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ORIGINAL PAPER

# Status of the regal fritillary (*Speyeria idalia*) and effects of fire management on its abundance in northeastern Kansas, USA

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**Abstract** The Regal Fritillary (*Speyeria idalia*), which once occupied prairies and meadows in North America from the upper Great Plains to the Atlantic coast, has disappeared in recent decades from nearly the entirety of the eastern half of its range and has declined westward. In the Great Plains, where the species is limited to native prairie remnants, several large populations are thought to exist, but patterns of occurrence and abundance in the region have not been described in detail. We surveyed prairies within a three county area of northeastern Kansas using distance-sampling along line transects and found Regal Fritillaries present at 70 of 87 sites. Population density varied considerably among sites but was generally much higher at those that had not been burned in the past year. Despite the loss of >99% of its original prairie landcover and the small sizes of remnants ($\bar{x} = 7.1$ ha), we estimate that our study area supports a globally significant population of ~12,000 adult individuals. Given the rapidity of decline of Regal Fritillary populations elsewhere, this study establishes important population benchmarks and a practical protocol for future monitoring efforts.

**Keywords** Distance sampling · Prescribed burning · Regal Fritillary *Speyeria idalia* · Tallgrass prairie remnants

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## Introduction

Once found in North America from the tall and mixed-grass prairies of the northern and central Great Plains and Midwest, eastward in tame meadows and wetlands to the Atlantic coast, the Regal Fritillary (*Speyeria idalia*) has suffered extraordinary decline. For reasons that are poorly understood, eastern populations crashed in the 1960s-early 1990s; today, only two localized populations remain east of Illinois and they are few, isolated, and declining east of the plains states and western Missouri (Debinski and Kelly 1998; Swengel and Swengel 2001; Williams 2002; NatureServe 2005). In the western portion of its range, where it is essentially a native prairie obligate, the Regal Fritillary underwent tremendous decline over the last two centuries as >95% of tallgrass prairie was destroyed (Samson et al. 1999), but does not seem to have experienced recent collapses (Royer and Marrone 1992; Swengel 1998; Mason 2001; NatureServe 2005). Because of its history of widespread extirpation, ongoing threats to existing populations from prairie loss and mismanagement, and the lack of documentation of stable populations anywhere, the species merits considerable conservation concern (Natural Heritage Inventory rank G3; NatureServe 2005).

Discussion of Regal Fritillary status in its western range has been vague; there are few descriptions of its abundance within the region, let alone studies of population numbers, sizes, or structure (but see Williams et al. 2003). It is "locally common in areas of southern North Dakota and most of South Dakota,'' occurring, respectively, at 23 of 65, and 28 of 29 prairies surveyed in 1991 (Royer and Marrone 1992). In Nebraska, it is rare or uncommon, but ''remains abundant in some localities, especially in wet riparian habitat along the Platte River'' (Nagel et al. 1991). In Kansas, the Regal Fritillary can be found through much of the state (Ely et al. 1986) and although no quantitative studies of regions or multiple sites have been published, it is reportedly ''a common resident of undisturbed or lightly grazed tallgrass prairie'' (Kopper et al. 2001a) in the eastern third, where it ranks ''among the most abundant large butterflies'' (Kopper et al. 2001b). Likewise, prairie remnants in western Missouri support high-density colonies that are thought to be relatively stable and well connected (Swengel 1998; NatureServe 2005).

Historically, tallgrass prairie covered ≥90% of Douglas, Leavenworth, and Miami counties in northeastern Kansas, but because of agricultural and other development, remnants ≥2 ha in size now constitute <0.5% of land cover (Kindscher et al. 2005), a condition generally representative of the eastern sixth of Kansas and adjoining western Missouri. The prairie that remains in this region survives in scattered small parcels, nearly all of them hay meadows, but since prairie hay has little value in the modern agricultural economy, prescribed burning has grown in popularity as a low-cost alternative to cutting for farmers and exurban landowners wishing to prevent their properties from becoming woody thickets. Increased awareness of the historic role of fire in prairie ecosystems has made it even more attractive to conservation oriented land managers, but prescribed burns kill Regal Fritillary larvae (the life stage present March–April when most burns are conducted), greatly reducing or even eliminating the species from sites (Kelly and Debinski 1998; Swengel 1998; Huebschman and Bragg 2000; Swengel and Swengel 2001). Because periodic fire is so useful, perhaps even essential, for prairie restoration and maintenance, the appropriate role of fire in managing sites that harbor prairie-obligate insects remains controversial (Schwartz 1998; Swengel 2001; Panzer 2002).

The goals of this study were to (1) describe Regal Fritillary occurrence and abundance within three northeastern Kansas counties, (2) investigate effects of prairie management, particularly prescribed burning, on regal density, and (3) test the practicality of conducting surveys using distance-sampling along line transects. Accomplishing the first two goals required visiting a large number of sites, hence our interest in distance-sampling as an alternative to mark-recapture as a means of abundance estimation. Distance-transect data, unlike traditional counts, can be used to correct for observer differences and detection probability according to distance and habitat, and make absolute density estimates. We found that the Regal Fritillary is still a common inhabitant of prairies in northeastern Kansas, particularly unburned sites. Our results provide a basis for detecting future population declines in the region and for comparisons with studies elsewhere.

## Methods

### Timing of fieldwork

The Regal Fritillary is univoltine; eggs are laid in September, the larvae overwinter in leaf litter, then feed on violets (*Viola* spp.) and pupate in early spring (Kopper et al. 2001a). In eastern Kansas, the first adults appear as early as 25 May (Ely et al. 1986), but females do not begin emerging until ~10 days after males, and numbers do not reach maximal levels until mid June (Kopper et al. 2001a). Peak visibility is during the second half of June, at which time males spend the day in flight, searching the vegetation for females (Kopper et al. 2001a). We found the 2005 season to be typical, first noticing regals on 27 May, 1, and 2 June in Leavenworth, Douglas, and Miami counties respectively, and on 26 May in central Kansas (Saline County).

### Line-transect surveys

We surveyed 87 tallgrass prairie remnants, totaling 618 ha, in three northeastern Kansas counties for Regal Fritillaries in mid June 2005 (14–15 and 20–21 June in Douglas; 22 June in Leavenworth; 23–24 June in Miami County). Sites were representative of prairie remnants regionally with regard to size (range 0.9–53.0 ha, $\bar{x} = 7.1$ ha, median 5.1 ha), quality (ranks of A, B, C, <C for 29, 47, 7, and 4 sites respectively according to within-site condition, and 0, 30, 41, and 16 sites according to element occurrence value), and management (nearly all were hay meadows, cut once annually in July; a few were pastures or idle, most of which were burned, probably in April). Quality of sites was determined using Natural Heritage program procedures (NatureServe 2002; Kindscher et al. 2005); condition rank depends on native species richness, exotic species abundance, and ecological processes (including disturbances), whereas element occurrence rank adds consideration of site size and

landscape context. Sites generally lacked any coverage by trees or shrubs, but often bordered such vegetation. Signs of recent fire (absence of litter, recently killed junipers, charred stems) were used to classify sites as burned since the last growing season versus unburned during that period (fall 2004-spring 2005; Table 1). Average sizes of burned (6.7 ± 1.07 ha) and unburned (7.2 ± 0.96 ha) sites were similar. One Douglas County prairie had both burned and unburned portions; we treated these as separate transects in analyses.

Transect centerlines (range 130–1300 m, $\bar{x} = 475$ m, median 450 m) ran the length of each (usually rectangular) site from one end to the other, and were located parallel to, and >30 m from, the edges of the site to each side of the line. Most transects consisted of two parallel segments located >60 m apart. Transects were not physically marked; a visual landmark was used to walk a fixed bearing, thereby defining a transect centerline, and a GPS unit used to measure transect lengths. All surveys were conducted by the same observer (AP), between 8:30 and 17:00 CST, under dry (no dew or recent precipitation), sunny, and warm (25–34°C) conditions, with winds <20 km/h. Surveys were done by walking along transect centerlines at ~4 km/h and recording the perpendicular distance to each individual (irrespective of its sex) seen ≤30 m from the line. Distances were estimated when ≤10 m, and measured with a laser rangefinder when greater; however, when butterfly densities were high, most distances were estimated, often in intervals of 5 m. If no Regal Fritillaries were detected prior to or while walking the transect at a site, we used binoculars for ~10 min to scan for the presence of the species (Flying individuals could be easily identified for several hundred meters).

## Abundance measures

The raw data from each site were converted to an index of relative abundance, individuals per 100 m transect, by multiplying total counts of individuals detected ≤30 m from the transect line by 100 m divided by transect length. Encounter rates for the study as a whole, and according to burn status, county, and combinations thereof, were calculated by averaging the rates of constituent sites.

We used DISTANCE, version 5.0, beta release 4 (Thomas et al. 2005) to estimate Regal Fritillary densities by following guidelines detailed by Buckland et al. (2001). Program DISTANCE fits a model detection function to the frequency distribution of perpendicular distances of individuals from the transect centerline; then, by accounting for the proportion of individuals present but not detected, it estimates the true density of individuals in the surveyed area. Preliminary models estimated the probability of detection at 30 m to be ~0.20, thereby indicating no need to truncate our data to a distance less than the transect width. A histogram of the data (Fig. 1) revealed obvious heaping of recorded distances at 5 m intervals, a structure we anticipated given the manner in which distances were estimated. In addition, a large number of detections occurred within a meter of the centerline (of 1,112 total, 52 were on the centerline and 64 were one meter distant) a condition that, in combination with an unrealistic paucity of detections between six and nine meters, generated a "spiked" histogram when we grouped the data into six (5 m) intervals, thus violating the broad "shoulder" shape criterion for reliable density estimation (Buckland et al. 2001, p. 42). Reducing the number of intervals to four achieved a better histogram shape and simplified

**Table 1** Abundances of Regal Fritillaries according to region and burn treatment. Values shown are encounter rates ($\bar{x}$ individuals per 100 m transect ±1 SE) according to equal weighting by site, density estimates ($\bar{x}$ individuals per ha ±1 SE) according to equal weighting by site, and density estimates weighted by transect length as calculated by program DISTANCE

| Region and treatment | Sites surveyed | Sites with regals | Encounter rate | Density | DISTANCE model estimates | | |
|---|---|---|---|---|---|---|---|
| | | *n* (%) | | | Density | 95% CI | df |
| Survey-wide (all sites) | 87 | 70 (80) | 2.7 ± 0.37 | 7.6 ± 1.03 | 7.6 ± 1.05 | 5.7–10.0 | 90 |
| Burned | 21 | 16 (76) | 0.9 ± 0.27 | 3.4 ± 1.04 | 2.9 ± 0.83 | 1.6–5.2 | 25 |
| Unburned | 66 | 54 (82) | 3.2 ± 0.46 | 8.9 ± 1.28 | 9.4 ± 1.31 | 7.1–12.3 | 71 |
| Douglas County (all) | 52 | 48 (92) | 2.9 ± 0.43 | 8.5 ± 1.18 | | | |
| Burned | 17 | 15 (88) | 1.1 ± 0.32 | 4.1 ± 1.22 | 3.4 ± 0.95 | 1.9–6.0 | 20 |
| Unburned | 35 | 33 (94) | 3.8 ± 0.55 | 10.6 ± 1.53 | 11.3 ± 1.52 | 8.6–14.8 | 37 |
| Leavenworth County[a] | 8 | 8 (100) | 7.1 ± 1.90 | 19.5 ± 5.26 | 20.2 ± 4.77 | 11.7–34.9 | 7 |
| Miami County (all) | 27 | 14 (52) | 0.9 ± 0.38 | 2.4 ± 1.05 | | | |
| Burned | 4 | 1 (25) | 0.1 ± 0.06 | 0.2 ± 0.21 | 0.2 ± 0.22 | 0.020–2.8 | 3 |
| Unburned | 23 | 13 (56) | 1.0 ± 0.44 | 2.7 ± 1.22 | 3.1 ± 1.42 | 1.2–7.7 | 22 |

[a] All sites unburned

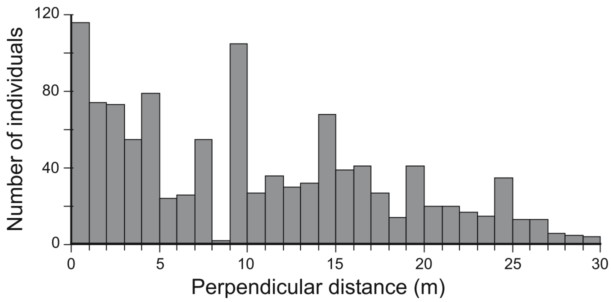


**Fig. 1** Number of Regal Fritillaries counted with respect to perpendicular distance from transect centerlines

modeling (with little effect on estimated density), so we used that grouping in subsequent work.

We created a variety of models by using all key functions available in DISTANCE combined with series expansions recommended for each (Buckland et al. 2001, p. 47). We used diagnostic tools in DISTANCE to assess models—Akaike's Information Criterion (AIC) to select adjustment terms and the most parsimonious model, and a $\chi^2$ test to check model fit to the data. The best model for the dataset as a whole (global model) was the uniform key function with cosine adjustment of order 1 (AIC = 2820.43; $\chi^2$ = 0.255, df = 2, $P$ = 0.88). However, after modeling separate detection functions according to burn status or county, then comparing the summed AIC scores to that of the global model, we found that separate models for burned and unburned prairie yielded a lower score (AIC = 2816.16), and were therefore preferable. The best model for unburned prairie was the half-normal key function (no adjustments; AIC = 2624.11; $\chi^2$ = 0.695, df = 2, $P$ = 0.71; Fig. 2a) whereas that for burned prairie was the uniform key function with cosine adjustments of orders 1 and 2 (AIC = 192.05; $\chi^2$ = 0.042, df = 1, $P$ = 0.84; Fig. 2b).

The density that DISTANCE calculates for the dataset used to select a model detection function is weighted by the transect lengths of samples. To calculate estimates based on equal weighting of sites, we used the models for unburned and burned prairie to estimate the density at each survey site according to its condition, then averaged appropriate combinations of those site estimates to calculate densities of Regal Fritillaries survey-wide and according to burn status, county, and combinations thereof. We estimated total numbers of Regal Fritillaries at sites by multiplying the density estimate by the area of each site (Kansas Biological Survey, unpub. data).

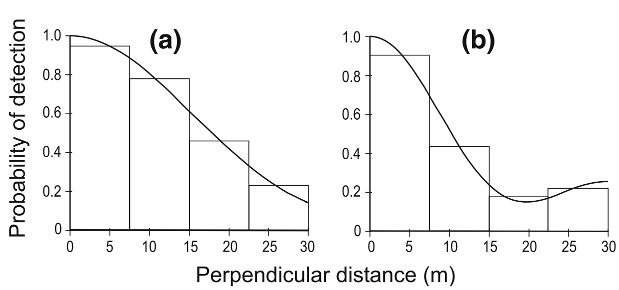


**Fig. 2** Modeled detection probability according to distance from transect centerline for Regal Fritillaries in (**a**) unburned and (**b**) burned prairies. Histograms of numbers of individuals detected are scaled to illustrate correspondence between models and data

### Abundance comparisons

By graphing the data and subsets thereof, and using regression analyses and ANOVA, we looked for effects of burn status, county, prairie size (area, log-area), prairie quality, date, and time of day on encounter rates. We examined the distribution of sites relative to one another, other prairies, and other landcover types (Kansas GAP; Cully et al. 2003) to look for geographic patterns in abundance.

To compare the density estimates for burned and unburned prairie calculated by DISTANCE, we used Welch's approximate $t$-test for samples with unequal variances (Sokal and Rohlf 1995). Following log-transformation [log(1+regals per 100 m)] to improve homogeneity of variances, we evaluated encounter rates with analysis of variance (ANOVA) using the general linear model in MINITAB, release 12.1 (Minitab, State College, Pennsylvania), and used the Tukey test in MINITAB to make pairwise comparisons of multilevel factors. To test for effects of burning and county, we included both terms in a single model (the former as a covariate). We could not include the burning × county interaction term in the model because we did not survey any burned prairies in Leavenworth county, but we tested for its significance using two models in which we *were* able to include the interaction term; in the first, by excluding the Leavenworth county data, and in the second, by pooling them with the Douglas county data. We did not perform ANOVAs using site densities because those estimates lacked independence, a common detection function model having been used for all sites within each burn category.

## Results

### Presence and numbers counted at sites

Regal Fritillaries were present at most sites (Table 1). We counted 1,112 regals at 70 of 87 surveyed prairie remnants; counts ranged 0–78 ($\bar{x} = 12.8$, median 5) individuals per site. Presence-absence was unrelated to whether sites were burned ($\chi^2 = 0.321$, df = 1, $P = 0.57$) but was very different by county (Table 1); regals were absent at some sites in both Douglas and Miami counties, but significantly more often in the latter ($\chi^2 = 17.223$, df = 1, $P < 0.001$). With the exception of one prairie in Douglas county, we detected regals ($\bar{x} = 15.9$, median 8 individuals) on the transect at each of the 70 sites at which we otherwise noted the species' presence.

Abundance and colony sizes at sites

Abundance ranged 0–17.0 ($\bar{x} = 2.7 \pm 0.37$ SE, median 1.28) individuals per 100 m transect, corresponding to densities of 0–46.9 ($\bar{x} = 7.6 \pm 1.03$ SE, median 1.28) individuals per hectare. Estimated colony sizes ranged 0–299 ($\bar{x} = 48.2 \pm 7.23$ SE, median 19.7) individuals per site (Fig. 3). Excluding the 20% of sites where regals were absent had little affect on these numbers (range 0–17.0, $\bar{x} = 3.3 \pm 0.43$ SE, median 2.00 individuals per 100 m; estimated colony size range 0–299, $\bar{x} = 59.9 \pm 8.41$ SE, median 29.2 individuals per site) because sites with higher abundances were progressively rarer than those with lower abundances, a pattern that held in survey-wide composite regardless of whether sites were burned (Fig. 4a).

Interactions between burning and county

ANOVA tests for the effect of burn status × county did not find this interaction significant ($F = 1.03$, df = 1 and 75, $P = 0.31$; $F = 1.41$, df = 1 and 83, $P = 0.24$), although the power of these tests was limited by sample size. Regal Fritillary encounter rates were lower in burned prairie in each of the counties that allowed for comparison (Table 1). This difference was significant in Douglas (one-way ANOVA: $F = 18.00$, df = 1 and 50, $P < 0.001$), but not Miami ($F = 1.78$, df = 1 and 25, $P = 0.19$) county; however, the latter result may owe more to test power than degree of effect.

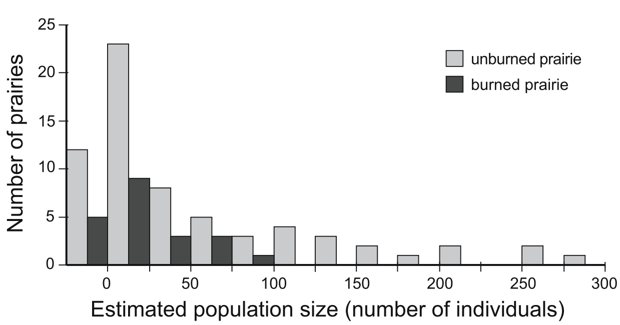


**Fig. 3** Distribution of surveyed prairies according to burn status and the estimated size of the adult Regal Fritillary population present. The first pair of bars indicates prairies at which no individuals were observed

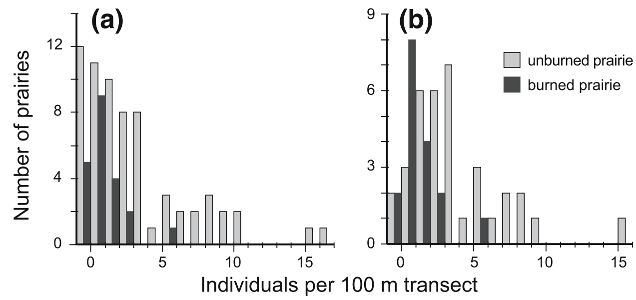


**Fig. 4** Distribution of surveyed prairies according to Regal Fritillary density and burn status (**a**) survey-wide and (**b**) in Douglas County. The first pair of bars in each graph indicates prairies at which no individuals were observed

Effects of burning

Regal Fritillaries were detected 4.5× more frequently in unburned prairie (1,032 individuals in 30,550 m of transect) than in burned prairie (80 individuals in 10,680 m of transect), although when calculated from averages of equally weighted site encounter rates this difference was reduced to 3.6× (Table 1). The 3.2× difference seen between density estimates from DISTANCE models (Table 1) was smaller still because the probability of detecting individuals in burned prairie (0.43 ± 0.042 SE) was estimated to be lower than in unburned prairie (0.60 ± 0.017 SE), yet this difference between density estimates for burned and unburned prairie was still substantial (6.5 ± 1.55 individuals/hectare) and significant ($t' = 4.173$, df ≈ 45, $P < 0.001$). Likewise, the effect of burning on encounter rates was significant ($F = 18.25$, df = 1 and 83, $P < 0.001$) in our ANOVA for effects of burn status and county.

As noted previously, regals were no more likely to be absent in burned than unburned prairie. Burning did, however, affect the high end of the range of abundances seen among sites (Fig. 4a); only one burned prairie (5% of the total), with 5.3 regals per 100 m transect, had an encounter rate over 2.4 regals per 100 m transect, whereas 29 unburned prairies (44% of the total), with abundances up to 17.0 regals per 100 m, exceeded that value. Because mean abundance varied significantly by county (see below), looking at the Douglas county data alone (Fig. 4b) may provide a more accurate picture of effects of burning on the distribution of abundances of regals among sites than does the survey-wide dataset, because in the latter, unburned Miami county prairies fill in much of the lower range of the distribution.

### Differences among counties

Mean Regal Fritillary abundance was highest in Leavenworth and lowest in Miami county (Table 1). The effect of county on encounter rates was significant ($F = 22.03$, df = 2 and 83, $P < 0.001$) in our ANOVA for effects of burn status and county; abundance was significantly lower in Miami county in pairwise comparisons with Douglas (Tukey test = 5.62, $P < 0.0001$) and Leavenworth (Tukey test = 5.32, $P < 0.0001$) counties. As previously noted, regals were significantly more often absent in Miami county than the others, but this phenomenon did not by itself account for differences in abundance. When we reanalyzed the data after excluding all sites where regals were absent, effects of county were still significant ($F = 8.93$, df = 2 and 66, $P < 0.001$) and abundance in Miami county was still significantly lower than in Douglas (Tukey test = 3.42, $P = 0.003$) and Leavenworth (Tukey test = 3.87, $P = 0.0007$) counties despite the fact that doing so disproportionately raised Miami county abundance; average abundance was 2.9 and 0.9 individuals per 100 m for Douglas and Miami counties respectively using all data, but were 3.2 and 1.6 individuals per 100 m when considering only sites where regals were present.

In contrast to the strict limit that burning imposed, each county had at least one site with very high abundance. The top three sites had 17.0, 15.6, and 10.1 regals per 100 m transect and were found, respectively, in Leavenworth, Douglas, and Miami counties, though the last case was quite extraordinary given that the second highest abundance found in Miami county was 2.4 regals per 100 m transect. At the other end of the spectrum, Miami county had many sites lacking regals, and Douglas county had a number of such sites, but the lowest abundance seen in a Leavenworth county prairie was 0.7 regals per 100 m transect.

### Effects of other factors

We found no effects of prairie size, prairie quality (either internal condition or element occurrence), date, or time of day on encounter rates, nor were there any suggestive patterns or associations with land cover types in the geographic distribution of abundance.

## Discussion

We found the Regal Fritillary to be a common resident of northeastern Kansas prairie remnants, occurring at 70 of 87 (80%) sites surveyed. Though abundance varied considerably among sites, the species' survey-wide density of 7.6 individuals per ha (Table 1) compares favorably to averages of 5.6 and 5.8 individuals per ha found, respectively, at large sites where the species was present in Iowa and the Dakotas (Kelly and Debinski 1998). We estimate the total adult population of our three county study area to be ~12,000 individuals, and believe that it constitutes only a small portion of a much larger metapopulation system in eastern Kansas and beyond.

Prescribed burning greatly reduced abundance (Table 1), presumably by eliminating larvae. In fact, past burns might explain the low abundance of regals at many "unburned" sites since populations can take several years to reach high levels after a fire (AP pers. obs., Swengel 1996; Swengel and Swengel 2001), but we did not have the site management histories necessary to explore this. We did notice that sites with high abundances generally had dense litter, indicating that they had not been burned in recent years, whereas unburned sites with low abundances usually had little litter, but this condition could also have been due to the sparser vegetation that also seemed to characterize some of those sites. The only Miami County site with high regal density (10.1 regals per 100 m transect) was a hay meadow that was exceptional, judging by its accumulation of litter and standing dead vegetation, for not having been hayed for a year or two, as well as the consequent presence of Henslow's Sparrows (*Ammodramus henslowii*). Interestingly, less than 400 m distant and on the other side of a highway, an equally large unburned prairie with much less litter and sparser vegetation had only 1.4 regals per 100 m transect.

That the two sites described above could have such different densities of regals despite their close proximity raises the question of the Regal Fritillary's dispersal capability, and whether densities at sites are more a reflection of local colony histories or of how successfully sites meet the habitat selection criteria of wide-ranging adults. Regals are strong flyers and sometimes disperse over tens of kilometers or more, though it is their tendency to remain within the bounds of their natal prairie, especially if it is surrounded by trees, croplands, or roads (Mason 2001; Ries and Debinski 2001; Shepherd and Debinski 2005). Nagel et al. (1991) noted that early in the season, males stayed in the area where they emerged, presumably to mate with females immediately upon their emergence. Such behavior, rather than habitat selection, perhaps explains our observation of 1.1 versus 6.3 regals per 100 m transect in burned and unburned portions of the only prairie where we encountered both treatments and no barriers to movement between them. Huebschman and Bragg (2000) found that it took four weeks for dispersal from the unburned to the burned areas of a large site to equalize densities.

Movement of at least a few individuals among sites seems the most likely mechanism to explain the lack of effects of prairie size or burn status on presence-absence in our study; the average distance between each prairie remnant in our study area and its nearest neighbor (sometimes located in an adjoining county) was 1.24 km, a distance well within the dispersal capabilities of the Regal Fritillary. Most remnants were substantially smaller ($\bar{x} = 7.1$ ha) than the 50–100 ha suggested necessary to support a viable population (NatureServe 2005), and the modest numbers at many sites clearly did not represent self-sustaining colonies (Fig. 3). On the other hand, the small sizes of sites did not preclude the existence of many colonies that were respectably large (27 sites with ≥50, and 15 sites with >100 individuals), considering that populations range-wide are thought to average 100–200 adults (NatureServe 2005). Indeed, the five largest colonies (203–299 individuals) occurred at sites of only 4.7–21.1 ha ($\bar{x} = 11.2$ ha, median 9.4 ha). Another possible explanation for these patterns is that the surrounding landscape, 38% of which is grassland of some sort (Cully et al. 2003), harbors regals to the extent that their occurrence and abundance is not so strongly determined by characteristics of the prairie remnants themselves. Except perhaps in southwestern Douglas County, where there is much degraded native and other rangeland, we do not think that nonprairie areas contribute much suitable breeding habitat. We observed a few regals in early summer at two prairie reconstructions in Douglas County, and in the fall at another, but have rarely encountered Regal Fritillaries outside native prairies, even when proximal to dense colonies, a fidelity to habitat noted elsewhere in the Midwest (Swengel 1997). A notable exception is an old landfill near the Kansas River in Douglas County that has been reclaimed as marsh and grassland and where we found regals to be abundant.

Only two sites were grazed in 2005. One, a burned site in Miami County, grazed by cattle, had no regals. The other, grazed by horses in Douglas County, was highly degraded yet had a respectable 5.0 regals per 100 m transect. We noted that regals were generally present and reasonably abundant at the several sites that had been grazed in the past even though all were of mediocre quality (very low forb abundance, much nonnative cool-season grass). One old pasture, with very poor species composition and numerous, though scattered, Eastern Red Cedars (*Juniperus virginiana*) up to 4 m in height, nevertheless hosted 3.1 regals per 100 m transect.

We were surprised to discover that Regal Fritillary occurrence and abundance differed among counties; indeed, we had no reason to expect regional differences in abundance within our study area, especially any that would correlate with county boundaries, and we have no explanation for this pattern. The trend of highest occurrence and abundance in Leavenworth County and lowest in Miami County corresponds to their locations from north to south (total distance ~110 km), but was not explained by average prairie size, quality, isolation, or total area, or by surrounding landcover types (nor were any of these factors, at least within the narrow range of values surveyed, correlated with differences in abundance among sites). Longer term studies are needed to discover whether these regional patterns are consistent year to year; sight records from five of our 27 Miami County study sites, made incidentally in the course of plant survey work in 2004, indicate regal presence at one site where we recorded it absent in 2005 and at much higher abundance than in 2005 at two others (KS Biol. Survey, unpub. data).

## Use of distance-sampling

Although it has not often been employed for butterfly population monitoring (Brown and Boyce 1998), we found distance-sampling along line-transects to be a practical and extremely efficient survey method. In contrast to the more widely-used ''Pollard walk,'' which limits observations to ≤5 m of the observer, use of distance-sampling and program DISTANCE let us count individuals up to 30 m away and thereby survey a much larger portion of each site than would otherwise have been feasible, then correct for declining detectability with distance. These tools also allowed us to correct for differences in detectability according to burn status (Fig. 2). The resulting density estimates, unlike Pollard indices and strip-transect counts, were easily converted to time point estimates of colony size (at their seasonal maxima) and can be directly compared to absolute density estimates from other studies and observers.

For density estimates from distance-sampling to be unbiased, four critical assumptions must be satisfied: (1) transects are placed randomly with respect to individuals, (2) all individuals on the transect centerline are detected, (3) distances are accurate, and (4) individuals are detected at their initial location, or their movement is random and slow with respect to the observer (Buckland et al. 2001). We are confident that our protocol satisfied the first assumption, but meeting the others was more problematic. Most detected individuals were flying, though usually fairly slowly, so we walked transects at a relatively brisk pace (~4 km/h) to reduce effects of regal movement and help minimize double-counting. Whereas every effort was made to record distances to where individuals were first seen, we cannot have accomplished this goal perfectly, the expected consequence being overestimation of densities (Buckland et al. 2001). On the other hand, since we regularly flushed regals from the vegetation along transect centerlines, it is likely that a few did not flush or flushed too late to be noticed, leading to underestimation of densities. As previously explained, the raw distance data exhibited heaping at 5 m intervals (see Methods; Fig. 1), but grouping the data into intervals effectively dealt with this issue.

Of greatest concern with respect to accurate density estimation was the large percentage of detections at the transect centerline. One cause may have been biased observer attention to the centerline in the course of keeping track of its (unmarked) location, but another possibility is that they reflect rapid decline with distance in success of flushing hidden individuals, particularly females. Although the sex ratio of the Regal Fritillary is presumed to be evenly balanced (NatureServe 2005), counts of males usually vastly outnumber females. Male to female detection ratios were 381:26 at a Kansas site through late June (Kopper et al. 2001a), 222:8 at a Nebraska site through mid July (Nagel et al. 1991), and 473:21 at eight Iowa prairies in late July (Kelly and Debinski 1998). The ratio was 183:353 at six sites in the Dakotas (Kelly and Debinski 1998), but this was in mid August when females begin actively seeking oviposition sites and by which time many males have died. We did not record the sexes of individuals, but did notice that some females flushed from the transect centerline whereas nearly all individuals seen more distantly were flying in the fashion typical of patrolling males. That the detection functions of the sexes are likely quite different poses no inherent problem for modeling the detectability of the species, but if females were mainly detected on the transect centerline it is likely that we underestimated regal densities as a consequence of averaging the observed increase in total detections within a meter of the transect centerline (Fig. 1) over the first (7.5 m) distance interval. Future survey efforts should investigate this issue by recording, at least at a few representative sites, the sex ratio of flying versus flushed individuals on the transect centerline and at 5 m distance.

We were somewhat surprised that detectability declined more rapidly with distance in burned than unburned sites (Fig. 2). Perhaps this difference resulted from the generally taller and denser vegetation of burned sites; despite the large size and conspicuousness of regals, even patrolling males were frequently missed beyond a few meters because their flight was typically <50 cm above the ground *through* vegetation reaching 60–100 cm in height. We wondered if this apparent effect of treatment was somehow an affect of density on the shape of the detection function, but separate models for high and low density (≥2.5 versus <2.5 regals per 100 m transect) unburned sites were practically equivalent (probabilities of detection were 0.60 and 0.62, respectively) and were not preferred, based on AIC scores, over a single function for the pooled data.

## Conservation status in Kansas

Eastern Kansas apparently harbors a healthy Regal Fritillary metapopulation of a size and character unlike anything heretofore described in the literature. Extant prairies total 672 ha at 113 sites in Douglas, 254 ha at 35 sites in Leavenworth, and 430 ha at 61 sites in Miami County (Kindscher et al. 2005) and thus comprise only 0.3% of landcover, yet based on our estimates of average regal density by county, the population of our study area is likely ~12,000 individuals. Discussion of the status of this species has been dominated by its plight further east, for example in Iowa, where regals were found at 11 of 52 surveyed sites, only five of which had populations over 50 individuals (Debinski and Kelly 1998). Framed within such a context, the passing mentions in the literature of the existence of several large populations in the Great Plains states (e.g., Williams 2002; NatureServe 2005; Shepherd and Debinski 2005) do not adequately convey their categorically different nature.

The Regal Fritillary population of our study area is likely just a small portion of a much larger system. In our experience, the status of prairies and regals in our study area is representative of most counties along each side of the Kansas–Missouri border. Just 40–80 km west of our study area, in the Flint Hills, we have found regals to be generally quite scarce even though the region contains 1.6 million ha of native tallgrass prairie (Knapp and Seastedt 1998). Historically, the Flint Hills must have had a regal population of unimaginably large proportions, and probably still would except that nearly all its prairie is rangeland, most of which is burned annually or biannually to maximize beef yields (Robbins et al. 2002; Reinking 2005). Nevertheless, the region still harbors many significant colonies at locations spared such frequent burning (e.g., Konza Prairie Research Natural Area, Chase County Lake). Further west, we have observed very large and dense regal populations in the lowlands and sand prairies of central Kansas (e.g., McPherson County Lake, Quivira National Wildlife Refuge), and found the species to be a common resident of the native mixed-grass rangelands of the Smoky Hills. In May–June 2005, we regularly observed regals while conducting a grassland bird study at Smoky Hill Air National Guard Range, Saline County. Densities were low, though on one occasion we found nine individuals nectaring at a ~12 $m^2$ *Asclepias* patch. At 39 sites (on 18–20, 25–26 June), we counted all regals within 30 m while walking back along our bird survey transects; sample sizes were small and variability high, so effects were not significant, but the trend was for mean abundance (individuals per 100 m transect ± SE, number of transects) to be lower at burned idle sites (0.08 ± 0.055, $n = 8$) than unburned grazed (0.20 ± 0.074, $n = 10$), unburned idle (0.26 ± 0.093, $n = 9$), and unburned hayed (0.31 ± 0.104, $n = 12$) sites.

The future status of the Regal Fritillary in northeastern Kansas is tied to the future of prairie, which in this rapidly developing region proximal to greater Kansas City is far from assured; only 6 ha of prairie remain in the two Kansas counties that adjoin our study area and include parts of that metropolitan area (Kindscher et al. 2005), and only a few prairies in our study area are on public lands or are otherwise protected by conservation organizations or easements. In Douglas County, high quality prairie was reduced from 794 ha (110 sites) in 1988 to 565 ha (89 sites) in 2005, a loss of 29% (Kindscher et al. 2005). Some sites were destroyed by conversion to rowcrops or nonnative pasture, but since many prairies are located on hills that are attractive sites for exurban home building, a disproportionate share have been lost to that use and accompanying yard development. The loss of prairie in our study area has had significant impacts: one of only two prairies with populations of the federally threatened Western Prairie Fringed Orchid (*Platanthera praeclara*) was plowed in 1990, and the last population of Greater Prairie-Chickens (*Tympanuchus cupido*) disappeared in 2003–2004 (AP, pers. obs.). Over the past two decades, we noticed no decline in regal populations at sites that we visited regularly, but we did not systematically measure abundances prior to this study. Kelly and Debinski (1998), however, conducted a mark-recapture survey at one of our study sites, Akin Prairie, in mid July 1996 and found 14.3 regals per ha, a density equivalent to our estimate of 15.8 ± 3.02 regals per ha on 14 June 2005.

The greatest threat to Regal Fritillary persistence in our study area is prairie destruction, but prescribed burning is also a concern. Currently, neither the small sizes of prairies nor use of prescribed fire limits the occurrence of regals, but if prairies become fewer, their isolation from one another might increase to the point that recolonization of sites no longer keeps pace with local extinctions. Likewise, if use of prescribed fire replaces hay management at more sites, the metapopulation dynamics of the region might be disrupted since high density sites would be fewer and more isolated, the overall population of the region would be reduced, and because burned sites are population sinks to the extent that immigrant females colonize them in the year before a burn. Negative effects of fire would be greatly reduced if only a portion of each site were burned in a given year, both because mortality would be reduced and because population rebound would be less dependent on immigrant females, but only two of the 21 burned sites we found employed partial burning. One of these sites, managed with patch burning, had by far the highest regal density of any burned site (5.3 regals per 100 m transect), and the other site would have had the second highest abundance (3.7 regals per 100 m transect) had we averaged the counts from burned and unburned portions rather than treating them as different sites.

With this study, we demonstrate that northeastern Kansas harbors a Regal Fritillary population of tremendous size and conservation significance despite the loss of >99% of its native prairie, and conversely, the collective importance of remaining prairies, however small, for the conservation of this (and likely other) declining prairie-obligate species. Given the rapidity of the Regal Fritillary's decline elsewhere, this study establishes important population benchmarks and a protocol for future monitoring efforts. Much remains to be understood about the factors that govern population densities and their interconnectivity. We hope that this first effort to describe local patterns in the species' occurrence and abundance within a small portion of its western range brings attention to some of these opportunities.

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## References

Brown JA, Boyce MS (1998) Line transect sampling of Karner blue butterflies (*Lycaeides melissa samuelis*). Environ Ecol Stat 5:81–91

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundances of biological populations. Oxford University Press, New York

Cully J, Egbert SL, Harrington J, Hoernemann T, Kaufman G, Lauver C, Martinko E, Price KP (2003) The Kansas Gap Analysis Project: final report. Kansas Cooperative Fish and Wildlife Research Unit, Manhattan

Debinski DM, Kelly L (1998) Decline of Iowa populations of the Regal Fritillary (*Speyeria idalia*) Drury. J Iowa Acad Sci 105:16–22

Ely C, Schwilling MD, Rolfs ME (1986) An Annotated List of the Butterflies of Kansas. Fort Hays Studies (Science) 7, Fort Hays State University, Fort Hays, Kansas

Huebschman JJ, Bragg TB (2000) Response of Regal Fritillary (*Speyeria idalia* Drury) to spring burning in an eastern Nebraska tallgrass prairie, USA. Nat Areas J 20:386–388

Kelly L, Debinski DM (1998) Relationship of host plant density to size and abundance of the Regal Fritillary *Speyeria idalia* Drury (Nymphalidae). J Lepidopt Soc 52:262–276

Kindscher K, Busby WH, Delisle JM, Dropkin JA, Freeman CC (2005) A Natural Areas Inventory of Douglas, Johnson, Leavenworth, Miami, and Wyandotte Counties in Northeast Kansas. Open-File Report No. 124. Kansas Biological Survey, Lawrence

Knapp AK, Seastedt TR (1998) Grasslands, Konza Prairie, and long-term ecological research. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, pp 3–15

Kopper BJ, Margolies DC, Charlton RE (2001a) Life history notes on the Regal Fritillary, *Speyeria idalia* (Drury) (Lepidoptera: Nymphalidae), in Kansas tallgrass prairie. J Kansas Entomol Soc 74:172–177

Kopper BJ, Shu S, Charleton RE, Ramaswamy SB (2001b) Evidence for reproductive diapause in the fritillary *Speyeria idalia* (Lepidoptera: Nymphalidae). Ann Entomol Soc Am 94:427–432

Mason KR (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

Nagel HG, Nightengale T, Dankert N (1991) Regal Fritillary butterfly population estimation and natural history on Rowe Sanctuary, Nebraska. Prairie Nat 23:145–152

NatureServe (2002) NatureServe element occurrence data standard. NatureServe, Arlington, VA. http://www.natureserve.org/prodServices/eodata.jsp. Cited 28 Sept 2006

NatureServe (2005) Comprehensive report: *Speyeria idalia* (Regal fritillary). NatureServe explorer: an online encyclopedia of life. Version 4.7. NatureServe, Arlington, VA. http://www.natureserve.org/explorer. Cited 24 May 2006

Panzer R (2002) Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. Conserv Biol 16:1296–1307

Reinking DL (2005) Fire regimes and avian responses in the central tallgrass prairie. Stud Avian Biol 30:116–126

Ries L, Debinski DM (2001) Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. J Anim Ecol 70:840–852

Robbins MB, Peterson AT, Ortega-Huerta MA (2002) Major negative impacts of early intensive cattle stocking on tallgrass prairies: the case of the Greater Prairie-Chicken (*Tympanuchus cupido*). N Am Birds 56:239–244

Royer RA, Marrone GM (1992) Conservation status of the Regal Fritillary (*Speyeria idalia)* in North and South Dakota. United States Department of the Interior, Fish and Wildlife Service, Denver, Colorado

Samson FB, Knopf FL, Ostlie WR (1999) Grasslands. In: Mac MJ, Opler PA, Puckett Haecker CE, Doran PD (eds) Status and trends of the nation's biological resources biological resources division, U. S. Geological Survey, Reston, Virginia, pp 437–445

Schwartz M (1998) Letter. Ecology forum: effects of fire and hay management on butterflies. RX Fire Notes 7:7–10

Shepherd S, Debinski DM (2005) Reintroduction of Regal Fritillary (*Speyeria idalia*) to a restored prairie. Ecol Restor 23:244–250

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York

Swengel AB (1996) Effects of fire and hay management on abundance of prairie butterflies. Biol Conserv 76:73–85

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

Swengel AB (1998) Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biol Conserv 83:77–89

Swengel AB (2001) A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodivers Conserv 10:1141–1169

Swengel AB, Swengel SR (2001) A 10-year study to monitor populations of the Regal Fritillary, *Speyeria idalia*, (Lepidoptera: Nymphalidae) in Wisconsin, U.S.A. Great Lakes Entomol 34:97–115

Thomas L, Laake JL, Strindberg S, Marques FFC, Buckland ST, Borchers DL, Anderson DR, Burnham KP, Hedley SL, Pollard JH, Bishop JRB, Marques TA (2005) Distance 5.0. Beta Release 4. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance. Cited 24 May 2006

Williams BL (2002) Conservation genetics, extinction, and taxonomic status: a case history of the Regal Fritillary. Conserv Biol 16:148–157

Williams BL, Brawn JD, Paige KN (2003) Landscape scale genetic effects of habitat fragmentation on a high gene flow species: *Speyeria idalia* (Nymphalidae). Mol Ecol 12:11–20