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Disentangling effects of fire, habitat, and climate on an endangered prairie-specialist butterfly☆

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ABSTRACT

Tallgrass prairie, arguably the most fire-dependent system in North America, is a Biome that has been essentially eliminated and is now exceedingly rare. Absent frequent disturbance, remnant tallgrass prairie rapidly converts to a dominant cover of woody plants. This creates unique challenges for conservation of prairie-specialist insects dependent on increasingly small and isolated habitats prone to direct and indirect threats from climate variability, habitat degradation, and management activities; or lack thereof. Regal fritillary butterflies (*Speyeria idalia*) exemplify this problem, with sharp population declines in recent decades and considerable disagreement on management practices, particularly in the use of prescribed burning to maintain habitat. Spanning 20-years (1997–2016), we evaluated regal fritillary populations within seven sites in relation to fire, habitat, and climate records to better understand these interacting effects on interannual and long-term population changes. Though fire had short-term negative effects on regal fritillary abundance, habitat quality was one of the most important factors explaining populations and was positively associated with prescribed fire. Burning every 3–5 years maximized regal fritillary abundance, but even annual burning was more beneficial to regal populations than no burning at all. Unburned refugia are important in maintaining populations, but creating and maintaining high quality habitat with abundant violets (*Viola* spp) and varied nectar sources, may be the most impactful management and conservation tool. Regal fritillary butterflies were consistently more than twice as abundant on high quality habitats and this relationship held across, and often dwarfed the effects of, various prescribed fire regimes or climate variability.

1. Introduction

The tallgrass prairie ecosystem is one of the most endangered in the world, largely as a result of conversion to agriculture (Noss et al., 1995). Remaining prairie is often located in small, isolated patches, and face a variety of threats, including a lack of fire. Although grassland plants and insects evolved with fire (Debinski et al., 2011), its appropriate use has been a topic of extensive debate, particularly in the tallgrass prairie ecoregion where habitat degradation and loss has been severe (Panzer, 2002; Debinski et al., 2011; Swengel et al., 2011). Conservationists are now presented with a paradox where the compatibility of burning prairie patches, necessary for maintaining them, and conserving insect populations, dependent upon prairie, are being questioned. The importance of arthropod communities, particularly butterflies, to serve as indicators of ecosystem function and to evaluate processes, like fire, is becoming more widely recognized (Moranz et al., 2012). In practice, however, this has been challenging as the effects of climate, management practices, and habitat on insect populations are confounded factors, operating over various temporal scales, but often examined in isolation and over short durations.

Prairie-specialist butterflies, many of which have experienced decades long declines, may be particularly vulnerable to interacting effects of climate, management, and habitat (Swengel et al., 2011). These species are also useful for evaluating these factors as they are sensitive to environmental variation, they have tight linkages to host and nectar plants, and populations respond rapidly to habitat changes (Simonson et al., 2001; Pywell et al., 2004). The regal fritillary (*Speyeria idalia* Drury; hereafter "regal" or "regals") is an example of a prairie-specialist butterfly that has experienced sharp declines in recent years which cannot be reliably attributed to any single cause. Once one of the most common prairie and grassland butterflies in the eastern United States (Hammond and McCorkle, 1984; Johnson, 1986), regals are now severely depleted or locally extinct east of the Mississippi River (Sims, 2017) and are being considered for federal listing under the

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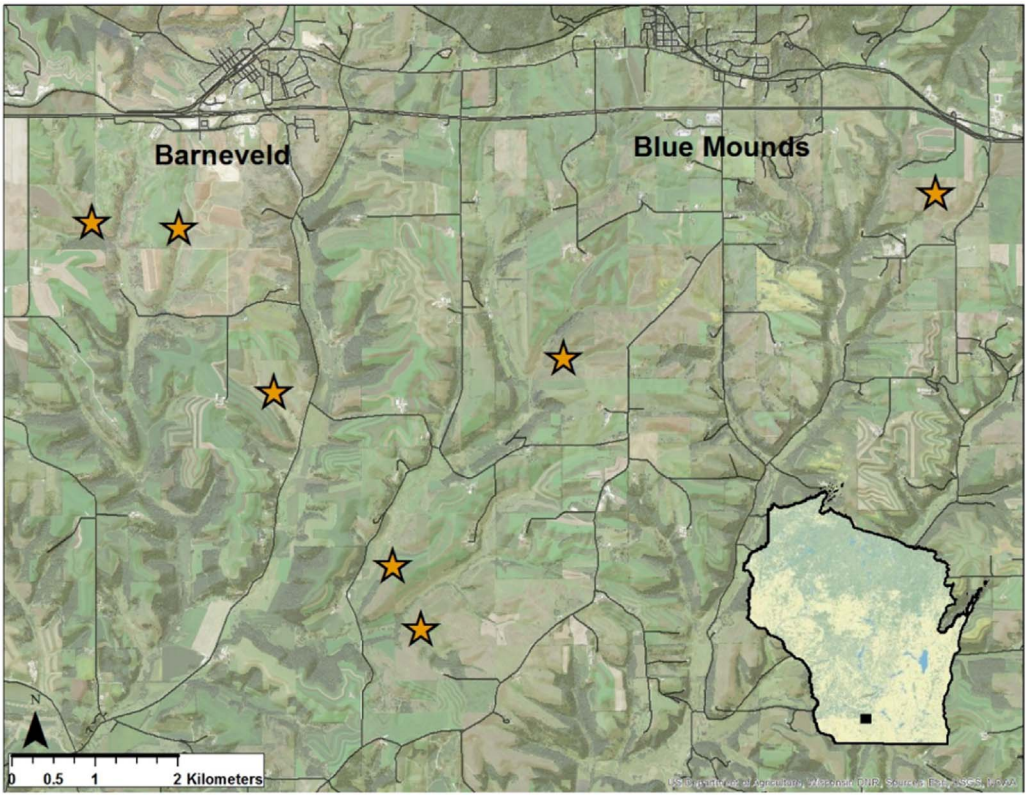

Fig. 1. Regal fritillary butterfly study sites (n = 7) in southern Wisconsin where surveys were conducted between 1997 and 2016.

Endangered Species Act (USFWS, 2015).

In the eastern tallgrass prairie region, examination of fire as a causal factor for declines often includes long-term population monitoring and inferred fire effects (Swengel, 1996; Swengel and Swengel, 2017) or evaluating population reductions on burned versus unburned (or longer unburned) areas and subsequent post fire recovery (Swengel, 1996; Swengel, 1998; Huebschman and Bragg, 2000; Powell et al., 2007; Vogel et al., 2010). These studies report significantly lower regal fritillary densities (but not absence) on recently burned areas, followed by rapid recovery (ca. 1–3 years). Researchers and managers have expressed concern that these short-term population decline and recovery cycles linked to fire may eventually lead to extirpation, especially in the most reduced and fragmented habitats (Swengel, 1996; Swengel, 1998; Swengel and Swengel, 2017). Establishing fire sensitivity and post fire recovery times is important, but this information alone provides limited insights into how fire shapes long-term population dynamics (Panzer, 2002). Similarly, many of these same studies were conducted over relatively short timescales, thus lacking a complete understanding of the interrelationships among recovery, habitat, and fire effects. This is important as fire interacts with habitat quality in important ways that may not be immediately evident.

Historical habitat loss is generally accepted as an ultimate cause for declining regal populations; however, degradation or loss of remaining quality habitat for larvae and adults is also an ongoing, proximate cause of declines (Sims, 2017). All suitable regal habitats must include adequate abundance of violets (larval) and flower (adults) food sources (Sims, 2017). Regal larvae feed exclusively on violets (*Viola* sp.) with well documented relationships between regal abundance and violet density (Debinski and Kelly, 1998; Beilfuss and Harrington, 2001) as well as nectar diversity (Huebschman, 1998). Ironically, relatively few studies in the eastern tallgrass region have quantified violet density (but see Debinski and Kelly, 1998; Kopper et al., 2000; Ferster and Vulinec, 2010; Swartz et al., 2015). Prescribed fire is known to increase flower production and increase prairie violet growth and seed production (Lovell et al., 1983). In southwest Missouri evidence suggested that butterfly abundance was not directly related to management activities but rather to native plant cover that was positively associated with burning (Moranz et al., 2012; Moranz et al., 2014). Similarly, in northwest Indiana local restorations, including fortuitous habitat improvements by an aggressive weedy annual species of violet (*Viola bicolor*), precipitated an unprecedented landscape scale expansion of regals and post-burn recovery time decreased from 1 to 2 years, prior to restorations, to less than one year (Shuey et al., 2016). Thus, understanding the impacts of fire on regal populations requires understanding effects of fire on habitat quality.

Increased climate variability may affect both regal and violet populations, particularly in marginally suitable habitats (Boggs and Inouye, 2012; Sims, 2017), and could represent one of the greatest threats to survival (Breed et al., 2013). While historical distributions of regals covered a wide range of climate conditions, some have speculated that recent increases in sporadic detection records may be an artifact of climate variability (Swengel and Swengel, 2017). Climate controls on regal abundance are poorly understood and long-term datasets are needed to elucidate patterns.

We analyzed a 20-year dataset to better understand variability of the prairie-specialist regal fritillary butterfly over a period of rapid population declines within a highly fragmented landscape. Our primary objectives were to:

(1) Determine the relative contribution and direction (positive or negative effect) of various parameters related to time, prescribed fire, habitat quality, and climate variability on regal fritillary population dynamics.
(2) Examine longer term regal fritillary response to prescribed burning (up to 8 years following burns) including burn frequency, burn area, and distance to unburned habitat in isolation and in conjunction with habitat and climate variables.