



## Severe decline and partial recovery of a rare butterfly on an active military training area



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### ABSTRACT

Global patterns of land-use change have led conservationists to rely increasingly on human-dominated landscapes for biodiversity conservation. One set of such landscapes, military training areas, hold promise for conservation as they are widespread and often harbor rare habitat types. However, military training areas are often heavily impacted and are not managed primarily for conservation. We sought to evaluate the effectiveness of a military training area for conservation by assessing the population of an extremely rare butterfly, the eastern regal fritillary (*Speyeria idalia idalia*), for which the sole viable population is within Fort Indiantown Gap National Guard Training Center in Pennsylvania, USA. Long-term monitoring data exist for this butterfly, but analysis has been complicated by the non-conformity of count data to standard statistical assumptions, the natural history of these butterflies, and challenges inherent to monitoring on a military training area. To address these complications, we used a novel multi-step process with zero-inflated generalized additive mixed models in a Bayesian framework. Data included 23,492 transect walks over 18 years. Our results provide the first comprehensive analysis of population trajectories for *S. idalia*, and indicate that after a long decline, populations have increased and, more recently, levelled. Temporal concordance of the increase with the onset of intensive logging and prescribed burning suggests the importance of large-scale, active management efforts. These results further clarify that, with active management of an appropriate scale, even the busiest military training areas can serve as effective sites for conservation. Thus, such areas may be underexploited for biodiversity conservation.

### 1. Introduction

In response to the ongoing and accelerating global extinction, conservationists have for decades focused extensively on establishing and managing reserves with the explicit goal of biodiversity protection. However, setting aside new reserves is not always possible, since few ecosystems that are relatively unaffected by anthropogenic change remain in some biomes (Millennium Ecosystem Assessment, 2005) and existing land uses may preclude the establishment of reserves in other areas. Further, human-dominated landscapes provide movement pathways critical to species' metapopulation structure, and may harbor high levels of biodiversity in their own right (Perfecto and Vandermeer, 2008). Thus, the effective use of human-dominated landscapes for conservation has become a key component of biodiversity conservation strategies (Lundholm and Richardson, 2010; Turner, 2010). Among such landscapes, military training areas have the potential to be exceptionally important, given their spatial extent: military training areas

are among the largest land use category owned by governments globally (Zentelis et al., 2017), and may cover as much as 5–6% of the Earth's land surface area (Zentelis and Lindenmayer, 2015). The potential utility of military training areas for conservation remains unclear, however (Zentelis and Lindenmayer, 2015).

Military training areas are often heavily impacted by past and present training activities (Lawrence et al., 2015), and with a critical primary mission of national defense, any biodiversity conservation efforts undertaken on such lands are typically considered, at best, a secondary priority (Zentelis et al., 2017). Nonetheless, military training areas do retain some features that could promote biodiversity conservation. Land managers on military training areas must meet legal obligations relating to environmental conservation and endangered species management on federal lands (Stein et al., 2008; Durant, 2010). Military training areas' clear delineation as publicly-owned lands typically prevents transformation of natural habitats within their boundaries to agriculture or residential development, as often occurs on the

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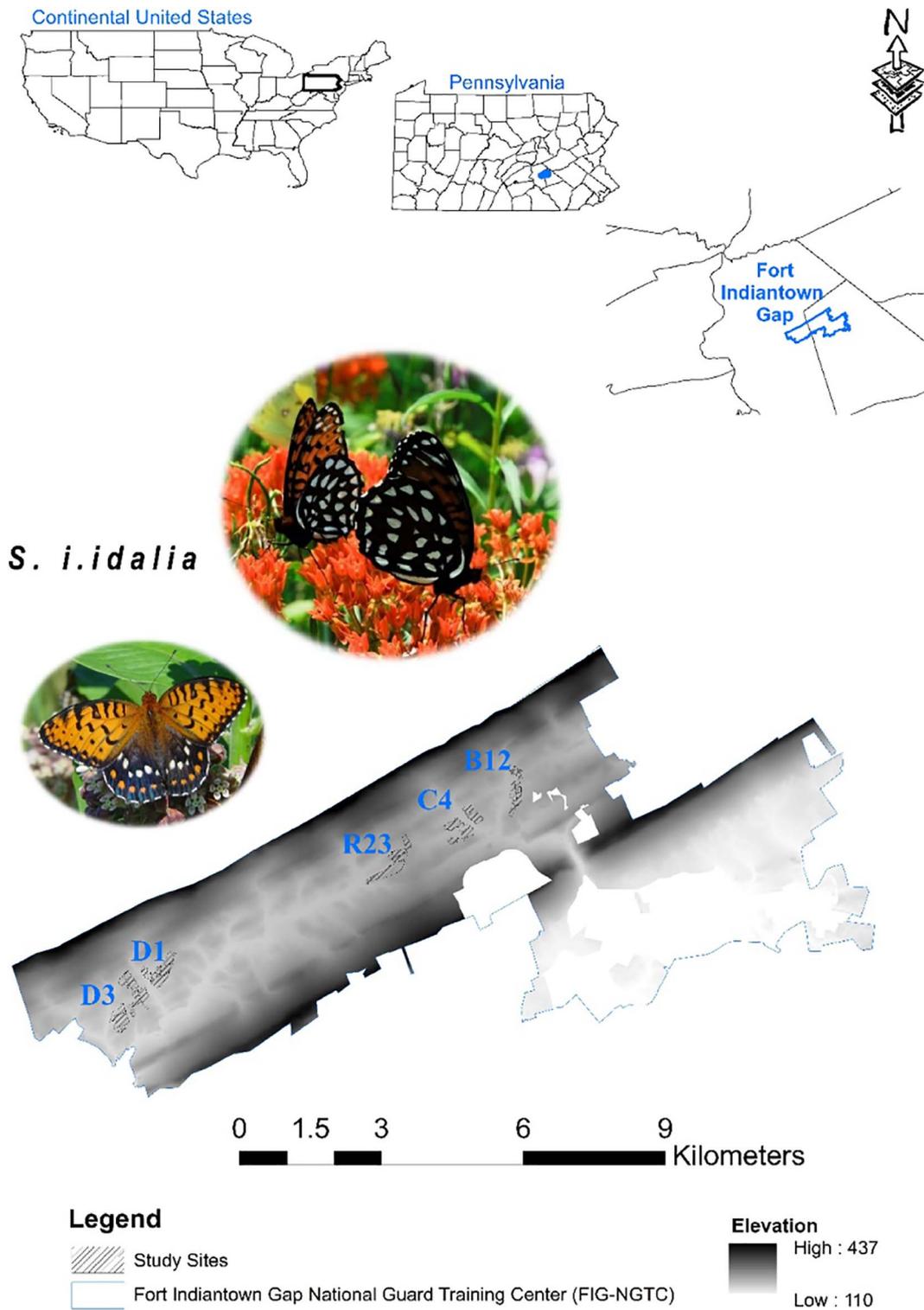


Fig. 1. Spatial representation of the study system in the United States, Pennsylvania, Fort Indiantown Gap National Guard Training Center (FIG-NGTC). Five sites (grasslands) and the study organism *Speyeria idalia idalia*. Photo credits: Joe Hovis (male), Department of Military and Veterans Affairs; photo by Tom Cherry (male and female), Pennsylvania Department of Military and Veterans Affairs.

surrounding landscape (Stein et al., 2008). To ensure realistic and diverse environments for training while also providing buffer areas, military training areas are often managed to maintain multiple habitat types (Warren et al., 2007; Stein et al., 2008; Aycrigg et al., 2015), including globally rare ones like grasslands (IUCN, 1996). To maintain a level of secrecy and to ensure public safety, as well as to avoid contact with unexploded ordnance and other hazardous conditions, military

training areas often impose strict restrictions on public and commercial access, limiting potential habitat degradation (Lawrence et al., 2015). Finally, military training areas may retain some key ecological processes of natural landscapes that are essential to native species, such as high fire frequency in grasslands (Warren et al., 2007). Each of these features are responsible for the highly heterogeneous landscapes that persist on military training areas, which, in turn, support high species

richness, a number of rare disturbance-adapted communities, and in some cases high concentrations of threatened species (Warren et al., 2007; Zentelis et al., 2017).

A particularly salient test of the utility of military training areas for conservation is the case of the eastern regal fritillary (*Speyeria idalia idalia*). *S. idalia*, a distinct subspecies of the declining regal fritillary *S. idalia* (Williams, 2001; Keyghobadi et al., 2013), is a rare North American grassland butterfly that previously ranged from West Virginia to Massachusetts (Swengel and Swengel, 2016). However, following large-scale development and agricultural transformation of its prairie habitat, suppression of fires necessary to prevent succession of grasslands with woody species, and direct impacts from spraying with pesticides, populations of this subspecies collapsed (Swengel, 1996; Swengel and Swengel, 2016). Since at least the mid-1990s, only a single viable population has remained in southeastern Pennsylvania, located wholly within the borders of the Fort Indiantown Gap National Guard Training Center (FIG-NGTC) (Ferster and Vulinec, 2010; Keyghobadi et al., 2013; Shuey et al., 2016), which in 2015 was the busiest military training area in the USA with over 700,000 personnel days of training and activity (FIG-NGTC, 2017). Thus, the land is under heavy demand and conservation efforts for the *S. idalia* must compete for space and attention with intensive military use.

Monitoring data on the status of *S. idalia* have been collected since 1998. Comprehensive analyses of these data, however, have been complicated by several factors. First, as for other wildlife monitoring programs, data do not conform to several assumptions of traditional statistical methods: count data involve non-normal errors, spatial nesting of sampling and repeated surveys of the same transects produce non-independent data with correlated errors, and population changes over time may be non-linear (Fewster et al., 2000; Zuur et al., 2009; Ingersoll et al., 2013). Further, the effect of multiple observers and turnover in personnel over an extended monitoring program can lead to a high observer error (Zuur et al., 2009). Second, butterflies may often express phenological patterns, such as seasonal peaks and troughs in activity, that result in differential detection across repeated surveys of the same site. This effect is further complicated in regal fritillaries, where a different phenology characterizes each sex (Powell et al., 2007). Rapid movements or cryptic behavior may also result in an inability to discern the sex of a detected individual. Further, butterflies can be highly responsive to ephemeral weather changes like cloud cover, leading to bouts of inactivity (Puntenney and Schorr, 2016). This may result in an abundance of zero counts during surveys which, if not accounted for, may bias density estimates. Finally, monitoring programs on military training areas have some inherent challenges. For instance, the presence of training activities onsite, especially ones involving live fire, may mean intermittent access to survey sites, resulting in unbalanced survey designs. In addition, changing management to support the primary training mission or the discovery of unexploded ordnance may permanently block access to a site, requiring shifts in survey routes.

In this study, we sought to improve understanding of the effectiveness of military training areas for conservation. Specifically, our primary goal was to assess the population trajectory of *S. idalia* for the last 18 years (1998–2015) at FIG-NGTC. We therefore developed a rigorous analytical strategy to model *S. idalia* population patterns at this active military training area, and to graphically render population patterns. A secondary goal was to assess the potential role of training activities, management actions, and environmental changes on the population during this time period. Comparison of population patterns with the known timing of key factors suspected to influence the butterfly or its habitat over time enabled evaluation of whether data were consistent with a causal relationship between the population change and its putative cause (Fewster et al., 2000; Ingersoll et al., 2016).

## 2. Methods

### 2.1. Study system

The study area was FIG-NGTC (40°26'13.15"N, 76°34'33.8"W), a military training area on the Appalachian Plateau physiographic region (Fig. 1). The landscape of the study area consists of a mosaic of forests and semi-natural grasslands extending over 6920 ha with altitudes ranging from 180 to 241 m (Division, 2002). The climate is humid continental with February the driest and May the most humid month. The target organism, *S. idalia*, is a large, diurnal, sexually dichromatic, non-migratory butterfly of the family Nymphalidae (Fig. 1). It inhabits native prairie and human modified mesic sites such as moist meadows and pastures (Keyghobadi et al., 2013) that include abundant larval host plants (violets, *Viola* spp.) and nectar species (primarily milkweed, *Asclepias* spp., and thistle *Cirsium* spp.) (Kelly and Debinski, 1998; Ferster and Vulinec, 2010; Swartz et al., 2015). It is a univoltine butterfly species and it flies in the warm summer months between mid-June and mid-September (Selby, 2007).

### 2.2. Datasets

Systematic surveys for *S. idalia* at FIG-NGTC during 1998–2015 were completed by trained biologists and volunteers in five established transects (at sites named B12, C4, D1, D3, R23) within grasslands. B12, D3, and R23 were included from the onset of the monitoring program in 1998. C4 was included in the study system in 1999 and D1 in 2002. Transect length ranged from 1557 m to 3515 m, and each transect (or site) was further divided into 13–35 sections (Supporting Information, Appendix S1). Three transects (B12, D3, R23) have been managed since late 1999 and one more (D1) since 2002 under an agreement that prohibits most military training activities and motorized vehicle use directly upon these sites, though adjacent sites continue to be heavily used. The agreement also allows for grassland management techniques (e.g., prescribed fires) to be applied by the wildlife personnel of FIG-NGTC to maintain the open character of these habitats (Ferster and Vulinec, 2010). Because of unexploded ordnance from previous training events, a small portion of site R23 was reoriented in 2003 and almost half of D3 was reoriented in 2006.

Data were from standardized weekly surveys using the Pollard Walk method (Pollard and Yates, 1993). Surveys were conducted from June until September when butterflies were active and access was granted along transects by the military training area. Because *S. idalia* is a large butterfly that is often readily detectable and can be identified to species and sex from a distance, all observations within 18.3 m (20 yards) on either side of the transect were included. Where individuals were observed, but sex could not be attributed in the field, we recorded them as of unknown sex. Because climate plays a key role in population trends of butterflies, we considered two climatic variables, annual temperature and an aridity index (Peñuelas et al., 2007; Donoso S. et al., 2016). These and other measurements taken during transect walks are presented in the Supporting Information (Appendix S2, S3).

### 2.3. Data analysis

We developed an analytical strategy for estimating population trajectories, by first assigning sex to unknowns with logistic regression, then modeling population change using sex-specific, zero-inflated, generalized additive mixed models, and finally graphically rendering population trajectories. First, because individuals of unknown sex were a non-negligible (3.1%) portion of the dataset, and excluding them could potentially cause bias by sex if one sex were strongly over-represented among the group of individuals of unknown sex, we used a

mixed effect logistic regression model (Agresti, 2013) to assign likely sex to all unknown detections on the basis of timing, and environmental and other covariates (Supporting Information, Appendix S4). Second, separate modeling of counts over time in males and females allowed us to account for differences in phenology, ecological traits and detectability by sex (i.e., females are more cryptic and have a lower detection rate; K.Z., M.T.S., V.P.T., E.N.M. & B.J.S., unpublished data in Supporting Information, Appendix S5). Third, the zero-inflated format accounted for the extensive number of zero counts resulting from survey design and butterfly natural history. Fourth, the generalized format ideally suited count data, which typically have non-normal errors (Zuur et al., 2009). Fifth, the mixed-effect format provided a means to cope with non-independent observations including repeated measurements and the nesting inherent in the sampling design, as well as inter-observer differences (Zuur et al., 2015). Sixth, the additive component enabled us to model a non-linear population trajectory rather than solely assuming a linear population trend (Ingersoll et al., 2013). Seventh, the use of smoothing terms allowed us to systematically model possible deviation from linearity (Ingersoll et al., 2013). Finally, graphical rendering of the model facilitated the interpretation of the timing, direction, and magnitude of population changes over time.

#### 2.4. Modeling of population trajectories

We modeled population trajectories of males and females separately to minimize possible bias derived from the different phenology, activity patterns and detectability of each sex. The excessive number of zeroes (82.8% of walks of transect sections) created a large spike at zero giving us an early warning of likely zero inflation (Zuur et al., 2015; Zuur and Ieno, 2016). Further, generalized linear analyses using a zero-inflated Poisson distribution performed better (i.e., dispersion parameter closer to one, results not shown) than Poisson or negative binomial analyses without zero inflation. We thus focused on a zero-inflated framework for the analysis.

To address the non-linear trends that emerged during data exploration (Supporting Information, Appendix S6), and to accommodate the zero-inflated count data with a dependency structure, we used zero-inflated Poisson generalized additive mixed models (ZIPGAMMs). Our ZIPGAMMs combined two parts: (a) a Poisson generalized additive mixed model that evaluated the count process (count part) and (b) a binary generalized additive mixed model that accommodated excess zeroes by estimating the probability of a positive count (binary part) (Zuur et al., 2015; Zuur and Ieno, 2016). Therefore, we used mixture models that allowed for a distinction between true and false zeros: true were the zeros where the animal was not present and false zeros when the animal was present but not detected because, for instance, sampling took place at the wrong time or the observer had poor visibility. If all zeros can be explained by the covariates in the count part then the binary part can be dropped. However, when zeros cannot be explained by the covariates in the count part they have high probability of being false zeros, and these probabilities are estimated and accounted for in the binary part of the model. We considered a global model that would better answer the ecological questions “what drives detection/lack of detection of *S. i. idalia*” and once we have a detection “what drives its density”. For our model, the starting point was a zero-inflated Poisson (ZIP) distribution for *S. i. idalia* counts.

$$N_{ijk} \sim \text{ZIP}(\mu_{ijk}, \pi_{ijk})$$

where  $N_{ijk}$  is the expected density of *S. i. idalia* in section  $k$  in transect  $j$  in year  $i$  and follows a zero-inflated distribution. The mean is  $\mu_{ijk}$  with a log link function for the count part, and  $\pi_{ijk}$  using a logistic link function for the binary part. If the probability of a false zero is 0, the  $\pi_{ijk} = 0$  which in turn will give a classical two-way nested Poisson GAMM. We

used the following global model for the total density of *S. i. idalia*:

$$\log(\mu_{ijk}) = \alpha + f(\text{Year}_{ijk}) + f(\text{Julian}_{ijk}) + \text{Period}_{ijk} + a_j + b_{jk}$$

$$\log \text{it}(\pi_{ijk}) = \gamma + \text{Month} + \text{Temperature}_{ijk} + \text{lengthSite}_{ijk} + a_j + b_{jk}$$

$$a \sim N(0, \sigma_{\text{site}}^2) \text{ and } b_{jk} \sim N(0, \sigma_{\text{section}}^2)$$

The term  $f()$  stands for the smoothing function (O'Sullivan splines), the error term  $a_j$  for the random intercept of site (transect) and  $b_{jk}$  for the random intercept of section within site. Both parts of the model contain an intercept ( $\alpha, \gamma$ ). To minimize inter-observer differences, we excluded surveys conducted by volunteers with low experience ( $\leq 3$  transect walks in total). We estimated the posterior distributions for all parameters in a Bayesian format using Markov chain Monte Carlo methods (MCMC) (Supporting Information, Appendix S7). We then graphically rendered population trajectories and 95% credible intervals. These procedures were performed in R version 3.1.1 (R Core Team., 2016) and JAGS (Plummer, 2003) via the R package rjags (Plummer et al., 2006; Lunn et al., 2009).

#### 2.5. Hypothesized associations of population change with putative causes

We evaluated whether training, management, and environmental factors suspected of affecting the population of *S. i. idalia* were temporally concordant with observed changes in the population trajectories (Fewster et al., 2000; Ingersoll et al., 2016). We hypothesized that military training (disturbance from training, transformation of adjacent land) would have both positive and negative effects on the population, but result in net increases in population density of this disturbance-adapted butterfly species. Also, despite potential negative direct effects of systematic management interventions (mechanical thinning, prescribed fire) on butterflies (McElderry et al., 2015), these interventions were expected to increase the density of its larva host and nectar plants over time. Thus, we hypothesized that these systematic management interventions would improve the quality of the habitat and lead to a net increase in this rare butterfly's population overall. In addition, since butterflies are known to react quickly to changing climate conditions (Devictor et al., 2012), we further hypothesized that weather alterations (year-to-year changes) would trigger population fluctuations.

### 3. Results

In 23,492 walks of transect sections, 9607 eastern regal fritillary individuals were detected, of which 3279 were females, 6019 were males, and 309 were of an unknown sex. Our model selection approach for logistic regression enabled us to attribute 260 (84%) of the unknowns to male or female (Supporting Information, Appendix S4). No directional change over time in annual temperature was evident (Mann-Kendall Test;  $t = -15, P = 0.3$ ) but the aridity index decreased significantly over the study period (Mann-Kendall Test;  $t = 53, P = 0.03$ ) (Supporting Information, Appendix S3). The evaluation of the fit of the global model and further diagnostics are given in the Supporting Information (Appendix S7).

#### 3.1. Males

The probabilities of false zeroes per regression parameter in the binary part of the model for males are given in Fig. 2a; these are zeroes that cannot be explained by the count part of the model (i.e., zeroes resulting from processes other than those determining actual density). The probabilities of false zeroes were highest for the month of September and lowest for the month of July, while probabilities were intermediate for all other variables. Credible intervals were largest for September, at the end of the study season.

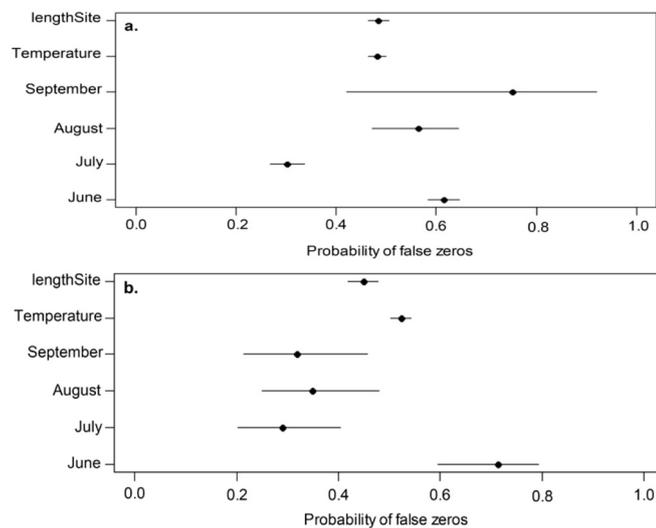


Fig. 2. The values of false zero probabilities per regression variable (y-axis) of the binary part of the model for males (a) and females (b) and the 95% credible interval, calculated and converted to the logistic scale; dots correspond to posterior means values and horizontal lines to 95% credible interval values. The values shown are the probabilities of false zeros, i.e., the zeros that cannot be explained by the count part of the model.

Table 1

The posterior means, standard errors, and credible intervals for the linear regression parameters in the count and binary part of the models. Underlined are important parameters (i.e. when credible intervals do not include the zero value).

			Mean	SE	2.5%	97.5%
Binary part	Males	June	0.47	0.07	<u>0.34</u>	<u>0.61</u>
		July	-0.84	0.09	<u>-1.00</u>	<u>-0.68</u>
		August	0.25	0.17	-0.11	0.60
		September	1.11	0.68	-0.32	2.43
		Temperature	-0.07	0.04	-0.15	0.00
	Females	lengthSite	-0.06	0.04	-0.14	0.02
		June	0.95	0.24	<u>0.46</u>	<u>1.40</u>
		July	-0.94	0.24	<u>-1.40</u>	<u>-0.46</u>
		August	-0.66	0.25	<u>-1.13</u>	<u>-0.16</u>
		September	-0.80	0.28	<u>-1.35</u>	<u>-0.23</u>
Count part	Males	lengthSite	-0.21	0.06	<u>-0.34</u>	<u>-0.09</u>
		First period	-4.74	1.38	<u>-8.75</u>	<u>-2.46</u>
		Second period	1.05	0.21	<u>0.66</u>	<u>1.44</u>
	Females	Third period	1.58	0.35	<u>0.88</u>	<u>2.24</u>
		First period	-3.67	0.67	<u>-4.87</u>	<u>-2.31</u>
		Second period	0.36	0.24	-0.13	0.83
		Third period	0.96	0.34	<u>0.31</u>	<u>1.63</u>

First period contains data between 1998 and 2002, second period contains data between 2003 and 2006 and third period between 2007 and 2015; lengthSite: is the length of the site (transect).

The posterior means, standard errors and 95% credible intervals of the regression parameters of the binary and count part of the model are in Table 1. For males, in the binary part of the model, the month of June was positively associated with detections of *S. idalia* and July was negatively associated with detections of this species. In the count part, there was a strong negative influence of the first period (1998–2002) and weaker positive influences of the second and third periods on male detection (Table 1).

Overall, males had a non-linear trend with year (Fig. 3a) and Julian date (Fig. 4a). For the analysis of seasonal variation (within-year change by Julian date), one seasonal peak of male detections was observed between the end of June and the beginning of July, followed by a decrease to the lowest point in September. In the analysis of long-term (across-year) change, a slightly increasing trend the first four years (1998–2001), was followed by sharp decrease until 2007. The population fluctuated from 2007 to 2011, then increased after 2011. Both

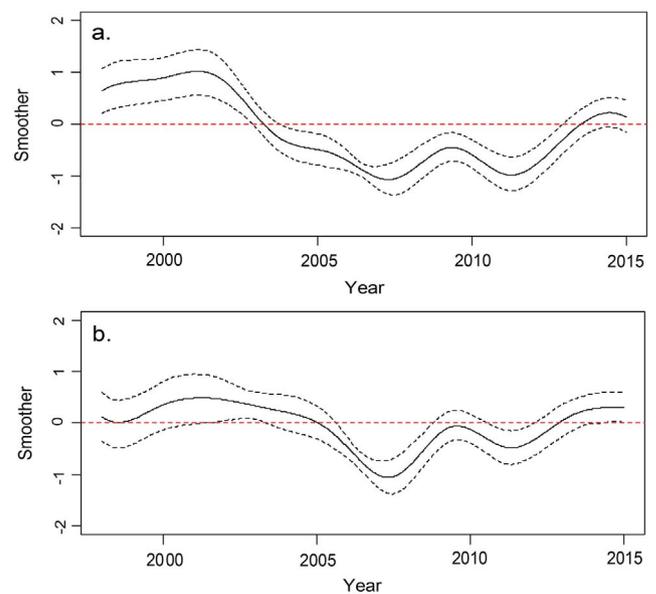


Fig. 3. Estimated smoother  $f(Year_{ijk})$  for (a) males and (b) females and 95% credible intervals of *Speyeria idalia idalia* population. The horizontal dotted line indicates the overall mean value. Credible intervals not including the horizontal dotted line at any point implies the population differed from the grand mean.

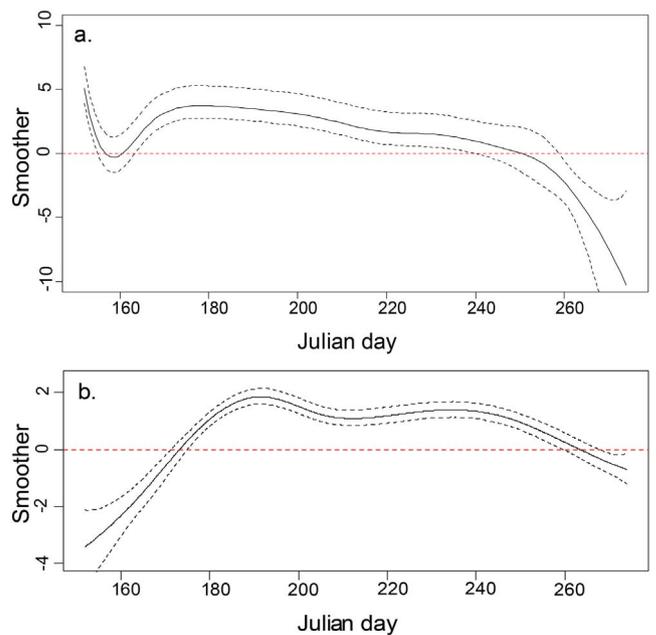


Fig. 4. Estimated smoother  $f(Julian_{ijk})$  for (a) males and (b) females and 95% credible interval of *Speyeria idalia idalia* population. The horizontal dotted line indicates the overall mean value. Credible intervals not including the horizontal dotted line at any point implies the population differed from the grand mean.

seasonal and long-term trends were significant, since the zero line did not always fall within the 95% confidence intervals of the smoothers.

### 3.2. Females

In the binary part of the model for females, the probabilities of false zeroes were highest in June and lowest in the other months, while length of site and temperature had intermediate probabilities (Fig. 2b). Each of these regression parameters was important (Table 1), and the month of June was positively associated with detections of *S. idalia* while the months of July, August and September were negatively associated with detections of this species. Higher temperatures and

shorter transects were also weakly positively associated with *S. idalia* detections. In the count part, there was a strong negative influence of the first period (1998–2002) and a weak positive influence of the last period (2007–2015) on female detection (Table 1).

For the analysis of seasonal variation, there was a significant change, with the first seasonal peak of detections of females reached between 29 June and 19 July, followed by a decline and then a second peak on 28 August (Fig. 4b). In the analysis of long-term change, females had a significant, non-linear trend with year (Fig. 3b) and Julian date. A slightly increasing trend was observed in the first four years (1998–2001), followed by a gradual decline to 2005, and a steep decline to 2007. From this point onwards, the population trajectory generally increased to the end of the study period, except for a brief decrease from 2009 to 2011.

## 4. Discussion

### 4.1. Population trajectories

The *S. idalia* population exhibited non-linear change in trajectory over time. Trajectories since 1998 indicate three periods of increase (1998–2001, 2007–2009, 2011–2014) and two periods of decline (2001–2007, 2009–2011). The most marked change in the population was the extended period of decline beginning in 2001, which brought the population from its peak density to its lowest recorded density in 2007. The trajectories also indicate that more recently (2011–2014), a partial recovery has occurred, though the increasing trend had begun to level by 2014. The non-linear pattern suggests a likely responsiveness of the population to external factors (explored further below). The recent increases are positive news for this sole remaining population of *S. idalia*, even if the population remains somewhat depleted relative to 2001.

As expected given that they represent the same species, changes in male and female trajectories coincided temporally. Inflection points in the population pattern (2001, 2007, 2009, 2011, 2014) were the same in both sexes. The tight temporal concordance from two distinct modeling efforts increases confidence in the accuracy of observed population trends.

The magnitude of observed changes differed by sex, however, with changes in males generally more pronounced, especially during 2001–2007 and 2011–2014. The greater observed changes could indicate that males have a higher sensitivity to factors promoting population change. More likely, males may be more detectable, and thus changes in their densities more apparent. As in other studies of *S. idalia* (Kelly and Debinski, 1998; Kopper et al., 2001), we detected far more males than females during transect walks. Further, both capture and recapture data for *S. idalia* during a mark-recapture program in 2014 had a strong skew toward males (Supporting Information, Appendix S5), suggesting bias in detection and capture that may result from male patrolling or courtship behavior (James, 2016; Takeuchi, 2017).

Credible intervals in both sexes were of consistent width throughout the study period, with two exceptions. Intervals were wider early in the study period (prior to about 2003), implying greater uncertainty (Kéry, 2004), perhaps due to the lower number of observed sites (a fourth site was added in 1999 and a fifth in 2002), the greater reliance on less experienced volunteers and other surveyors early in the study period, or greater spatial variability in population pattern at that time. Intervals were smaller during 2003–2004 and 2006–2007 in males and 2005–2006 in females, suggesting an unambiguous pattern of decline.

The probability of false zeroes (i.e., walks where no butterflies were detected when they were present during at least part of the year) was high in June and low in July for both sexes. This is readily explainable by the phenology of *S. idalia*: activity was variable in June as the season began, but peaked in July. The probability of false zeroes was also low in August and September in females, likely representing increased activity during oviposition (Kopper et al., 2001). The

probability of false zeroes was also highly uncertain in males in August and especially September, probably because many males die after mating in July. Accounting for zero-inflation from butterfly phenology in the binary part of the model ensures that the count part represents true density of butterflies during active periods.

### 4.2. Associations between putative causes and population change

While butterfly population changes could be influenced by unmeasured environmental factors and could have a random component, we consider it likely that training and management activities were important contributors to population change. This is because of the magnitude of population changes and the often close temporal concordance of these changes with changes in training activities or management. In particular, several factors may have contributed to population changes in *S. idalia* early in the study period through their effects on vegetation structure (Van Swaay et al., 2016). Initially, training activities involving tank and troop movements may have led to frequent disturbances that favored early successional grassland habitat suitable for *S. idalia*. These activities may thus have contributed to the relative stability of the butterfly population during this period, but they were discontinued in most sites after the 1998 season (Ferster and Vulinec, 2010). Declines occurring from 2001 to 2007 may have been related to woody encroachment on grassland habitat. In response, a small-scale manual effort to remove woody vegetation was undertaken in an attempt to delay succession, but this was later considered insufficient for the scale of the managed habitat and was abandoned in 2003. From 2004 onwards, prescribed fires ignited by hand were used to maintain the open structure of grasslands (Selby, 2007). In the appropriate season and frequency, prescribed fires can limit the loss of herbaceous plant species to woody encroachment (Huebschman and Bragg, 2000), and indirectly favor the persistence of grassland-dependent organisms like *S. idalia*. However, fires may also cause direct mortality to *S. idalia* if burning takes place during life stages when they cannot fly away from oncoming flames (Moranz et al., 2014). Burning in some early years (prior to butterfly surveys in 2005 and 2007) took place in May, most likely in the last instar stage of *S. idalia* when mobility is low (Edwards, 1879). This may have caused direct mortality and population declines. Weather patterns may have reinforced these declines. Butterflies are well known to react quickly to year-to-year weather variation (Suggitt et al., 2011), and this extended period of decline included the two most arid years (2001, 2007) of the study period.

The increases we observed in 2008–2009 could be reasonably attributed to vegetation structure changes that occurred near two of the survey routes (sites D1, C4). Specifically, extensive disturbance occurred as range construction and logging converted forested tracts to open grassland habitats adjacent to the study areas. Host plants for *S. idalia* larvae (*Viola* spp.) and nectar plants (*Asclepias* spp., *Cirsium* spp., *Monarda fistulosa*) for adults became widespread as a result of this disturbance, likely favoring growth in the *S. idalia* population not only in the adjacent, recently-cleared areas but also in the grassland areas under study. Unpublished data have clearly demonstrated that frequency of fire had a significant positive effect on the presence of violets (Adamidis et al., unpublished data).

In 2010, a different fire regime, by aerial ignition, was first applied in the study area, replacing the prescribed fires ignited by hand. Burning in the first year (prior to butterfly surveys in 2010) was again in May, during a period of limited mobility for *S. idalia* larvae, which may have had a temporary negative effect on the population. Potential direct mortality from this burn may have driven short-term declines in the *S. idalia* population.

In subsequent years, burning by aerial ignition was conducted later in the season, and the aerial ignition approach enabled prescribed fires to cover a much greater surface area of grasslands than had been covered previously when prescribed fires were set by hand ignition. The

cumulative effect of these more extensive burns on *S. idalia* habitat over several years, combined with the greater experience of the management team and the more established working relationship between land managers and the military trainers may have driven increases in the species' trajectory after 2011. Overall, changes in population trajectories were temporally concordant with key changes in management regime, suggesting that active management, and particularly intensive management efforts of a scale sufficient to affect large habitat areas, may strongly impact the *S. idalia* population on this active military training area.

#### 4.3. Implications for analysis of long-term monitoring data

Analysis of the data posed several challenges, including analysis challenges typical of wildlife monitoring data generally (Fewster et al., 2000; Zuur et al., 2009; Ingersoll et al., 2013) as well as challenges specific to butterfly monitoring data, and to research on military training areas. The extensive monitoring data on *S. idalia* was collected over 18 years with great effort, time, and expense, but had not previously been analyzed comprehensively, in part because of these analytical challenges. We suspect that many other wildlife monitoring datasets remain unanalyzed for similar reasons (e.g., as discussed in Ellison et al., 2003). Or, where such analyses of wildlife monitoring data have been completed, a biased shortcut may have been employed that ignored one or more statistical complexities, limiting inference and hindering opportunities for publication in the peer-reviewed literature. Our approach combines several techniques that have been recently developed and presented in the statistical literature (Zuur et al., 2015; Zuur and Ieno, 2016), but to our knowledge, this set of techniques, and ZIPGAMMs in particular, have not previously been applied to wildlife monitoring data (but see Gardner et al., 2008 for a linear model). Our approach, therefore, provides a roadmap for analyzing data with common practical problems of monitoring datasets generally, as well as those pertaining to butterflies and research on military training areas more specifically (e.g., sex-specific variation in detection, changes to sampling areas, zero-inflation, non-normal distributions, random effects).

#### 4.4. Implications for conservation on military training areas

Our results suggest conservation approaches that may effectively accommodate both conservation of *S. idalia* and human activities at FIG-NGTC, and that could be replicated on other military training areas. The continued use of prescribed fire with aerial ignition could maintain fire-adapted grasslands, providing both the openness needed for training and suitable habitat for grassland-dependent species like *S. idalia*. Care must be taken, though, in timing the application of fire treatments to avoid direct mortality of target species like *S. idalia* and other non-target species during periods of low mobility.

Although the range construction and logging that occurred in the middle of the study period was a one-time event to support military training needs, it highlighted how strongly disturbance-adapted populations like *S. idalia* may respond to nearby managed disturbance and especially to the resulting increases in key resources, like the disturbance-adapted host and nectar plants favored by *S. idalia*.

Conservation strategies are most efficient when concentrating in endangered species where habitat requirements are known (Ochoa-Hueso et al., 2014). However, care must be taken to avoid an approach creating a uniform habitat or designing a specialized strategy to conserve only a single species. Such an approach could benefit the target species at the cost of the broader ecological community, as other species in the community have differing habitat requirements. Further, as a practical matter, the same land must serve multiple conservation purposes (Grumbine, 1994), and thus key conservation objectives for military training areas include maintaining or increasing biodiversity values broadly (Zentelis et al., 2017).

More broadly, this study supports the idea that multiple land uses can coexist sustainably on a military training area, including both military training and maintenance of a globally threatened species. Continued coexistence over time may depend upon focused and sustained management attention; in this study, the target species underwent a prolonged decline prior to the onset of effective management of a sufficient scale. More recently, support of the military branch for management efforts, and close coordination between land managers and military personnel on the military training area have been essential components of the recovery of *S. idalia* and its continued persistence on site. Similar management efforts and coordination to benefit conservation are likely possible on many military training areas. Opportunities may be especially ripe on military training areas where listed species are already present or where military personnel are motivated to avoid the restrictions on land use and training that may accompany future listing of rare or declining species.

While military training areas are not primarily managed for biodiversity, they represent a vast, largely untapped resource for conservation globally (Zentelis et al., 2017). Their large spatial extent and their distribution in diverse ecosystem types, could secure the success of programs similar to this one, suggesting that conservation on military training areas could be a viable and underexploited option. Biodiversity conservation may be viable on existing military training areas is also appealing, because it may involve only one or a few landowners, and because it may avoid the need to engage in the challenging process of establishing new protected areas. Conservation biologists should therefore encourage active, targeted management of military training area lands as a means to expand conservation of threatened organisms, especially those experiencing sustained threat elsewhere.

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#### Appendix S1–S7. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2017.09.026>.

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