & Malikul 1992). However, there seem to be a variety of observations concerning the optimal moisture characteristics of prairie sites. While one writer (Clark 1932) suggests that the species favors dry prairies, another (Royer 1988) maintains that they are usually found in damp prairie environments, and others (Ebner 1970, Layberry et al. 1998) connect them with both types of sites in the same geographic areas. These apparent contradictions suggest that regal fritillaries are sensitive to moisture conditions at both extremes. In a wet year, spring flooding will drown the larvae at wet sites, but they will starve if violets senesce early due to insufficient moisture at dry sites (Bliss & Schweitzer 1987). Such susceptibility to site moisture and annual precipitation may explain Holland’s 1901 observation about the intermittent presence of the regal fritillary: "at times it is apparently common, and then for a succession of seasons is scarce."

Defining suitable habitat for butterflies has proven to be more difficult than previously thought, because the immature stages of most species need intricately precise conditions for survival (Thomas 1991, Weiss & Murphy 1990). For example, larvae of the European butterfly genus *Boloria*, violet-feeding relatives of the *Speyeria*, have highly specific microhabitat requirements, involving small differences in temperature, amount of direct sunlight, host plant maturity, ground cover, and humidity. In contrast, the apparently haphazard oviposition habits of the regal fritillary (Clark 1932, Opler & Krizek 1984, Scott 1986, Wagner 1995), which often deposits eggs on non-host plants or on bare ground with no violets in sight, do not initially suggest that larvae will be sensitive to microhabitat characteristics. Indeed, such random egg-laying implies to the observer that the location is irrelevant to the survival of the larvae. But if regal fritillary larvae did, in fact, have such generalized requirements for overwintering, it should be relatively simple to create a suitable environment for captive breeding. However, as Wagner (1995) relates, overwintering has proven fatal to larvae in captive breeding programs, both in laboratory conditions and in field trials. Despite numerous attempts by various researchers, captive propagation of regal fritillaries has proven infeasible (Williams 1999, Debinski & Drobney 2000). Regal fritillaries exhibit amazing fecundity; one female in captivity laid 2,494 eggs, more than twice the number recorded for any other species (Wagner et al. 1997). In her apparently random placement of hundreds of eggs, the regal fritillary may be maximizing her reproductive potential by choosing multiple variations in microhabitat characteristics.

In order to safeguard regal fritillaries, each preserve should include a mosaic of microhabitats for oviposition sites, spread over a sufficient area to give at least some of the regal fritillary larvae on the preserve an opportunity to survive localized prescribed burns, diverse weather conditions, and other stochastic events. Such site diversity is especially critical if adult dispersal proves to be limited, as this study suggests. It is to be hoped that detailed autecological studies will eventually clarify the exact habitat requirements of regal fritillary larvae, but the insect's precipitous decline in eastern states indicates it would be better to err on the side of caution.

In December of 1991, when a group of scientists met to review the status of the regal fritillary in New England and New York, they did not realize that the insect was already gone from the area (Wagner et al. 1997), even though apparently suitable habitat remained. In many of the states in which regal fritillaries have been extirpated, the species disappeared before it was even listed as threatened or endangered (Williams 1999). These details bear disturbing similarity to several accounts of extinctions in Britain and Europe (Thomas 1991), where butterfly species have vanished despite the persistence of their habitats and their host plants. Systematic annual monitoring of known populations in this state should be the first line of defense against a comparable fate for regal fritillaries in Minnesota.

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Table 1. Prairie study sites and their corresponding ownership, size, and location

Site #	Site Name	Ownership	Size (ha)	Location
1	**Dalby WMA1**	State of Minnesota	16	NE 1/4,NE 1/4, Sect. 15, Rockwell Township, Norman County
2	**Dalby WMA2**	State of Minnesota	32	S 1/2, SW 1/4, Sect. 11, Rockwell Township, Norman County
3	**Frenchmans Bluff**	The Nature Conservancy	16	S 1/2, SE 1/4, Sect. 18, Flom Township, Norman County
4	**Twin Valley**	The Nature Conservancy	97	W1/2 (east of marsh), Sect. 23, Rockwell Township, Norman County
5	**Neal WMA**	State of Minnesota	304	SE 1/4, Sect. 24, Rockwell Township, and SW 1/4, Sect. 19, Home Township, Norman County
6	**Cupido WMA**	State of Minnesota	227	W 1/2,NE 1/4, Sect. 25, Rockwell Township, Norman County
7	**Ulen WMA**	State of Minnesota	65	N 1/2, NW 1/4,Sect. 30, Ulen Township, Clay County
8	**Felton**	Clay County	122	S 1/2,Sect. 31, Hagen Township, and N 1/2 Sect. 6, Keene Township, Clay County
9	**Bicentennial**	Clay County	65	SW 1/4, Sect.5, Keene Township, Clay County
10	**Blazing Star**	The Nature Conservancy	53	SW 1/4, Sect.5, Keene Township, Clay County
11	**Flowing 36**	State of Minnesota	16	NE 1/4, Sect.5, Keene Township, Clay County
12	**Cromwell WMA**	State of Minnesota	28	SW 1/4, SW 1/4 Sect. 36, Flowing Township, Clay County
13	**Buffalo River 13**	State of Minnesota	65	W 1/2, NE 1/4, Sect. 1, Cromwell Township, Clay County
14	**Buffalo River 14**	State of Minnesota	71	SW 1/4, Sect 10, Riverton Township, Clay County
15	**Buffalo River 15**	State of Minnesota	81	Sect 10 & 11 (north of Buffalo River), Riverton Township, Clay County
17	**Bluestem17**	The Nature Conservancy	130	N 1/2 of NW 1/4, Sect. 14, Riverton Township, Clay County
18	**Bluestem18**	The Nature Conservancy	32	E1/2 of NE 1/4 of NE 1/4, Sect 14, Riverton Township, Clay County
19	**Bluestem19**	The Nature Conservancy	49	W 1/2, Sect 15, Riverton Township, Clay County

Table 2. Values averaged for all (two or three) observations at each site

Site #	Temp (C)	Sun	Avg. wind speed (kph)	Survey Length (hrs)	Site Moisture	Violets per plot	Nectar plants per k.	Habitat area (k^2) accessible within 50 m.	Habitat area (k^2) accessible within 500 m.	Habitat area (k^2) accessible within 1000 m.	Habitat area (k^2) accessible within 5000 m.	Contiguous habitat area (k^2)	Contiguous habitat area (k^2), roads as barriers	Regals per hour
1	23.33	1.00	5.83	0.83	mesic	0.05	540.50	1.26	2.71	3.77	24.08	2.71	2.07	0.00
2	25.33	0.83	6.83	0.98	mesic	4.20	903.93	1.34	1.34	3.78	27.55	2.71	0.64	1.76
3	22.33	0.68	3.33	1.10	dry	4.20	881.50	1.22	1.23	2.13	12.74	1.93	1.42	3.87
4	31.50	0.55	6.75	1.25	wet	11.67	848.00	0.90	0.92	11.95	24.53	0.88	0.88	4.00
5	24.50	0.95	7.00	1.88	wet	4.59	1005.99	10.81	10.87	11.23	22.47	12.97	4.02	2.00
6	22.33	0.82	6.17	2.12	mesic	2.73	351.27	10.81	10.98	11.17	27.45	12.97	4.69	2.60
7	27.33	0.82	5.17	1.44	wet	5.72	175.89	3.68	4.28	4.59	39.51	4.56	1.06	0.00
8	29.33	0.87	8.50	1.83	dry	2.23	737.09	6.22	11.62	18.35	29.80	26.75	17.85	18.22
9	24.50	0.82	7.92	1.02	dry	1.11	401.43	6.56	12.78	18.17	29.82	26.75	17.85	27.32
10	25.67	0.83	9.00	1.96	dry	0.91	871.24	6.56	11.04	12.78	34.65	26.75	17.85	23.80
11	29.67	1.00	3.00	0.81	dry	0.45	167.89	4.25	4.99	4.99	18.24	4.42	0.17	16.55
12	27.33	0.70	7.33	0.89	wet	2.46	1220.89	0.17	0.25	0.52	9.20	0.10	0.10	1.52
13	28.33	0.87	7.33	1.39	mesic	5.11	265.50	15.94	19.47	22.51	31.50	14.53	3.61	1.24
14	25.00	0.70	7.50	1.11	mesic	1.22	141.14	15.77	22.40	22.55	34.44	1.65	1.65	1.33
15	26.33	0.83	5.83	1.92	mesic	2.47	525.79	14.15	15.77	15.98	34.31	14.53	3.61	0.19
17	26.00	0.60	4.50	2.82	mesic	1.94	415.77	14.12	14.23	16.01	31.86	14.53	3.61	1.62
18	27.00	0.60	5.83	1.00	mesic	1.71	535.78	14.12	14.31	16.02	32.00	14.53	3.61	18.33
19	29.67	0.98	4.50	1.17	mesic	0.81	362.42	14.12	14.21	14.26	30.32	14.53	0.61	2.33

Table 3. Complete data for 1998 and 1999 field seasons

SITE AND SURVEY DATA											BUTTERFLY DATA						
#	Name	moisture	Area (Ha)	Date	Year	Sun	Cloud cover	Temp. C.	Avg. wind speed (kph)	Wind gusts (kph)	Hrs.	Regals	Regals/ hour	Other fritillar -ies	Other species (# indivs.)	Blooming nectar plants per km (1999)	Violets per plot (1999)
1	Dalby WMA1	mesic	16.2	7/22/1998	1998	1.00	0.05	21	4.0	11	0.83	0	0.0	0			
1	Dalby WMA1	mesic	16.2	7/28/1999	1999	1.00	0.50	26	10.5	15	0.92	0	0.0	0	51	831.00	0.05
1	Dalby WMA1	mesic	16.2	8/17/1999	1999	1.00	0.10	23	3.0	6	0.75	0	0.0	0	10	250.00	0.05
2	Dalby WMA2	mesic	32.4	7/22/1998	1998	1.00	0.02	22	8.0	14	0.75	1	1.3	0			
2	Dalby WMA2	mesic	32.4	7/28/1999	1999	1.00	0.00	31	10.5	15	1.27	5	3.9	0	61	1405.71	4.20
2	Dalby WMA2	mesic	32.4	8/17/1999	1999	0.50	0.50	23	2.0	4	0.93	0	0.0	2	23	402.14	4.20
3	Frenchmans Bluff	dry	16.0	7/24/1998	1998	0.95	0.02	21	2.0	4	1.75	14	8.0	15			
3	Frenchmans Bluff	dry	16.0	7/28/1999	1999	1.00	0.00	23	3.5	9	0.83	3	3.6	29	24	715.00	4.20
3	Frenchmans Bluff	dry	16.0	8/18/1999	1999	0.10	0.70	23	4.5	12	0.72	0	0.0	4	65	1048.00	4.20
4	Twin Valley	wet	97.2	7/24/1998	1998	0.10	0.35	27	4.5	10	1.00	0	0.0	0			
4	Twin Valley	wet	97.2	7/29/1999	1999	1.00	0.00	36	9.0	12	1.50	12	8.0	7	82	848.00	11.67
5	Neal WMA	wet	304.0	7/24/1998	1998	0.90	0.20	27	9.0	12	1.25	4	3.2	13			
5	Neal WMA	wet	304.0	8/5/1999	1999	1.00	0.10	22	5.0	8	2.50	2	0.8	6	49	1005.99	4.59
6	Cupido WMA	mesic	227.0	7/22/1998	1998	0.45	0.85	23	12.0	16	1.75	4	2.3	0			
6	Cupido WMA	mesic	227.0	7/29/1999	1999	1.00	0.00	25	6.5	8	3.00	9	3.0	16	146	587.64	2.73
6	Cupido WMA	mesic	227.0	8/19/1999	1999	1.00	0.10	19	0.0	0	1.62	4	2.5	5	50	114.91	2.73
7	Ulen WMA	wet	65.0	7/22/1998	1998	0.95	0.30	26	10.0	14	1.50	0	0.0	1			
7	Ulen WMA	wet	65.0	8/5/1999	1999	1.00	0.00	29	3.0	8	1.33	0	0.0	1	22	307.14	5.72
7	Ulen WMA	wet	65.0	8/17/1999	1999	0.50	0.50	27	2.5	10	1.50	0	0.0	3	20	44.64	5.72
8	Felton (Cty)	dry	121.5	7/21/1998	1998	0.60	0.70	27	7.5	13	1.50	61	40.7	26			
8	Felton (Cty)	dry	121.5	7/28/1999	1999	1.00	0.00	34	13.0	18	2.00	15	7.5	14	68	668.54	2.23
8	Felton (Cty)	dry	121.5	8/10/1999	1999	1.00	0.25	27	5.0	6	2.00	13	6.5	14	116	805.63	2.23
9	Bicentennial (part 1)	dry	64.8	7/21/1998	1998	0.90	0.05	25	6.0	8	1.50	21	14.0	3			
9	Bicentennial (part 2)	dry	64.8	7/21/1998	1998	0.50	0.70	28	8.0	12	0.50	14	28.0	4			
9	Bicentennial (part 1)	dry	64.8	7/27/1999	1999	1.00	0.00	21	9.0	12	0.90	29	32.2	10	21	189.00	1.11
9	Bicentennial (part 2)	dry	64.8	7/27/1999	1999	1.00	0.00	28	13.5	15	0.90	29	32.2	13	16	252.10	1.11
9	Bicentennial (part 1)	dry	64.8	8/10/1999	1999	1.00	0.30	20	6.0	11	1.25	29	23.2	10	174	689.00	1.11
9	Bicentennial (part 2)	dry	64.8	8/10/1999	1999	0.50	0.25	25	5.0	6	1.08	37	34.3	20	134	475.63	1.11
#	Name	moisture	Area (Ha)	Date	Year	Sun	Cloud cover	Temp. C.	Avg. wind speed (kph)	Wind gusts (kph)	Hrs.	Regals	Regals/ hour	Other fritillar -ies	Other species (# indivs.)	Blooming nectar plants per km (1999)	Violets per plot (1999)
10	Blazing Star	dry	53.0	7/21/1998	1998	0.50	0.50	28	8.0	12	2.00	33	16.5	4			
10	Blazing Star	dry	53.0	7/27/1999	1999	1.00	0.00	27	10.5	20	1.50	33	22.0	14	53	760.94	0.91
10	Blazing Star	dry	53.0	8/10/1999	1999	1.00	0.05	22	8.5	13	2.37	78	32.9	26	154	981.55	0.91
11	Flowing 36	dry	16.2	7/25/1998	1998	1.00	0.05	29	4.0	10	1.00	37	37.0	1			
11	Flowing 36	dry	16.2	7/21/1999	1999	1.00	0.10	32	0.0	12	0.75	5	6.7	0	47	273.68	0.45
11	Flowing 36	dry	16.2	8/8/1999	1999	1.00	0.30	28	5.0	9	0.67	4	6.0	0	25	62.11	0.45
12	Cromwell WMA	wet	28.0	7/25/1998	1998	1.00	0.05	31	4.0	10	0.66	3	4.5	0			
12	Cromwell WMA	wet	28.0	7/21/1999	1999	1.00	0.00	26	10.0	14	1.22	0	0.0	0	39	1843.04	2.46
12	Cromwell WMA	wet	28.0	8/8/1999	1999	0.10	0.30	25	8.0	12	0.78	0	0.0	0	29	598.73	2.46
13	Buffalo River StatePark13	mesic	65.0	7/23/1998	1998	0.65	0.00	21	0.0	8	1.50	1	0.7	0			
13	Buffalo River StatePark13	mesic	71.0	7/20/1999	1999	1.00	0.10	32	12.0	14	1.53	2	1.3	0	76	364.33	5.11
13	Buffalo River StatePark13	mesic	71.0	8/6/1999	1999	0.95	0.50	32	10.0	14	1.15	2	1.7	2	49	166.67	5.11
14	Buffalo River StatePark14	mesic	71.0	7/21/1998	1998	0.10	0.80	27	10.0	15	1.00	0	0.0	0			
14	Buffalo River StatePark14	mesic	65.0	7/21/1999	1999	1.00	0.10	24	9.0	13	1.33	0	0.0	0	44	168.99	1.22
14	Buffalo River StatePark14	mesic	65.0	8/8/1999	1999	1.00	0.50	24	3.5	10	1.00	4	4.0	0	20	113.29	1.22
15	Buffalo River StatePark15	mesic	81.0	7/20/1998	1998	1.00	0.15	29	10.0	20	3.50	2	0.6	0			
15	Buffalo River StatePark15	mesic	81.0	7/20/1999	1999	0.50	0.75	30	2.0	10	1.60	0	0.0	3	40	901.05	2.47
15	Buffalo River StatePark15	mesic	81.0	8/8/1999	1999	1.00	0.20	20	5.5	9	0.66	0	0.0	0	12	150.53	2.47
17	Bluestem17	mesic	129.6	7/23/1998	1998	0.50	0.85	24	1.5	8	2.50	3	1.2	0			
17	Bluestem17	mesic	129.6	7/19/1999	1999	0.30	0.90	27	4.0	8	2.95	1	0.3	1	160	301.79	1.94
17	Bluestem17	mesic	129.6	8/6/1999	1999	1.00	0.10	27	8.0	12	3.00	10	3.3	1	73	529.75	1.94
18	Bluestem18	mesic	32.4	7/23/1998	1998	0.80	0.50	24	10.0	12	1.00	23	23.0	0			
18	Bluestem18	mesic	32.4	7/19/1999	1999	0.00	0.50	25	0.0	0	1.00	2	2.0	0	56	525.49	1.71
18	Bluestem18	mesic	32.4	8/6/1999	1999	1.00	0.40	32	7.5	9	1.00	30	30.0	2	68	546.08	1.71
19	Bluestem19	mesic	48.6	7/25/1998	1998	0.95	0.05	29	2.0	10	1.00	6	6.0	0			
19	Bluestem19	mesic	48.6	7/19/1999	1999	1.00	0.50	29	7.5	11	1.00	1	1.0	0	63	215.03	0.81
19	Bluestem19	mesic	48.6	8/5/1999	1999	1.00	0.50	31	4.0	10	1.50	0	0.0	2	59	509.80	0.81

		Nectar plants observed in bloom									Plot surveys: violets (larval food plants) and nectar plants in all plots								
#	Name	Blazing Star	Thistle	Wild Bergamot	Milk-weed	Cone-flower	Wood Lily	Total bloom-ing	Route length (km)	Blooming nectar plants per km (1999)	Number of plots survey -ed	Violets	Violets per plot (1999)	Blazing Star	Thistle	Wild Berga-mot	Milk-weed	Cone-flower	Wood Lily
1	Dalby WMA1																		
1	Dalby WMA1	777	19	0	35	0	0	831	1	831.00	20	1	0.05	0	0	0	163	0	0
1	Dalby WMA1	242	8	0	0	0	0	250	1	250.00	20	1	0.05	0	0	0	163	0	0
2	Dalby WMA2																		
2	Dalby WMA2	1682	286	0	0	0	0	1968	1.4	1405.71	20	84	4.20	0	16	20	96	0	0
2	Dalby WMA2	499	64	0	0	0	0	563	1.4	402.14	20	84	4.20	0	16	20	96	0	0
3	Frenchmans Bluff																		
3	Frenchmans Bluff	0	62	649	0	4	0	715	1	715.00	20	84	4.20	72	14	0	0	0	0
3	Frenchmans Bluff	999	49	0	0	0	0	1048	1	1048.00	20	84	4.20	72	14	0	0	0	0
4	Twin Valley																		
4	Twin Valley	1060	5	0	207	0	0	1272	1.5	848.00	24	280	11.67	0	17	12	84	1	0
5	Neal WMA																		
5	Neal WMA	2680	153	24	0	0	0	2857	2.84	1005.99	64	294	4.59	14	57	6	21	1	0
6	Cupido WMA																		
6	Cupido WMA	1192	59	0	365	0	0	1616	2.75	587.64	60	164	2.73	0	160	0	230	0	3
6	Cupido WMA	238	78	0	0	0	0	316	2.75	114.91	60	164	2.73	0	160	0	230	0	3
7	Ulen WMA																		
7	Ulen WMA	325	19	0	0	0	0	344	1.12	307.14	36	206	5.72	3	8	0	1	4	0
7	Ulen WMA	46	4	0	0	0	0	50	1.12	44.64	36	206	5.72	3	8	0	1	4	0
8	Felton (Cty)																		
8	Felton (Cty)	2	366	0	49	1007	0	1424	2.13	668.54	48	107	2.23	6	36	0	21	50	0
8	Felton (Cty)	1447	260	0	0	9	0	1716	2.13	805.63	48	107	2.23	6	36	0	21	50	0
9	Bicentennial (part 1)																		
9	Bicentennial (part 2)																		
9	Bicentennial (part 1)	0	49	0	0	140	0	189	1	189.00	36	40	1.11	1	0	0	14	29	1
9	Bicentennial (part 2)	0	16	0	0	284	0	300	1.19	252.10	36	40	1.11	1	0	0	14	29	1
9	Bicentennial (part 1)	657	28	0	0	4	0	689	1	689.00	36	40	1.11	1	0	0	14	29	1
9	Bicentennial (part 2)	545	18	0	0	3	0	566	1.19	475.63	36	40	1.11	1	0	0	14	29	1
#	Name	Blazing Star	Thistle	Wild Bergamot	Milk-weed	Cone-flower	Wood Lily	Total bloom-ing	Route length (km)	Blooming nectar plants per km (1999)	Number of plots survey -ed	Violets	Violets per plot (1999)	Blazing Star	Thistle	Wild Berga-mot	Milk-weed	Cone-flower	Wood Lily
10	Blazing Star																		
10	Blazing Star	1185	489	0	14	85	0	1773	2.33	760.94	32	29	0.91	8	43	0	40	1	3
10	Blazing Star	1953	327	0	0	7	0	2287	2.33	981.55	32	29	0.91	8	43	0	40	1	3
11	Flowing 36																		
11	Flowing 36	14	59	96	87	4	0	260	0.95	273.68	20	9	0.45	0	22	3	27	0	0
11	Flowing 36	29	25	5	0	0	0	59	0.95	62.11	20	9	0.45	0	22	3	27	0	0
12	Cromwell WMA																		
12	Cromwell WMA	0	384	894	178	0	0	1456	0.79	1843.04	24	59	2.46	6	56	44	22	0	0
12	Cromwell WMA	0	346	27	100	0	0	473	0.79	598.73	24	59	2.46	6	56	44	22	0	0
13	Buffalo River StatePark13																		
13	Buffalo River StatePark13	9	286	0	328	0	0	623	1.71	364.33	36	184	5.11	1	90	0	0	0	0
13	Buffalo River StatePark13	139	146	0	0	0	0	285	1.71	166.67	36	184	5.11	1	90	0	0	0	0
14	Buffalo River StatePark14																		
14	Buffalo River StatePark14	17	181	0	69	0	0	267	1.58	168.99	36	44	1.22	0	17	0	0	0	0
14	Buffalo River StatePark14	140	39	0	0	0	0	179	1.58	113.29	36	44	1.22	0	17	0	0	0	0
15	Buffalo River StatePark15																		
15	Buffalo River StatePark15	0	455	10	215	175	1	856	0.95	901.05	36	89	2.47	42	36	0	0	7	0
15	Buffalo River StatePark15	105	38	0	0	0	0	143	0.95	150.53	36	89	2.47	42	36	0	0	7	0
17	Bluestem17																		
17	Bluestem17	277	313	0	194	58	0	842	2.79	301.79	72	140	1.94	0	33	0	72	3	5
17	Bluestem17	635	825	18	0	0	0	1478	2.79	529.75	72	140	1.94	0	33	0	72	3	5
18	Bluestem18																		
18	Bluestem18	26	291	89	94	36	0	536	1.02	525.49	24	41	1.71	0	8	0	15	3	0
18	Bluestem18	399	153	0	5	0	0	557	1.02	546.08	24	41	1.71	0	8	0	15	3	0
19	Bluestem19																		
19	Bluestem19	117	25	0	186	0	1	329	1.53	215.03	32	26	0.81	2	1	0	5	5	0
19	Bluestem19	764	16	0	0	0	0	780	1.53	509.80	32	26	0.81	2	1	0	5	5	0

Table 4. Predictors of regal fritillary abundance

Predictor	Coefficient (SE)	Student's *t*	*P*
Constant	1.15 (1.55)	0.74	0.4689
Dry	8.78 (3.54)	2.47	0.0258
Contiguous habitat area (roads considered as barriers)	0.73 (0.26)	2.76	0.0146

N = 18, adj. R^2 = 0.6843