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Abstract. The >2,570,000-ha Flint Hills ecoregion of Kansas, USA, harbors the largest remaining contiguous tract of tallgrass prairie in North America, a unique system, as the remainder of North America's tallgrass prairie has succumbed to development and conversion. Consequently, the loss and degradation of tallgrass prairie has reduced populations of many North American prairie-obligate species including the regal fritillary (*Speyeria idalia*) butterfly. Population abundance and occupied range of regal fritillary have declined >99%, restricting many populations to isolated, remnant patches of tallgrass prairie. Such extensive decline has resulted in consideration of the regal fritillary for protection under the Endangered Species Act. Although it is widely accepted that management practices such as fire, grazing, and haying are necessary to maintain prairie ecosystems, reported responses by regal fritillary to these management regimes have been ambiguous. We tested effects of prescribed fire across short, moderate, and long fire-return intervals as well as grazing and haying management treatments on regal fritillary density. We also tested the relative influence of habitat characteristics created by these management regimes by measuring density of an obligate host plant (*Viola* spp.) and canopy cover of woody vegetation, grasses, forbs/ferns, bare ground, and litter. We found density was at least 1.6 times greater in sites burned with a moderate fire-return interval vs. sites burned with short and long fire-return intervals. Overall management regardless of fire-return interval did not have an effect on density. Percent cover of grass had the strongest positive association, while percent cover of woody vegetation had the greatest negative effect on density. Our results indicate that patch-burning is a viable and perhaps even ideal management strategy for regal fritillary in tallgrass prairie landscapes. Additionally, these results elucidate the importance of fire, particularly when applied at moderate-return intervals to regal fritillary, and corroborate a growing suite of studies that suggest fire is perhaps not as detrimental to populations of regal fritillary as previously believed.

Key words: butterfly conservation; distance sampling; Flint Hills; Fort Riley Military Reservation; grassland management; Kansas; prescribed burning; regal fritillary; *Speyeria idalia;* tallgrass prairie.

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Introduction

Once covering ~67 million ha, native tallgrass prairie communities in the United States have been reduced to approximately 4% of their former range (Samson and Knopf 1994). Native tallgrass prairie communities have succumbed to conversion to cropland, plant community succession, urban development, and invasion by herbaceous and woody plant species (Samson and Knopf 1994). While most other extant tallgrass prairie remains primarily in isolated fragmented patches, the >2,570,000-ha Flint Hills ecoregion of Kansas, USA, represents the principal remaining contiguous tract of tallgrass prairie in North America (Reichman 1987). Nevertheless, the Flint Hills have also suffered drastic losses with tallgrass prairie retaining as little as 37% of the historic extent in the Flint Hills/Osage Plains region (Samson et al. 2004).

It is widely accepted that North American grassland ecosystems were historically shaped and maintained by disturbances such as fire and grazing by large native ungulates (Fuhlendorf and Engle 2001). Subsequently, grassland management practices such as prescribed fire, livestock grazing, and haying play critical roles in maintaining native prairie in the absence of ecological drivers that historically shaped them (Samson et al. 1998, Fuhlendorf and Engle 2004, Toombs et al. 2010). These disturbances are considered necessary for prairies to maintain their open structure, depress invasive species spread, prevent woody encroachment, and promote overall productivity (Vogel 1974, Shuey 1997). Loss or infrequent occurrence of these drivers negatively affects tallgrass prairie ecosystems and disturbance-dependent flora and fauna (Collins 1992, Briggs and Knapp 1995, Fuhlendorf and Engle 2004).

The regal fritillary (*Speyeria idalia*; hereafter "regal" or "regals") is a large, nonmigratory butterfly considered a prairie-obligate species (Hammond and McCorkle 1983, Powell et al. 2007, Selby 2007). Regals have a single generation per year with adult flight commencing in the spring and continuing through early fall when females begin to oviposit (Klots 1951, Tilden and Smith 1986, Wagner et al. 1997). During immature stages, regal larvae exclusively feed on violets (*Viola* spp.; Klots 1951, Hammond 1974, Ferris and Brown 1981). Regal larvae can feed on a variety of violet species, but specific violet species tend to dominate within different populations (Selby 2007). In the Midwest and Great Plains, USA, larvae are reported to predominantly feed on bird's-foot (*Viola pedata*) and prairie violet (*Viola pedatifida*; Swengel 1997, Kelly and Debinski 1998, Dole et al. 2004, McCullough et al. 2017); however, larvae have also been documented using wild pansy (*Viola tricolor*; Shuey et al. 2016) and common blue violet (*Viola sororia*; Caven et al. 2017, McCullough et al. 2017).

The range of the regal once extended from Oklahoma, USA, northward to the border of Canada, and eastward to the Atlantic coast (NatureServe 2005, Selby 2007). Despite its historically broad geographic distribution, populations of this once common butterfly have declined considerably (~99%; NatureServe 2005). While the species has been nearly extirpated in the eastern portion of its range, western populations can be locally abundant and the species is considered secure in Kansas (Ely et al. 1986, Marrone 2002, Selby 2007). Exact causes of regal declines remain unclear, but it is suspected that habitat loss and fragmentation through grassland conversion, high-intensity grazing, frequent and intensive burning, and haying are the greatest ongoing threats to populations (Hammond 1995, Swengel 1996, 1998, NatureServe 2005, Selby 2007, Vogel et al. 2007). Previously, the regal was listed as a Category II species under the U.S. Endangered Species Act (ESA) of 1973 until this category was eliminated in 1996 (USFWS 1996). Continued range-wide declines and persistent threats to remaining populations from habitat loss and degradation prompted the U.S. Fish and Wildlife Service to initiate a status review of the regal in September 2015 in response to a petition to list the species as threatened under the ESA (USFWS 2015).

Effects of management, particularly prescribed fire, on prairie butterflies and other invertebrates remain a controversial subject despite past studies (Dana 1991, Swengel and Swengel 1999, Panzer 2002). Extirpation of regal populations has been documented following complete burns of prairie remnants (Swengel 1996, Swengel and Swengel 2001*a*, Powell et al. 2007, Swengel et al. 2011). This observation has led to the postulation that fire may be eliminating larvae, significantly depressing and even extirpating populations among those sites (Swengel 1996, 1998, Kelly and Debinski 1998, Huebschman and Bragg 2000, Swengel and Swengel 2001*b*, Powell et al. 2007). Even rotational burning—where some patches are burned while other patches remain unburned creating a mosaic across the landscape—has been shown to lead to decreases in regal abundance. It is worth noting this was seen at study sites <30 ha and within a converted landscape matrix (Swengel and Swengel 2001*a*). The apparent sensitivity of regals to prescribed fire in the literature has led some to advocate the use of permanent non-fire refugia managed with mowing or haying to conserve the species and their habitat as these practices have been reported to be more favorable to prairie-specialist butterflies (Swengel 1996, Swengel and Swengel 2007, Swengel et al. 2011).

Counter to previous work that is often conducted in isolated tallgrass prairie remnants, the Flint Hills present a unique opportunity to study this imperiled butterfly within a landscape-scale prairie framework. Given the necessity of disturbance processes such as fire, grazing, and haying to the persistence of tallgrass prairie and the ambiguous effects these practices appear to have on prairie-obligate invertebrates, such as the regal, our objectives were twofold. First, we quantified effects of fire-return interval (short, one to two years; moderate, three to five years; or long, ≥10 yr) and overall management regime (hayed, burned, and grazed) on adult regal density. Second, we tested the relative influence of habitat characteristics created by these management practices on density of adult regals.

Methods

Study areas

This study was conducted during 2012 and 2014–2016 in northeastern Kansas, at the Fort Riley Military Reservation (FRMR; Geary and Riley counties) and Konza Prairie Biological Station (KPBS; Riley County; Fig. 1). Both the FRMR and KPBS are located within the northern portion of the Flint Hills physiographic region. Generally, the Flint Hills are characterized by large rolling hills and rocky flint-filled soils (Anderson and Fly 1955). The elevation of the Flint Hills varies and is higher than surrounding areas due to the flint within this region's bedrock that resists erosion. Elevation in the Flint Hills ranges from ~246 to 512 m above sea level. The underlying flint and limestone deposits also made this region undesirable for crop cultivation, helping to conserve the region as the largest remaining contiguous tract of tallgrass prairie in North America (Reichman 1987). The vegetative community is dominated by big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) along with other perennial grasses, woody species, and a wide variety of native herbaceous forbs (Towne 2002). The climate is characterized by hot dry summers and cold winters with temperatures ranging from −40°C to 49°C. Annual precipitation varies widely (average annual precipitation = 83.82 cm), and droughts are common (Abrams and Hulbert 1987). During the course of our study, temperatures ranged from −22°C to 41°C. In 2012, there were drought conditions and annual precipitation was low (total precipitation in 2012 = 47.8 cm). Annual precipitation increased in the following years of the study to 66.8, 104.5, and 98.5 cm for 2014, 2015, and 2016, respectively. The landscape surrounding the FRMR and KPBS encompasses numerous drainages, two large reservoirs, and broadly distributed urban and rural developments.

The FRMR is ~41,000 ha with approximately 29,000 ha managed for multiple uses including conservation and outdoor recreation activities. The FRMR is divided into training areas that are managed using a combination of burning and haying regimes. We partitioned the FRMR into four study sites that were comprised of several training areas. Prescribed burns are typically conducted from 15 August to 30 April annually, but occasional wildfires from live-fire military training occur throughout the year. Many grassland fields within training areas are leased for hay harvest. Haying at the FRMR occurs from 15 July to 15 August each year. Hayed sites are largely dominated by native, warm-season grasses, which may be hayed during even-numbered years only, odd-numbered years only, or annually. Training areas that comprised the four study sites at the FRMR all received prescribed burning at either the short, moderate, or long fire-return intervals, and only transects within the annually hayed sites were included in analyses. In order for transects to be included in the hayed treatment category, ≥50% of the transect had to be hayed. We placed one transect per training area in each of the four study sites. The average size of a training area among the four study sites was 269 ha with a range of 95–636 ha for surveyed areas (Fig. 1, Table 1).

The KPBS is a 3487-ha tract of tallgrass prairie co-owned and operated by the Division of

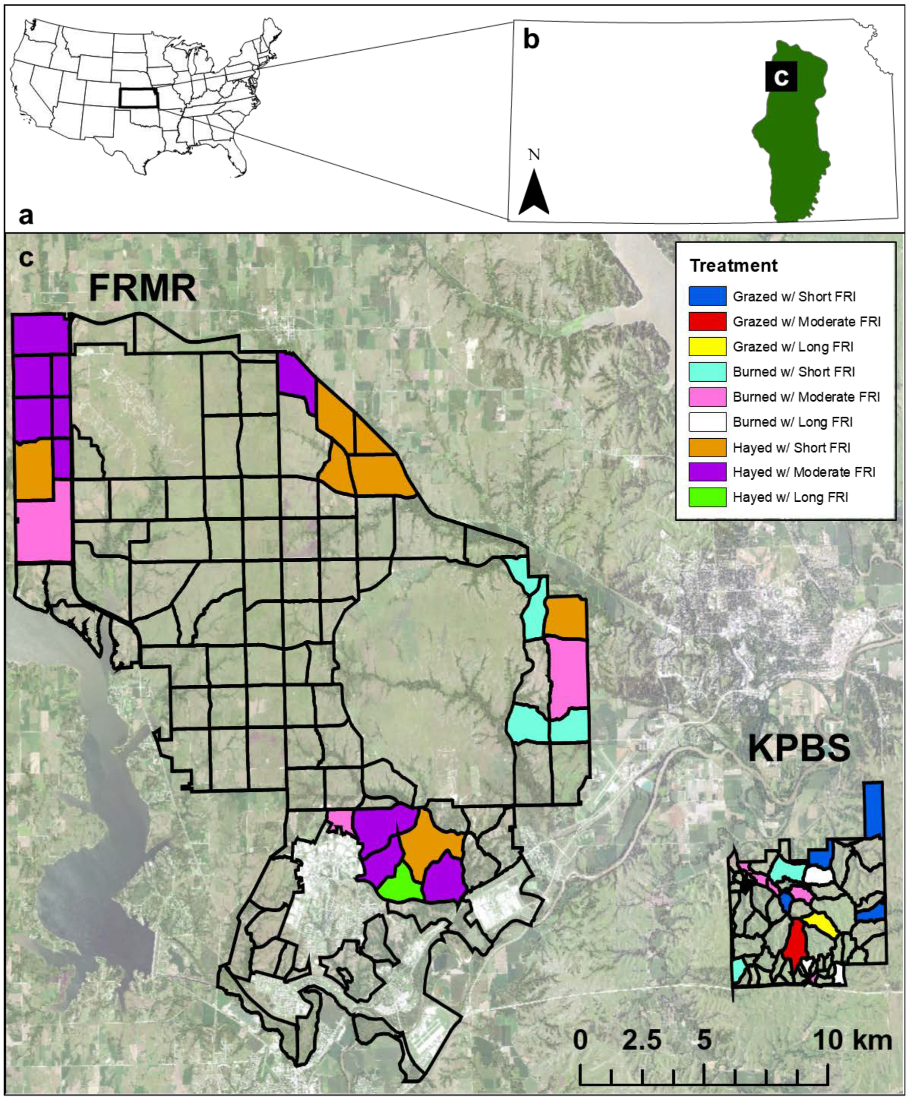

Fig. 1. Study area and surrounding landscape in northeast Kansas. (a) Map of the United States with Kansas highlighted in bold black. (b) Enlargement of Kansas. The green region spanning across the eastern part of Kansas indicates the Flint Hills ecoregion. (c) The study area showing locations of the Fort Riley Military Reservation (FRMR) and Konza Prairie Biological Station (KPBS). The color-coded sections within the FRMR and KPBS indicate sites within each where regal fritillary (*Speyeria idalia*) survey transects were located during 2012 and 2014–2016. Colors indicate treatment (hayed, burned, and grazed) and fire-return interval (FRI; short, one to two years; moderate, three to five years; or long, ≥10 yr) of each site.

Biology, Kansas State University, and The Nature Conservancy. The KPBS has been a National Science Foundation Long-Term Ecological Research Site since 1981, and watersheds are experimentally managed with various grazing and burning regimes (Knapp et al. 1998). Grazing treatments include the use of native bison (*Bison bison*) or cattle (*Bos taurus*), or no grazing. Watersheds with cattle are stocked with cow–calf pairs at a light-to-moderate stocking rate of one pair per 3.24 ha for approximately five months each year. Cattle stocking rates at the KPBS are typical of the Flint Hills region (Owensby 2010, KDA 2017, Miller 2018). Bison are present

Table 1. The number of transects surveyed in each treatment for regal fritillary (*Speyeria idalia*) at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA, 2012, 2014–2016.

Treatment	No. of transects surveyed by year				No. of regal fritillary	Total area (ha)
	2012	2014	2015	2016		
Burned short	2	4	6	0	34	877
Burned moderate	3	4	4	5	116	1341
Burned long	1	0	2	2	2	142
Grazed short	4	1	3	1	71	344
Grazed moderate	1	1	1	1	17	135
Grazed long	1	0	1	1	10	83
Hayed short	0	3	7	6	54	2089
Hayed moderate	0	9	10	4	140	2381
Hayed long	0	1	1	1	7	191
Total	12	23	36	21	451	7583

Note: Included are the total area stratified by overall management regime (hayed, burned, and grazed) and fire-return interval (short, one to two years; moderate, three to five years; or long, ≥10 yr) and the total number of regal fritillary observed in each treatment group.

year-round at a rate of approximately one bison per 6.07 ha. Although bison and cattle differ in a number of ways including grazing and movement patterns (Kohl et al. 2013), previous bison–cattle comparison studies have demonstrated that their effects on the plant community can be similar and differences are more likely due to how they are managed rather than species (Towne et al. 2005, Fuhlendorf et al. 2018). Additionally, because cattle grazed only five months of the year and bison grazed year-round during the course of our study, it is difficult and beyond the scope of this research to determine whether variation in the tallgrass prairie's response and subsequently any effect on regals is a reflection of the species of grazer or their respective management. In turn, for the purposes of this study, bison and cattle units were treated collectively as grazed to broadly demonstrate the response of regal density to the presence of a large herbivore on the landscape. Prescribed burns are applied at one-, two-, three-, four-, and 20-yr intervals within management units defined by watersheds, and most fires are ignited during spring. The KPBS was treated as a single study site (Fig. 1). Among the watersheds surveyed, all received prescribed burning at either the short, moderate, or long fire-return intervals, and six were grazed by either cattle (n = 3) or bison (n = 3). Similar to the FRMR, we placed one transect per watershed surveyed. The average size of a watershed surveyed at the KPBS was 70 ha with a range of 12–167 ha (Table 1).

Regal fritillary surveys

We surveyed 41 different line transects distributed throughout the FRMR and KPBS study sites for regals during their annual flight period (late May–early August) in 2012 and 2014–2016. Line transects were 500 m to >1 km in length and stratified by management regime and fire-return interval. Transects were surveyed twice in 2012 (13–22 June and 12–18 July), three times in 2014 (18 June–2 July, 3–18 July, and 21 July–4 August), and six times in 2015 (8–23 June, 24 June–1 July, 6–14 July, 16–22 July, 23–30 July, and 30 July–8 August) and 2016 (1–22 June, 23 June–1 July, 6–15 July, 18–26 July, 27–31 July, and 4–9 August; Table 1). Successive survey bouts did not begin until all transects for the current bout had been surveyed. All surveys were conducted between 08:30 and 18:30 CST, under sunny and warm conditions, when temperatures were ≥17°C if the sky was overcast, and winds <20 km/h on the Beaufort scale. Surveys were conducted by walking transect centerlines and recording the perpendicular distance from the centerline to each regal within ≤30 m of each side. The distance at which each regal was first detected from the transect centerline was estimated within intervals of 0–5 m, >5–10 m, >10–20 m, and >20–30 m.

Vegetation surveys

We used a module-nested plot sampling method to characterize vegetation along the line transects (Table 2). Each module consisted of one

100-m^2 plot with two 10-m^2 and two 1-m^2 embedded subplots. We measured one density and six cover variables during field surveys. We measured the density of prairie violets as number of prairie violets/100 m^2. Cover of woody (trees and shrubs) vegetation, herbaceous plants, grasses, forbs/ferns, bare ground, and litter were measured within plots appropriate for plant basal area. Although ferns were included in with forb cover, they made up a very small percentage of the overall coverage within the category. Cover variables were estimated using nine cover classes: 0–0.9%, 1–1.9%, 2–4.9%, 5–9.9%, 10–24.9%, 25–49.9%, 50–74.9%, 75–95%, and >95%, which were converted to midpoints for the analysis. Vegetation data were collected every 100 m along line transects in 2014–2016. We surveyed two module vegetation plots at each vegetation survey point. Modules were placed on both sides of the line transect at 90° angles.

Statistical analysis

We conducted distance sampling using function distsamp in package Unmarked (Fiske and Chandler 2011) in R (version 3.2.2; R Development Core Team 2016) to estimate regal density as a function of combinations of grassland management practices and vegetation characteristics (Royle et al. 2004). Due to the variation in transect length, regal density estimates were weighted by transect length in the models. To identify which models best explained observed patterns in regal density, we used an information-theoretic framework to compare, rank, and select the best-fitting models (Burnham and Anderson 2002). We used the second-order variant of Akaike's information criterion adjusted for small sample sizes (AIC_c) to compare the relative fit of alternative models. We compared AIC_c values from models using the key functions uniform, half-normal, and hazard rate to determine the best-fitting detection function. We calculated delta AIC_c (ΔAIC_c) and Akaike weights (w_i), to evaluate support for each model (Burnham and Anderson 2002). We used AIC_c to rank models and selected the best-fitting models as those with the lowest AIC_c scores (Buckland et al. 2001). We considered all models with a $\Delta AIC_c < 2$ from the top-ranked model to have support.

To evaluate effects of fire-return interval and overall management on regal density, we developed three ecologically relevant models: null (no effect), fire-return interval, and overall management. In the fire-return interval only model, management other than burning (haying or grazing) was ignored and regal density was estimated for the three levels of fire-return interval (short, one to two years; moderate, three to five years; or long, ≥10 yr). In the overall management model, fire-return interval was ignored and regal density was estimated for the three overall management regimes (hayed, burned, and grazed). All data were modeled with the hazard-rate detection function because this function best fit these data (all $\Delta AIC_c > 23$). In addition to our aforementioned primary analysis, we also tested for site effects because of the spatial confoundment within our study sites (i.e., haying only occurred at the FRMR and grazing only occurred at the KPBS). For these analyses, we separated the FRMR and KPBS study sites and compared hayed vs. unhayed at the FRMR and grazed vs. ungrazed at the KPBS. These data were also

Table 2. Habitat variables measured in the regal fritillary (*Speyeria idalia*) study at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA, 2014–2016.

Habitat variable	Plot size† (m^2)	Description
Viola pedatifida density	100	Number of *V. pedatifida*
Tree cover	100	Percentage of total woody plant canopy cover greater than 2.5 m in height
Shrub cover	10	Percentage of total woody plant cover less than 2.5 m in height
Herb cover	1	Percentage of total herbaceous plant cover
Grass cover	1	Percentage of total graminoid plant cover
Forb and fern cover	1	Percentage of total herbaceous plant cover excluding graminoids
Bare ground cover	1	Percentage of total exposed soils and rock cover
Litter cover	1	Percentage of total dead vegetative litter cover

† Data were collected within nested vegetation sampling modules every 100 m along transects surveyed for regal fritillary.

modeled with the hazard-rate detection function (all $\Delta AIC_c > 2$).

Finally, we tested the relative influence of the seven measured habitat variables on regal densities. Prior to testing the influence of habitat variables on regal density, we employed the Pearson correlation coefficient to test for statistical correlation among these variables. Correlated variables ($|r| > 0.60$) were not included in the same models. Following removal of models with correlated variables, we constructed all possible combinations of additive models to test the effect of the habitat variables on regal density.

Results

Effects of fire-return interval and management on regal fritillary density

We made 451 observations of regals along the 41 different transects surveyed throughout the course of this study and detected regals at 38 of 41 (92%) transects (Table 1). Survey-wide density estimates produced for the FRMR and KPBS reported regal density to be ~0.53 ± 0.073 (standard error [SE]) individuals per ha at the FRMR and ~0.52 ± 0.076 (SE) individuals per ha at the KPBS. In 2015 and 2016, when sample bouts were conducted at approximately two-week intervals, we found regal density peaked during sample bout two (~23 June–1 July; Fig. 2). We detected regals along line transects in all treatment categories, but the highest ranked model testing the effect of fire-return interval and grassland management on regal density was the fire-return interval only model (AIC_c 1379.95, $K = 5$, $w_i = 1.00$). All remaining models had $\Delta AIC_c > 61$ units from the highest ranked model. This model revealed that regal densities were greatest in areas that were burned with a moderate fire-return interval (Fig. 3). Although the 95% confidence interval of the moderate fire-return interval category overlapped with the short fire-return interval category, regal density was at least 38% and 77% greater than in sites with short and long fire-return intervals, respectively (Fig. 3). Density estimates produced from our overall management model revealed that the density of regals did not differ among sites that were hayed, grazed, or burned indicating that regals responded similarly to disturbance type when fire-return interval was ignored (Fig. 4). Likewise, regal density estimates did not differ between grazed and ungrazed sites at the KPBS (Fig. 5a) or hayed and unhayed sites at the FRMR (Fig. 5b).

Effects of habitat characteristics on regal fritillary density

We did not consider models that included both grass and bare ground as these habitat variables were negatively correlated ($r = -0.67$). We tested all possible combinations of additive models using the revised habitat variables ($n = 47$). The model that best fit these data was the grass + woody + litter model ($AIC_c = 1086.35$, $K = 6$, $w_i = 0.49$). Although one other model (grass + woody + litter + forb; $AIC_c = 1087.74$, $K = 7$, $w_i = 0.25$) had $\Delta AIC_c < 2$, we did not consider this model to have support as the forb parameter in this model was spurious and did not explain enough variation to warrant its inclusion and thus should not be interpreted as having any ecological effect (Arnold 2010). The remaining alternative models lacked support and had $\Delta AIC_c > 2$ from the top model. Among the variables included in the top model, percent

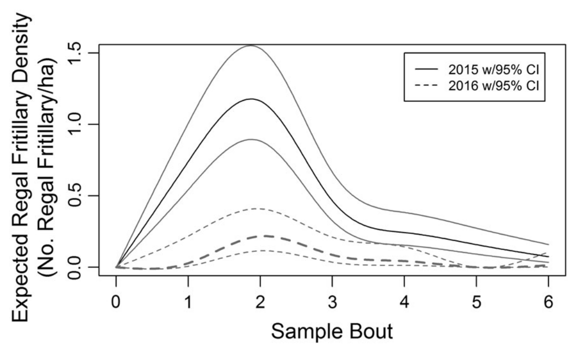

Fig. 2. Density estimates (no./ha) of regal fritillary (*Speyeria idalia*) with 95% confidence intervals across six sample bouts from surveys conducted in 2015 and 2016 at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas. Transects were surveyed six times in 2015 (8–23 June, 24 June–1 July, 6–14 July, 16–22 July, 23–30 July, and 30 July–8 August) and 2016 (1–22 June, 23 June–1 July, 6–15 July, 18–26 July, 27–31 July, and 4–9 August). Density estimates and 95% confidence intervals were calculated using function distsamp in package Unmarked in program R. Estimates were weighted by transect length (i.e., survey effort).

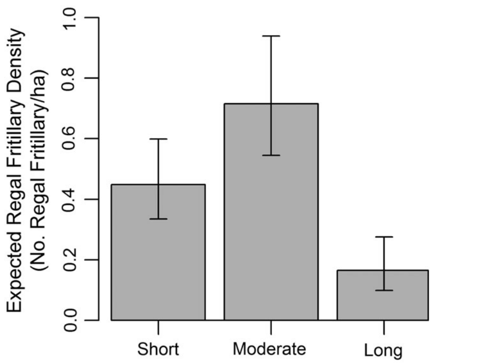

Fig. 3. Density (no./ha) estimates of regal fritillary (*Speyeria idalia*) grouped by fire-return interval (short, one to two years; moderate, three to five years; or long, ≥10 yr) from surveys during 2012 and 2014–2016 at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA. Density estimates and 95% confidence intervals were calculated using function distsamp in package Unmarked in program R. Estimates were weighted by transect length (i.e., survey effort).

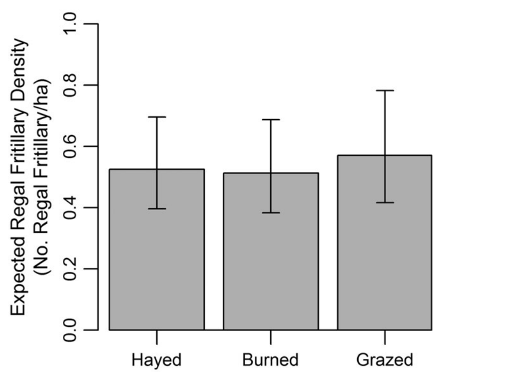

Fig. 4. Density (no./ha) estimates of regal fritillary (*Speyeria idalia*) grouped by overall management from surveys during 2012 and 2014–2016 at the Fort Riley Military Reserve and Konza Prairie Biological Station in northeastern Kansas, USA. Density estimates and 95% confidence intervals were calculated using function distsamp in package Unmarked in program R. Estimates were weighted by transect length (i.e., survey effort).

grass cover had the strongest association with regal density ($\beta = 0.49 \pm 0.14$ SE); as average percent grass cover increased, the estimated density of regals increased (Fig. 6a). Regal density ($\beta = 0.38 \pm 0.08$) also increased with average

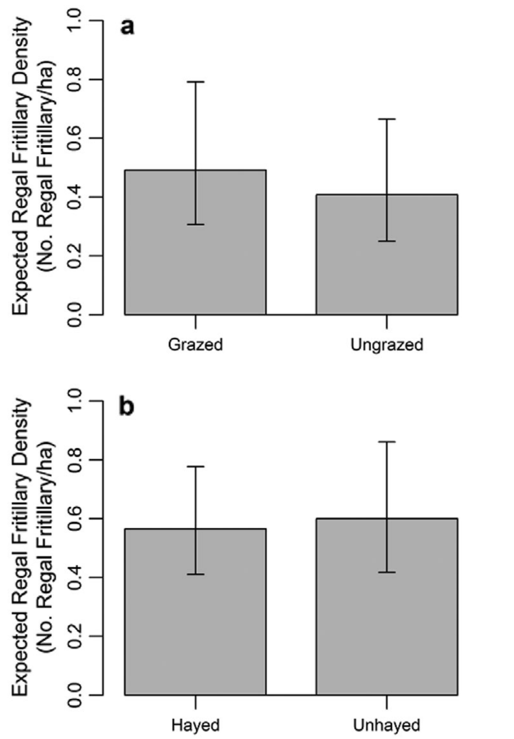

Fig. 5. Density (no./ha) estimates of regal fritillary (*Speyeria idalia*) grouped by site-specific management regimes from surveys during 2012 and 2014–2016 at the Fort Riley Military Reserve (FRMR) and Konza Prairie Biological Station (KPBS) in northeastern Kansas, USA. (a) Density estimates of regal fritillary grouped by grazed and ungrazed management treatments at the KPBS. (b) Density estimates of regal fritillary grouped by hayed and unhayed management treatments at the FRMR. Density estimates and 95% confidence intervals were calculated using function distsamp in package Unmarked in program R. Estimates were weighted by transect length (i.e., survey effort).

percent litter cover (Fig. 6b). Conversely, average percent woody cover had a negative effect on regal density ($\beta = -0.34 \pm 0.16$; Fig. 6c). Neither average density of prairie violet nor average percent cover of forbs had an effect on regal density ($\beta = -0.04 \pm 0.08$ and $\beta = -0.06 \pm 0.12$, respectively).

Discussion

We tested potential effects of prescribed burning across short, moderate, or long fire-return

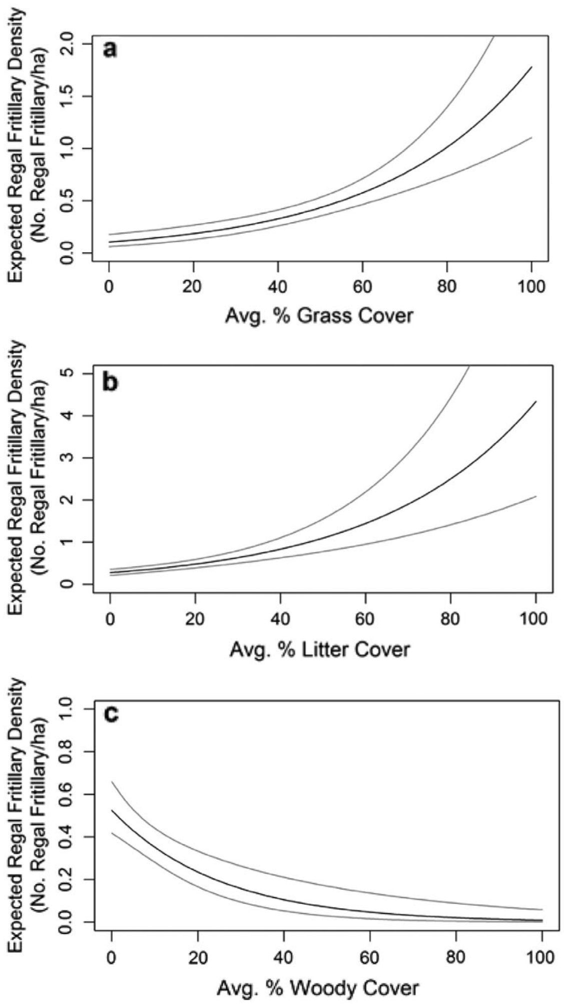

Fig. 6. Relative influence of the habitat features contained in the top-ranked model relating vegetation cover to regal fritillary (*Speyeria idalia*) density. Habitat features were measured using a module-nested plot method every 100 m along transects located at the Fort Riley Military Reservation and Konza Prairie Biological Station in northeastern Kansas, USA, 2014–2016. All habitat variables were estimated as average percent cover. The average percent cover of the habitat features for panels (a), (b), and (c) is displayed on the *x*-axis.

intervals as well as overall management regime on regal density in study sites located within the landscape-scale tallgrass prairie in the northern Flint Hills. Our analysis revealed areas that received prescribed burning at the moderate fire-return interval supported at least 1.6 times greater density of regals vs. sites burned with short and long fire-return intervals. We found that management regime, when underlying fire-return interval was ignored, had no effect on regal densities. We also tested for effects of vegetation features created by these management practices on regal densities. Our vegetation results indicated that percent cover of grass had the strongest positive association while percent cover of woody vegetation had the greatest negative effect on regal density. These results are consistent with vegetation response to moderate fire-return intervals and bolster our finding that fire, when applied at moderate-return intervals, is an important driver of regal densities.

Fire-return interval

The perceived adverse responses to fire demonstrated by regals and other grassland-obligate invertebrates have led some to advocate that the occurrence of fire was uncommon during the evolutionary history of these species (Schlicht and Orwig 1998, Nekola 2002, Swengel et al. 2011). However, there are multiple lines of evidence that indicate fire has been a crucial process in maintaining grasslands for millennia (Sauer 1950, Briggs et al. 2002, Anderson 2006). Some have even suggested that fire has decreased since the North American Great Plains was settled (Steinauer and Collins 1996, Samson et al. 2004). Moreover, research indicates that fire can promote the growth of forbs, including important nectar sources used by adult regals (Moranz et al. 2014), temporarily boost the density of larval host plants (Latham et al. 2007), control woody vegetation cover (Bragg and Hulbert 1976, Abrams and Hulbert 1987, Briggs et al. 2002, 2005, Lett and Knapp 2005), and promote the growth of the dominant warm-season grasses, especially big bluestem (Collins 1990). We propose two factors that explain these interpretation inconsistencies when it comes to determining effects of prescribed fire on regal populations.

First is the scale of the observation, and second is the timing of the observation (Latham et al. 2007, Moranz et al. 2014). Issues with interpretation of fire effects appear to arise when small, relatively isolated prairie remnants are burned in their entirety and regal abundance declines or the species disappears from such sites entirely

(Swengel 1996, Swengel and Swengel 2001*a*, Powell et al. 2007, Swengel et al. 2011). Due to the extensive conversion and fragmentation of grassland ecosystems, it is common for research on grassland flora and fauna to be conducted at small remnant patches of prairie (Huebschman and Bragg 2000 [97 ha]; Swengel and Swengel 2001*a* [<30 ha]; Powell et al. 2007 [0.9–53 ha]; Moranz et al. 2014 [60–105 ha]; Henderson et al. 2018 [19–41 ha]) that are often not well connected to surrounding prairie. Observations of regals declining immediately following burns have led to the assumption that fire kills regal larvae (Swengel 1996, 1998, Kelly and Debinski 1998, Huebschman and Bragg 2000, Swengel and Swengel 2001*b*, Powell et al. 2007, Swengel et al. 2011, Moranz et al. 2014). However, observations of regal larvae in areas that had been burned ≤61 d prior to detection suggest that prescribed fire does not necessarily result in complete larvae mortality and persistence of regals on recently burned sites is likely a function of both larval survival and adult recolonization (McCullough et al. 2017).

Unlike larvae, adult regals are much more mobile and have strong flight capabilities (Zercher et al. 2002, Selby 2007). Their vagility affords them the ability to occupy or abandon sites as conditions and resources change, which can confound assessments of how a management strategy affects their presence and abundance (Swengel 1996). For example, Moranz et al. (2014) surveyed four grassland sites in Missouri, USA, for regals during three survey periods (~5–9 June, 25–27 June, and 17–26 July) and found regal density increased following dormant-season fire. Conversely, Swengel (1996) surveyed for regals in the same region during early adult flight (14–19 June) and found that prairie-specialist numbers including the regal were greater in hayed vs. burned prairies. Moranz et al. (2014) suggested that sampling only once during the early adult flight may have not given regals enough time to recolonize the burned sites and resulted in the observed decreased density among those sites. Numerous studies have found that adult regals can and do recolonize sites following burns. Although reported recovery times vary, research indicates that recolonization can occur as quickly as four weeks postburn (Huebschman and Bragg 2000) and numbers may reach pre-burn levels or greater within two to four years (Henderson et al. 2018). The observed peak flight density during sample bout two (~23 June–4 July) coupled with the positive response by regals to moderate fire-return intervals in our study support these conclusions. Thus, sampling during a single portion, especially shortly after a fire, of the flight period may lead to inaccurate conclusions regarding treatment effects on adult butterfly densities.

Patch size can play an important role in predicting butterfly abundance (Hanski 1994, Hanski et al. 1994, Wahlberg et al. 1996, Sutcliffe et al. 1997) including regals (Kelly and Debinski 1998, Mason 2001, Caven et al. 2017). For instance, one study found that contiguous size of grassland accounted for 60% of the variation in regal abundance (Mason 2001). We hypothesize that the observed positive responses of regals to moderate fire-return intervals in this study are likely due to not only survey timing but also experimental scale. Similar hypotheses have been proposed for regals regarding differences among findings of the effects of prescribed fire (Latham et al. 2007, Moranz et al. 2014, Henderson et al. 2018). In contrast to the aforementioned studies that were conducted on very small, isolated remnant patches of prairie, our study sites were much larger and embedded within a landscape comprised largely of native tallgrass prairie. Despite their strong flight capabilities and ability to disperse great distances, regals are not adapted for the heavily developed matrix of urban development and croplands that commonly surround prairie remnants (Selby 2007). Likewise, the propensity of regals to remain in native prairie and sensitivity to non-natural habitat boundaries such as row crops, tree lines, and roads (Ries and Debinski 2001, Caven et al. 2017) may explain why recolonization can happen in some contexts such as the contiguous grassland within the Flint Hills but not others. Consequently, the probability of regals successfully reaching distant unburned prairie after a site has been burned and repopulating them quickly is relatively low. Accordingly, small isolated populations of regals are likely to be most vulnerable to disturbances that were characteristic of the historic prairie landscape (Selby 2007, Caven et al. 2017).

Burning prairie remnants in their entirety have led to the extirpation of regals; subsequently, many advocate against using fire as a management strategy for conserving populations (Swengel 1996, Swengel and Swengel 2001*a*, Powell et al. 2007, Swengel et al. 2011). Alternatively, patch-burning has been applied successfully, even on relatively small, isolated prairie remnants (Huebschman and Bragg 2000, Powell et al. 2007, Moranz et al. 2014, Henderson et al. 2018). Although many studies have found patch-burning to be a viable management strategy for regals, the fire-return interval at which sites should be burned seems to be unclear. The majority of studies that found patch-burning to be a compatible management strategy for regals had sites that were burned on three- to five-year cycles (Huebschman and Bragg 2000, Moranz et al. 2014, Henderson et al. 2018). Yet, some have suggested that common three- to four-year burn cycles may be too short for regals to reach their maximum potential (Kelly and Debinski 1998, Swengel and Swengel 2007, Moranz et al. 2014) and recommend longer (i.e., greater than eight years) fire-return intervals and even permanent non-fire refugia to support peak regal densities (Swengel and Swengel 2007, Caven et al. 2017). However, delaying fire-return intervals greater than three years can lead to transitions from grasslands to shrublands and fire-return intervals greater than ten years, or complete fire suppression, can lead to the invasion of woody species and conversion from grasslands to woodlands (Ratajczak et al. 2016). Once woody species are established, conversion back to grasslands is difficult and more intensive fires or extensive use of mechanical or herbicide practices may be required to remove invaded woody species (Ratajczak et al. 2016). Our results support other recent research indicating that burning annually may be more beneficial to regals than complete fire suppression (Henderson et al. 2018). In turn, permanent non-fire refugia may be unnecessary if sites are managed with rotational patch-burning. Because woody species invasion is neither good for the persistence of the prairie or regals, implementation of fire-return intervals greater than three to five years should be monitored carefully for woody encroachment and perhaps should only be employed if supplemental management such as haying can be used to control woody species.

The burning strategy that best suits regals and their habitat (i.e., promotes the growth of grass, prevents woody encroachment, and encourages the growth of important forbs such as nectar sources and violet host plant species all while maintaining adjacent unburned patches of prairie) likely falls on a continuum relative to patch size. While burning small portions of pastures on longer rotations may work better to promote regals in small isolated prairies, burning greater portions of large intact prairies may be effective in other contexts, such as those found in this study. It is recommended that prescribed burns should affect no more than 20% of grassland habitat containing regals and unburned habitat patches that are known to be occupied by regals be in close proximity (Swengel et al. 2011). Therefore, implementation of patch-burning in remnant prairie tracts should be done with caution and respect to timing, intensity, and frequency (Selby 2007). To aid in development of specific conservation strategies, future research of regals, particularly adult regal ecology, may benefit from investigations conducted on large scales (e.g., landscape) with greater spatial replication and with respect to both disturbance and survey timing to fully assess effects of processes such as fire, grazing, and haying on populations. Determining minimum connectivity among patches of remnant prairie required for successful dispersal and recolonization may also prove to be beneficial.

Haying and grazing

Management practices such as haying and grazing have helped preserve prairie remnants by preventing excessive litter and woody encroachment in the absence of fire (Selby 2007, Begay et al. 2011). In Kansas prairies, haying practices have been shown to maintain the abundance of forbs and in general the practice often promotes biodiversity, particularly among forb species (Collins et al. 1998, Jog et al. 2006). In contrast, legumes such as lead plant (*Amorpha canescens*) and round-head lespedeza (*Lespedeza capitata*) appear to be vulnerable to mowing and haying practices (Begay et al. 2011). Both haying and light-to-moderate grazing practices have also been proposed to favor prairie-specialist butterflies (McCabe 1981, Swengel 1996, 1997, 2001*a*, *b*, Swengel and Swengel 2001*b*). Grazing also seems to promote the growth of the regal's larval host plant as studies have noted increased violet density in grazed prairies (Mello 1989, Debinski and Kelly 1998). It has even been suggested that the elimination of grazing in New England may have contributed to the loss and degradation of habitat and subsequently the extirpation of regals in several sites (Dunwiddie and Sferra 1991). Our results indicated that grazing and haying management had no effect on regal density when fire-return interval was ignored and density was modeled by overall management (i.e., hayed, burned, and grazed). These results would again point to fire as the underlying process driving regal densities particularly when applied at moderate-return intervals. Although our overall management model did not indicate that one management method was preferable for regals, it does suggest that management whether it be haying, burning, or grazing can be used in areas that contain regals without detrimental impacts on the species' abundance.

These results are encouraging as the majority of remaining tallgrass prairie in North America is held in private ownership and primarily managed for cattle production (Fuhlendorf and Engle 2004). Management strategies that are compatible with farmers, ranchers, and landowners will be most beneficial for regals in large working landscapes such as those found in the Flint Hills. Nonetheless, alternative management regimes such as haying and grazing can also have unfavorable effects on populations particularly when they are applied at high frequencies and aggressively. For example, high-intensity grazing may reduce or homogenize plant structure, and decrease plant diversity, and trampling eggs and larvae could also be factors (Hammond and McCorkle 1983, Royer and Marrone 1992, Dana 1997, Selby 2007). It is presumed that improperly timed haying may eliminate essential nectar sources when they are needed by adults, and reduce larval host plants and mowing an area too short may harm developing eggs and larvae (Selby 2007). Similar to fire, haying and grazing should be implemented with caution and respect to timing, frequency, and intensity. Our results highlight the need for further research on how regals respond to sites that are managed with patch-burning vs. sites that are managed exclusively with haying or grazing, which in previous studies have been suggested to be more favorable.

Habitat characteristics

Our vegetation models indicated that average percent grass cover had the strongest positive association with regal densities while average percent woody cover had the greatest negative effect on regal densities. Regals are commonly described as a prairie-specialist, indicator, or flagship species of pristine prairie habitat in the literature (Hammond and McCorkle 1983, Swengel 1996, Moranz et al. 2014, Henderson et al. 2018). Thus, these relationships are relatively unsurprising given that the presence of grass and absence of trees are the defining features of a prairie. Previous studies have reported similar findings regarding the importance of native grass species and lack of woody vegetation to regals. Particularly, warm-season grasses such as big bluestem have been found to be an important component of regal habitat (Mason 2001, Caven et al. 2017). In fact, big bluestem has been positively associated with regals and documented to be nearly twice as abundant on plots where regals were present vs. plots where they were absent (Caven et al. 2017). Likewise, others have documented the regals' negative response to woody vegetation. For instance, Ries and Debinski (2001) found that regals responded strongly to habitat edges including treelines and either avoided traversing them altogether or quickly returned if they did cross them. Even the presence of a single shrub species has been shown to decrease the likelihood of regals being present (Caven et al. 2017).

Unlike other species of Lepidoptera, regals rarely oviposit directly onto their larval host plant species and instead prefer to deposit eggs on the underside of detritus in shaded microsites (Kopper et al. 2000). Previous research has even suggested that regal larvae perish in the absence of litter accumulation, possibly from exposure (Wagner et al. 1997, Ferster and Vulinec 2010). Our models revealed that there was a positive relationship with average percent litter cover and adult regal density. These results coincide with a number of other studies that indicate litter buildup is an important component to regal habitat (Mason 2001, Davies et al. 2007, Powell et al. 2007, Vogel et al. 2007, Ferster and Vulinec 2010, Helzer 2012, Caven et al. 2017). Although fire and concentrated grazing decrease tallgrass dominance and litter buildup (Fuhlendorf and

Engle 2004), a complete lack of disturbance allows for heavy litter accumulation that can limit the availability of light and reduce the abundance and diversity of forbs (Collins 1992, Briggs and Knapp 1995). However, application of patch-burning and patch-burn grazing creates a heterogeneous shifting mosaic of vegetation patterns across the landscape where patches are in various states of successional recovery (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001). These practices allow the postburn sites to return to pre-burn states, where grasses dominate and litter accumulates to prefire levels within a few years (Fuhlendorf and Engle 2004).

Similarly, violets are also an important habitat component for regals, and a number of studies have shown a positive correlation between the abundance of violets and adult regals (Swengel 1997, Beilfuss and Harrington 2001, Henderson et al. 2018). However, the presence or absence of regals in sites cannot always be attributed to the abundance or presence of violets (Bliss and Schweitzer 1987, Ferge 1990, Debinski and Kelly 1998, Huebschman 1998, Ferster 2005, Latham et al. 2007). At the Fort Indiantown Gap National Guard Training Center in Pennsylvania, USA, violet host plant density was not different between sites that were densely populated with regals and similar habitat sites that contained fewer regals (Latham et al. 2007). In surveys of Midwest prairies, there was no significant correlation between host plants and regals (Swengel 1997). Our results indicated that average violet density had no effect on adult regal density and the variable was not included in our top vegetation model. While violet species are a critical habitat feature for populations of regals, it is arguably most important during the immature stages of development when violets are the sole food plant of larvae (Klots 1951, Hammond 1974, Ferris and Brown 1981). Even adult female regals do not preferentially orient to or oviposit directly on larval host plants (Kopper et al. 2000). Their vagility, propensity to "wander" (Selby 2007), and shifting requirement for resources besides violet species as adults may explain why some find no relationship between adult regals and violet host plant species.

The availability of appropriate nectar sources during adult flight is perhaps as important as the presence of larval host plants for an area to support butterfly populations (Opler and Krizek 1984, Selby 2007). This habitat requirement is especially important for long-lived butterflies such as the regal (Selby 2007), which not only utilize nectar sources for energy, but also likely use these food sources for production of eggs (Opler and Krizek 1984). The importance of nectar sources suggested by the regal literature led us to a priori hypothesize that average percent forb cover would be an important habitat feature in describing regal densities. However, average percent forb cover was not one of the variables included in our top vegetation model. Our data indicated that there was no relationship between regal density and average percent cover of forbs. This was surprising given that other studies often report a positive relationship between regals and forbs (Nagel et al. 1991, Huebschman 1998, Davies et al. 2007, Helzer 2012, Farhat et al. 2014, Moranz et al. 2014, Caven et al. 2017). Regal populations have been positively correlated with number of flower ramets (Vogel et al. 2010), diversity of known nectar resources (Huebschman 1998), proximity to habitat with high nectar resources (Davies et al. 2007), and even flower color (Swengel 1993). Regals use a number of plant species as nectar sources, but they appear to exhibit strong selection for specific nectar plants (Heitzman and Heitzman 1987, Nagel et al. 1991, Swengel 1993, Huebschman 1998, Royer 2004).

Our results may have been due to the broad measurement of forbs used in this study. Average percent forb cover was measured as a percent of total herbaceous cover excluding graminoids. Accordingly, the resulting average percent forb cover estimates were comprised of all forbs including those forbs that are not selected or unusable by regals. Additionally, when measuring forb cover, we did not consider whether forbs were in flower, thus providing a usable nectar source to regals. Perhaps, had we collected these data in a way that would have afforded us the ability to further examine the specific plant species within each category, the value of forbs in our models may have been improved. For example, we were unable to further breakdown the forbs category, which included subshrubs (i.e., leadplant). It is possible that we may have seen some improvement in our model and been better able to disentangle our results had we collected those data in such a way that allowed us to separate subshrubs from forbs and bin them with true shrubs (i.e., rough-leaved dogwood [*Cornus drummondii*]). Consequently, we may not have measured forb cover in a manner that was ecologically relevant to regals.

Conclusion

To conserve populations of regals, we must determine the underlying reason(s) for their declines, which apparently have yet to be attributed to any one particular cause (Henderson et al. 2018). Mixed results regarding the effects of prescribed management, principally fire, on populations of regals is a point of major conservation concern. Inconsistencies among findings have only heightened the confusion behind what is commonly referred to as the "prairie butterfly paradox," where butterflies like the regal appear to be sensitive to the very processes considered necessary to maintain their grassland habitat (Moranz et al. 2014). Understanding nuances of how management practices affect regals throughout their range and across spatial scales is imperative to their survival. Our study is one of the first to examine effects of prescribed management practices on regals within a landscape-scale prairie context. These results join a growing suite of recent research that indicates prescribed burning, particularly when applied in a shifting mosaic, may not be as detrimental to populations of regals as previously suggested (Huebschman and Bragg 2000, Powell et al. 2007, Moranz et al. 2014, Henderson et al. 2018). These processes may even be critical to maintaining the habitat quality and heterogeneity within grasslands that regals require for long-term persistence. Our data also suggest that incorporation of other management (e.g., haying and grazing) along with moderate fire-return intervals appears to be compatible with conservation of regals. Prior to large-scale habitat fragmentation, disturbances such as fire, haying, and grazing would have been unlikely to decimate populations of regals. Unfortunately, due to widespread habitat conversion and fragmentation, regal populations are much more sensitive to the historic disturbance processes that maintained their grassland habitat (Caven et al. 2017). Thus, these management regimes should be applied carefully, as regals may respond differently to their use in various parts of their range, where for instance grasslands are more fragmented and not as well connected. Due to the variability in how grassland vegetation and wildlife respond to disturbances across their range (Collins and Steinauer 1998, Pöyry et al. 2005), our results support the notion that conservation planners and land managers can and perhaps should use a variety of management strategies to achieve heterogeneity and quality grassland habitat in support of prairie-obligate species such as the regal.

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Literature Cited

Abrams, M. D., and L. C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. American Midland Naturalist 117:442–445.

Anderson, R. C. 2006. Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. Journal of the Torrey Botanical Society 133:626–647.

Anderson, K. L., and C. L. Fly. 1955. Vegetation-soil relationships in Flint Hills bluestem pastures. Journal of Range Management 29:306–308.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Begay, B., H. M. Alexander, and E. Questad. 2011. Effect of mid-summer haying on growth and reproduction in prairie forbs. Transactions of the Kansas Academy of Science 114:108–114.

Beilfuss, K. G., and J. A. Harrington. 2001. Distribution patterns of the regal fritillary butterfly (*Speyeria idalia* Drury) within a Wisconsin dry prairie remnant. Pages 191–196 *in* N. P. Bernstein and L. J. Ostrander, editors. Proceedings of the 17th North American Prairie Conference: Seeds for the Future, Roots of the Past. North Iowa Area Community College, Mason City, Iowa, USA.

Bliss, P., and D. F. Schweitzer. 1987. Element stewardship abstract for *Speyeria idalia*, regal fritillary. The Nature Conservancy Eastern Heritage Task Force, Boston, Massachusetts, USA.

Bragg, T. B., and L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19–24.

Briggs, J. M., G. A. Hoch, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586.

Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. American Journal of Botany 82:1024–1030.

Briggs, J. M. A. K., J. M. Knapp, J. L. Blair, G. A. Heisler, M. S. Lett. Hoch, and J. K. McCarron. 2005. An ecosystem in transition causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55:243–254.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of wildlife populations. Oxford University Press, Oxford, UK.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science and Business Media, New York, New York, USA.

Caven, A. J., K. C. King, J. D. Wiese, and E. M. B. Buckley. 2017. A descriptive analysis of regal fritillary (*Speyeria idalia*) habitat utilizing biological monitoring data along the big bend of the Platte River, NE. Journal of Insect Conservation 21:183–205.

Collins, S. L. 1990. Introduction: fire as a natural disturbance in tallgrass prairie ecosystems. Pages 3–7 *in* S. L. Collins and L. L. Wallace, editors. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, Oklahoma, USA.

Collins, S. L. 1992. Fire frequency and community heterogeneity in tallgrass prairie: a field experiment. Ecology 73:2001–2006.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747.

Collins, S. L., and E. M. Steinauer. 1998. Disturbance, diversity, and species interactions in tallgrass prairie. Pages 140–158 *in* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics, long-term ecological research in tallgrass prairie. Oxford University Press, New York, New York, USA.

Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. Journal of Range Management 51:258–264.

Dana, R. P. 1991. Conservation management of the prairie skippers *Hesperia dacotae* and *Hesperia ottoe*: basic biology and threat of mortality during prescribed burning in spring. Bulletin 594-1991. Minnesota Agricultural Experiment Station, St. Paul, Minnesota, USA.

Dana, R. P. 1997. Characterization of three Dakota skipper sites in Minnesota. Final report submitted to the U.S. Fish and Wildlife Service by the Natural Heritage and Nongame Research Program, Minnesota Department of Natural Resources. https://files.dnr.state.mn.us/eco/nongame/projects/consgrant_reports/1997/1997_dana.pdf

Davies, J. D., D. M. Debinski, and B. J. Danielson. 2007. Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. Landscape Ecology 22:1341–1354.

Debinski, D. M., and L. Kelly. 1998. Decline of Iowa populations of the regal fritillary (*Speyeria idalia*) Drury. Journal of the Iowa Academy of Science 105:16–22.

Dole, J. M., W. B. Gerard, and J. M. Nelson. 2004. Butterflies of Oklahoma, Kansas, and North Texas. University of Oklahoma Press, Norman, Oklahoma, USA.

Dunwiddie, P. W., and N. Sferra. 1991. Loss of rare butterfly and plant species in coastal grasslands. Natural Areas Journal 11:119–120.

Ely, C. A., M. D. Schwilling, and M. E. Rolfs. 1986. An annotated list of the butterflies of Kansas. Fort Hays Studies (Science) 7. Fort Hayes State University, Fort Hays, Kansas, USA.

Farhat, Y. A., W. M. Janousek, J. P. McCarty, N. Rider, and L. L. Wolfenbarger. 2014. Comparison of butterfly communities and abundance between marginal grasslands and conservation islands in the eastern Great Plains. Journal of Insect Conservation 18:245–256.

Ferge, L. A. 1990. Rare butterflies and moths of Wisconsin. Niche: Newsletter of the Wisconsin Bureau of Endangered Resources 4:1–3.

Ferris, C. D., and F. M. Brown. 1981. Butterflies of the Rocky Mountain states. University of Oklahoma Press, Norman, Oklahoma, USA.

Ferster, B. 2005. Regal fritillaries: news from the eastern front. American Butterflies 13:4–12.

Ferster, B., and K. Vulinec. 2010. Population size and conservation of the last eastern remnants of the regal fritillary, *Speyeria idalia* (Drury) [Lepidoptera, Nymphalidae]; implications for temperate grassland restoration. Journal of Insect Conservation 14:31–42.

Fiske, I. J., and R. B. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Fuhlendorf, S. D., C. A. Davis, R. D. Elmore, L. E. Goodman, and R. G. Hamilton. 2018. Perspectives on grassland conservation efforts: Should we rewild to the past or conserve for the future? Philosophical Transactions of the Royal Society B: Biological Sciences 373:20170438.

Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns: We propose a paradigm that enhances heterogeneity instead of homogeneity to promote biological diversity and wildlife habitat on rangelands grazed by livestock. BioScience 51:625–632.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604–614.

Hammond, P. C. 1974. An ecological survey of the nymphalid butterfly genus *Speyeria*. Thesis. University of Nebraska, Lincoln, Nebraska, USA.

Hammond, P. C. 1995. Conservation of biodiversity in native prairie communities in the United States. Journal of the Kansas Entomological Society 68:1–6.

Hammond, P. C., and D. V. McCorkle. 1983. The decline and extinction of *Speyeria* populations resulting from human environmental disturbances (Nymphalidae: Argynninae). Journal of Research on the Lepidoptera 22:217–224.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151–162.

Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762.

Heitzman, J. R., and J. E. Heitzman. 1987. Butterflies and moths of Missouri. Missouri Department of Conservation, Jefferson City, Missouri, USA.

Helzer, C. 2012. Regal fritillary butterflies in burned and grazed prairie. The Nature Conservancy. The Prairie Ecologist. http://prairieecologist.com/2012/11/13/regal-fritillary-butterflies-in-burned-and-grazed-prairie/

Henderson, R. A., J. Meunier, and N. S. Holoubek. 2018. Disentangling effects of fire, habitat, and climate on an endangered prairie-specialist butterfly. Biological Conservation 218:41–48.

Huebschman, J. J. 1998. The relationship between nectar sources and regal fritillary (*Speyeria idalia* Drury) butterfly populations. Thesis. University of Nebraska at Omaha, Omaha, Nebraska, USA.

Huebschman, J. J., and T. B. Bragg. 2000. Response of regal fritillary (*Speyeria idalia* Drury) to spring burning in an eastern Nebraska tallgrass prairie, USA. Natural Areas Journal 20:386–388.

Jog, S., K. Kindscher, E. Questad, B. Foster, and H. Loring. 2006. Floristic quality as an indicator of native species diversity within managed grasslands. Natural Areas Journal 26:149–167.

KDA (Kansas Department of Agriculture). 2017. Bluestem pasture release 2017. https://www.agmanager.info/land-leasing/land-rental.../bluestem-pasture-release-2017

Kelly, L., and D. M. Debinski. 1998. Relationship of host plant density to size and abundance of the regal fritillary butterfly, *Speyeria idalia* Drury (Nymphalidae). Journal of the Lepidopterists' Society 52:262–276.

Klots, A. B. 1951. A field guide to the butterflies of North America, east of the Great Plains. Houghton Mifflin Company, Boston, Massachusetts, USA.

Knapp, A. K., J. M. Briggs, J. M. Blair, and C. L. Turner. 1998. Patterns and controls of aboveground net primary production in tallgrass prairie. Pages 193–221 *in* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, editors. Grassland dynamics, long-term ecological research in tallgrass prairie. Oxford University Press, New York, New York, USA.

Kohl, M. T., P. R. Krausman, K. Kunkel, and D. M. Williams. 2013. Bison versus cattle: Are they ecologically synonymous? Rangeland Ecology and Management 66:721–731.

Kopper, B. J., R. E. Charlton, and D. C. Margolies. 2000. Oviposition site selection by the regal fritillary, *Speyeria idalia*, as affected by proximity of violet host plants. Journal of Insect Behavior 13:651–665.

Latham, R. E., D. Zercher, P. McElhenny, P. Mooreside, and B. Ferster. 2007. The role of disturbance in habitat restoration and management for the eastern regal fritillary (*Speyeria idalia idalia*) at a military installation in Pennsylvania. Ecological Restoration 25:103–111.

Lett, M. S., and A. K. Knapp. 2005. Woody plant encroachment and removal in mesic grassland: production and composition responses of herbaceous vegetation. American Midland Naturalist 153:217–231.

Marrone, G. M. 2002. Field guide to butterflies of South Dakota. South Dakota Department of Game, Fish, and Parks, Pierre, South Dakota, USA.

Mason, K. R. 2001. Comparison of prairie sites and classification of their habitat attributes in relation to abundance of the regal fritillary butterfly (*Speyeria idalia*). Minnesota Department of Natural Resources. http://files.dnr.state.mn.us/eco/nongame/projects/consgrant_reports/2001/2001_mason.pdf

McCabe, T. L. 1981. The Dakota Skipper, *Hesperia dacotae* (Skinner): range and biology, with special reference to North Dakota. Journal of the Lepidopterists' Society 35:179–193.

McCullough, K., G. Albanese, and D. A. Haukos. 2017. Novel observation of larval fire survival, feeding behavior, and host plant use in the regal fritillary, *Speyeria idalia* (Drury) (Nymphalidae). Journal of the Lepidopterists' Society 71:146–152.

Mello, M. J. 1989. Survey and ecology of *Speyeria idalia* (regal fritillary) on Block Island with notes on other species. Report # 89-9. Lloyd Center for Environmental Studies, South Dartmouth, Massachusetts, USA. Submitted to The Nature Conservancy, Rhode Island Field Office.

Miller, T. 2018. Stocking rates are the key! Natural Resources Conservation Service Kansas United States Department of Agriculture. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/ks/newsroom/features/?cid=stelprdb1266414

Moranz, R. A., S. D. Fuhlendorf, and D. M. Engle. 2014. Making sense of a prairie butterfly paradox: the effects of grazing, time since fire, and sampling period on regal fritillary abundance. Biological Conservation 173:32–41.

Nagel, H. G., T. Nightengale, and N. Dankert. 1991. Regal fritillary butterfly population estimation and natural history on Rowe Sanctuary, Nebraska. Prairie Naturalist 23:145–152.

NatureServe. 2005. NatureServe Explorer: an online encyclopedia of life. Version 7.0. Arlington, Virginia, USA. http://www.natureserve.org/explorer

Nekola, J. C. 2002. Effects of fire management on the richness and abundance of central North American grassland land snail faunas. Animal Biodiversity and Conservation 25:53–66.

Opler, P. A., and G. O. Krizek. 1984. Butterflies east of the Great Plains. Johns Hopkins University Press, Baltimore, Maryland, USA.

Owensby, C. 2010. Managing Kansas Flint Hills grasslands. Symphony in the Flint Hills Field Journal. https://newprairiepress.org/cgi/viewcontent.cgi?article=1009&context=sfh

Panzer, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. Conservation Biology 16:1296–1307.

Powell, A. F. L. A., W. H. Busby, and K. Kindscher. 2007. Status of the regal fritillary (*Speyeria idalia*) and effects of fire management on its abundance in northeastern Kansas, USA. Journal of Insect Conservation 11:299–308.

Pöyry, J., S. Lindgren, J. Salminen, and M. Kuussaari. 2005. Responses of butterfly and moth species to restored cattle grazing in semi-natural grasslands. Biological Conservation 122:465–478.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ratajczak, Z., J. M. Briggs, D. G. Goodin, L. Lei, R. L. Mohler, J. B. Nippert, and B. Obermeyer. 2016. Assessing the potential for transitions from tallgrass prairie to woodlands: Are we operating beyond critical fire thresholds? Rangeland Ecology and Management 69:280–287.

Reichman, O. J. 1987. Konza prairie: a tallgrass natural history. University of Kansas Press, Lawrence, Kansas, USA.

Ries, L., and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. Journal of Animal Ecology 70: 840–852.

Royer, R. A. 2004. Atlas of North Dakota butterflies. Northern Prairie Wildlife Research Center Online, Jamestown, North Dakota, USA. Version 29. http://www.npwrc.usgs.gov/resource/distr/lepid/bflynd/bflynd.htm

Royer, R. A., and G. M. Marrone. 1992. Conservation status of the regal fritillary (*Speyeria idalia*) in North and South Dakota. U.S. Fish and Wildlife Service, Denver, Colorado, USA.

Royle, J. A., D. K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. Ecology 85:1591–1597.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44:418–421.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 1998. Grasslands. Pages 437–445 *in* M. J. Mac, P. A. Opler, C. E. Puckett Haecker, and P. D. Doran, editors. Status and trends of the nation's biological resources. Biological Resources Division, U.S. Geological Survey, Reston, Virginia, USA.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. Wildlife Society Bulletin 32:6–15.

Sauer, C. O. 1950. Grassland climax, fire and management. Journal of Range Management 3:16–20.

Schlicht, D. W., and T. T. Orwig. 1998. The status of Iowa's Lepidoptera. Journal of the Iowa Academy of Science 105:82–88.

Selby, G. L. 2007. Regal fritillary (*Speyeria idalia* Drury): a technical conservation assessment. USDA Forest

Service, Rocky Mountain Region. http://www.fs.fed.us/r2/projects/scp/assessments/regalfritillary.pdf

Shuey, J. A. 1997. Dancing with fire: ecosystem dynamics, management, and the karner blue (*Lycaeides melissa samuelis* Nabokov) (Lycaenidae). Journal of the Lepidopterists' Society 51:263–269.

Shuey, J., E. Jacquart, S. Orr, F. Becker, A. Nyberg, R. Littiken, T. Anchor, and D. Luchik. 2016. Landscape-scale response to local habitat restoration in the regal fritillary butterfly (*Speyeria idalia*) (Lepidoptera: Nymphalidae). Journal of Insect Conservation 20:773–780.

Steinauer, E. M., and S. L. Collins. 1996. Prairie ecology: the tallgrass prairie. Pages 39–52 *in* F. B. Samson and F. L. Knopf, editors. Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Washington, D.C., USA.

Sutcliffe, O. L., C. D. Thomas, and D. Peggie. 1997. Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. Oecologia 109:229–234.

Swengel, A. B. 1993. Regal fritillary: prairie royalty. American Butterflies 1:4–9.

Swengel, A. B. 1996. Effects of fire and hay management on abundance of prairie butterflies. Biological Conservation 76:73–85.

Swengel, A. B. 1997. Habitat associations of sympatric violet-feeding fritillaries (*Euptoieta, Speyeria, Boloria*) (Lepidoptera: Nymphalidae) in tallgrass prairie. Great Lakes Entomologist 30:1–18.

Swengel, A. B. 1998. Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biological Conservation 83:77–89.

Swengel, A. B. 2001*a*. Regal weeds…the surprising value of an old field. Wisconsin Entomological Society Newsletter 28:1, 5.

Swengel, A. B. 2001*b*. Update on the regal fritillary in Wisconsin. Wisconsin Entomological Society Newsletter 28:1–2, 5.

Swengel, S. R., D. Schlicht, F. Olsen, and A. B. Swengel. 2011. Declines of prairie butterflies in the Midwestern USA. Journal of Insect Conservation 15:327–339.

Swengel, A. B., and S. R. Swengel. 1999. Observations of prairie skippers (*Oarisma Poweshiek*, *Hesperia dacotae*, *H. ottoe*, *H leonardus pawnee*, and *Atrytone arogos* Iowa) (Lepidoptera: Hesperiidae) in Iowa, Minnesota, and North Dakota during 1988–1997. Great Lakes Entomologist 32:267–292.

Swengel, A. B., and S. R. Swengel. 2001*a*. Effects of prairie and barrens management on butterfly faunal composition. Biodiversity Conservation 10:1757–1785.

Swengel, A. B., and S. R. Swengel. 2001*b*. A 10-year study to monitor populations of the regal fritillary, *Speyeria idalia*, (Lepidoptera: Nymphalidae) in Wisconsin, U.S.A. Great Lakes Entomologist 34: 97–115.

Swengel, A. B., and S. R. Swengel. 2007. Benefit of permanent non-fire refugia for Lepidoptera conservation in fire managed sites. Journal of Insect Conservation 11:263–279.

Tilden, J. W., and A. C. Smith. 1986. A field guide to western butterflies. Houghton Mifflin Company, Boston, Massachusetts, USA.

Toombs, T. P., J. D. Derner, D. J. Augustine, B. Krueger, and S. Gallagher. 2010. Managing for biodiversity and livestock. Rangelands 32:10–15.

Towne, E. G. 2002. Vascular plants of Konza Prairie Biological Station: an annotated checklist of species in a Kansas tallgrass prairie. SIDA 20:269–294.

Towne, E. G., D. C. Hartnett, and R. C. Cochran. 2005. Vegetation trends in tallgrass prairie from bison and cattle grazing. Ecological Applications 15:1550–1559.

USFWS (U.S. Fish and Wildlife Service). 2015. Status review for four Midwestern species. www.fws.gov/midwest/es/soc/Batch90daySept2015.html

USFWS (U.S. Fish and Wildlife Service). 1996. 50 CFR Part 17, Endangered and threatened wildlife and plants; review of plant and animal taxa that are candidates for listing as endangered or threatened. Federal Register 1:7596.

Vogel, R. J. 1974. Effects of fire on grasslands. Pages 139–194 *in* T. T. Kozlowski and C. E. Ahlgren, editors. Fire and ecosystems. Academic Press, New York, New York, USA.

Vogel, J. A., D. M. Debinski, R. R. Koford, and J. R. Miller. 2007. Butterfly responses to prairie restoration through fire and grazing. Biological Conservation 140:78–90.

Vogel, J. A., R. R. Koford, and D. M. Debinski. 2010. Direct and indirect responses of tallgrass prairie butterflies to prescribed burning. Journal of Insect Conservation 14:663–677.

Wagner, D. L., M. S. Wallace, G. H. Boettner, and J. S. Elkington. 1997. Status update and life history studies on the regal fritillary (Lepidoptera: Nymphalidae). Pages 261–275 *in* P. D. Vickery and P. W. Dunwiddie, editors. Grasslands of northeastern North America ecology and conservation of native and agricultural landscapes. Massachusetts Audubon, Lincoln, Massachusetts, USA.

Wahlberg, N., A. Moilanen, and I. Hanski. 1996. Predicting the occurrence of endangered species in fragmented landscapes. Science 273:1536–1538.

Zercher, D., P. McElhenny, and P. Mooreside. 2002. Habitat management plan for the regal fritillary (*Speyeria idalia*) at the Fort Indiantown Gap National Guard Training Center, Annville, Pennsylvania. 5-year implementation period: 2002–2006. Final plan prepared for the Pennsylvania Department of Military and Veterans Affairs, Fort Indiantown Gap, Environmental Section, Annville, Pennsylvania, USA.