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Climate Extremes, Vegetation Change, and Decoupling of Interactive Fire-Grazing Processes Exacerbate Fly Parasitism of Cattle

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Abstract

We assessed local horn fly (*Haematobia irritans* L.) and face fly (*Musca autumnalis* De Geer) communities on cattle in 2012 and 2013 relative to vegetation and climate data to understand how parasitism of cattle is influenced by change in climate and vegetation structure. We compared heterogeneity management using spatially and temporally discrete fires (i.e., patch-burning one-third of a pasture annually) to homogeneity management (i.e., burning entire pasture in 2012 then no burning in 2013), with cattle grazing all years in both treatments. Predicted emergence of horn flies and face flies was 24 and 34 d earlier in 2012 associated with earlier spring warming, a significant deviation from the five-year mean. Intraannual horn fly dynamics were explained by concurrent high ambient air temperature the day of observations, but face flies were explained by low ambient air temperatures and dry conditions 3 wk before observations. Importance values of information for the theoretic models including fire treatments ranged from 0.89 to 1, indicating that both horn flies and face flies are sensitive to habitat alterations and fire-driven animal movements. Ordination indicates herds on unburned pastures were dissimilar to herds on pastures burned with patchy fires or pastures burned completely and species-specific fly responses to different vegetation structure metrics. For example, horn flies were correlated with vegetation visual obstruction, and face flies were correlated with woody plant cover. Vegetation structure may be as important as climate in driving the dynamics of fly parasites of cattle.

Key words: community and ecosystem ecology, ecosystem, ectoparasite, habitat management, range entomology

Warming global surface temperature (Hansen 2012, Field 2014) is accompanying an increase in frequency and severity of drought, especially in the Northern Hemisphere (Thomas et al. 2004, Meehl and Tebaldi 2004, Burke and Brown 2008). Spring warming may also accelerate in western North America (Westerling et al. 2006). Concurrent with these changes in climate patterns, woody plant encroachment on grasslands globally has accelerated, caused potentially by changing climate, carbon dynamics, and land use (Archer et al. 1995, Bond and Keeley 2005, Engle et al. 2008, Buitenwerf et al. 2012). As woody plants encroach into grasslands, the plant community transitions from an herbaceous-dominated state to a state dominated by woody plants (Asner et al. 2003, Briske et al. 2005).

Change in weather patterns and the state transition of the plant community can negatively influence livestock grazing and dependent human livelihoods (Buitenwerf et al. 2012, Wang et al. 2014). The conspicuous effects of climate change and woody plant encroachment are reduced livestock performance and production resulting from heat stress, limited water availability, and reduced herbaceous forage required by ruminants (Brown-Brandl et al. 2006, Craine et al. 2010, Limb et al. 2010, Godber and Wall 2014, Thornton et al. 2014). Conversely, a more subtle effect of these global changes on livestock is the potential escalation of exposure to parasites and associated diseases (Thornton and Gerber 2010). While several studies have projected escalating human vulnerability to vector-borne diseases, a paucity of information on livestock vulnerability to parasites and vector-borne diseases exists in the literature (Sutherst 1998, Pickles et al. 2013). This is surprising because the role of temperature and moisture in parasite biology has been long understood because infestations are highly dependent on precipitation and temperature variation (Teskey 1969).

Climate change models have predicted up to a 244% increase in filth flies, specifically species within the family Muscidae, in Europe by 2080 (Goulson et al. 2005). The mechanisms driving predicted increases are weather, specifically temperature and rainfall (Stoffolano and Matthysse 1967, Teskey 1969, Ragland and Sohal 1975, Goulson et al. 2005). However, fly distribution also is associated with herbaceous and shrub vegetation, which flies use for thermal regulation, for egg laying, and for overwintering habitat, as well as host movement and characteristics (Huddleston et al. 1974, Krafsur and Moon 1997, Talley et al. 2009).

Projected increases in parasitic flies are a concern for animal welfare and economics because parasitic flies are considered the most damaging parasites of grazing livestock, causing >$2 billion US in economic loss annually in the United States alone (Huddleston et al. 1974, Byford et al. 1992). Moreover, simplistic global change models predicting parasite distributions based primarily on climatic variables is an unrealistic approach that ignores important habitat features and host population attributes (Pérez-Rodríguez et al. 2013). Simplistic global change models also neglect disturbance ecology and the potential effects of fire that may also disrupt fecal resources required by flies for reproduction (Scasta et al. 2014b).

Fly species within the family Muscidae are particularly injurious to livestock in North America and include horn flies (*Haematobia irritans*), face flies (*Musca autumnalis*), and stable flies (*Stomxys calcitrans*). Loss of blood, annoyance, and associated avoidance behaviors, reduced grazing time, and disease exposure cause livestock production losses (Harvey and Launchbaugh 1982, Buxton et al. 1985, Boland et al. 2008). Rapid development of resistance to insecticides and the lack of alternative control strategies that can be applied across broad landscapes will compromise effective control strategies (Wardhaugh 2005, Oyarzún et al. 2008). Restoring regular prescribed burning and allowing fire to interact with grazing can reduce cattle parasites, specifically horn flies and ticks (Scasta et al. 2012, Polito et al. 2013).

Because other studies indicate that global change may drive increasing pestiferous fly pressure, but no studies have empirically measured vegetation change and host–parasite dynamics of cattle and flies, we coupled a data set of parasitic flies on cattle with climate and vegetation data to better understand how flies on cattle are influenced by broad climate and vegetation structure changes. The timeframe of our study included opposite ends of the temperature gradient relative to the last century, with 2012 as the hottest year since 1895 based on the mean annual high temperature and the March to May high temperature and 2013 as the fourth coolest for March to May high temperature with spatio-temporally variable applications of fire. Our objectives in this study were to understand how 1) recent weather extremes influenced fly activity in the spring, 2) climate change via spring warming, hotter summers, and precipitation accumulation might influence seasonality of horn flies and face flies, and 3) different applications of prescribed fire alters vegetation structure and the parasitic fly species composition of cattle herds.

Materials and Methods

Study Site

Our experiment was initiated in 2007 in mesic grasslands in southern Iowa, USA (Scasta et al. 2014a), and parasites were evaluated in 2012 and 2013. Study sites were tallgrass prairie on glaciated plains composed of loess hills with glacial till side slopes. Mean pasture size was 27 ha and all pastures were seasonally grazed from May to September. Mean stocking rate (± SE) was 2.5 ± 0.2 animal unit months (AUM) per hectare, with 12 ± 1 mature female cows per pasture. All herds assessed in the experiment were composed of black Angus beef cows (*Bos taurus* L.). Pastures were managed with two applications of fire, 1) heterogeneity management or patch-burning one-third of a pasture annually, or 2) homogeneity management (i.e., burning the entire pasture in 2012 and not burning in 2013; Fuhlendorf and Engle 2001). All fires were conducted in the dormant season from March to early April. Our study was replicated at the pasture scale with three pastures and cattle herds in each treatment (Supp. Appendix Table 1 [online only]).

Data Collection

We conducted assessments of flies on beef cattle weekly in 2012 (May 30th–August 9th) and 2013 (May 20th–August 9th). Digital photographs of four randomly selected and different cows in each pasture, or ∼33% of each herd, were collected between 0700 a.m. and 1100 a.m. (Lima et al. 2002, Boland et al. 2008). The specific determinants of different preferences of horn flies to select animals include phenotypic traits such as body size (Steelman et al. 1996) and color (Steelman et al. 1991, Pruett et al. 2003). Another possible explanation for differential selection of certain animals is that horn fly distribution may depend on the feeding success of individual horn flies on a particular beef animal, possibly relating to the success of the anticoagulation mechanisms of the fly against the coagulation systems of that particular host (Pruett et al. 2003, Untalan et al. 2006). Therefore, a random selection of animals from each pasture replication would truly encompass the variation extremes of low fly carrier and high fly carrier animals. This in turn would also allow a true treatment effect to be seen and not skew the data toward low fly carrier animals. This is important for the objective of our study to detect herd variation through time as a function of climate and treatment-induced changes to vegetation—not individual animal variation *per se*. Similar protocols of randomly assessing cattle as a subset of the larger herd for quantifying population dynamics of parasitic flies have been applied in entomological studies of cattle (Harvey and Brethour 1979; Haufe 1982; Kinzer et al. 1984; Kunz et al. 1984; DeRouen et al. 2009, 2010; Li et al. 2011).

We collected images from <30 m and included the side and face of each cow to allow for evaluating various physical animal locations that are preferred by different species of flies (Scasta et al. 2015). A digital grid was overlain on images in the laboratory and digital zoom was used for identification and counting. Four species of pestiferous flies were assessed: horn flies (*Haematobia irritans* L.), face flies (*Musca autumnalis* De Geer), stable flies (*Stomoxys calcitrans* L.), and horse flies (*Tabanus* spp.).

Vegetation structure was measured annually in mid-July by assessing three aspects of vegetation structure that can be manipulated with fire and may influence flies. Vegetation structure included canopy cover of woody plants, which may influence thermal regulation and dispersion of flies (Krafsur and Moon 2008); canopy cover of herbaceous litter, a habitat feature important for reproduction of flies (Talley et al. 2009, Baldacchino et al. 2014); and visual obstruction, a measure of density and biomass of herbaceous vegetation, which is associated with organism perception of habitat (Marsh et al. 2014). Each vegetation structure type was measured at ninety total observation points that were equally spaced along permanent transects. Canopy cover of woody plants and herbaceous litter was determined by visually estimating canopy cover of 0.5-m^2 quadrats at each of the ninety observation points. Cover was estimated using the visual estimates of canopy cover classes: 0, <1%, 1–5%, 6–25%, 51–75%, 76–95%, and 96–100% using the categorical mid-points of 0, 1, 3, 16, 38, 63, 86, and 98 (Daubenmire 1959). Visual obstruction was measured with a nondestructive technique using a pole marked with 1-dm intervals (Robel et al. 1970). The pole was placed 4 m in each cardinal direction from the ninety observation points and observed from a height of 1 m from the soil surface for vegetation obstructing the observer's view (Robel et al. 1970, Vermeire and Gillen 2001).

To understand the effect of air temperature on emergence patterns of face flies and horn flies in our study, we determined cumulative degree-day thresholds for 2010–2014, the only years such data were available from a local weather station (Krafsur and Moon 1997). Temperature and moisture have been clearly identified in the scientific literature as drivers of parasite biology, particularly in the face of globally changing climate (Sutherst 2001). Therefore, to understand seasonal patterns for both fly species, we used weather data for times associated with our fly activity surveys as well as for 3 wk before fly image collection, considered the time lapsed required for the previous generational phase of egg lay and emergence (Goulson et al. 2005). Temperature is a key variable influencing insect emergence and parasitic activity (Wang 1964, Stoffolano and Matthysse 1967, Caldwell and Wright 1978). Thus, we collected the "concurrent" observed high and low temperature for each date that fly images were collected and the antecedent high and low temperatures observed 3 wk prior to each fly image collection date (aka "antecedent" high and low temperatures). Moisture, specifically rainfall, and relative humidity have both been documented to influence fly population dynamics (Benson and Wingo 1963, Goulson et al. 2005). Thus, precipitation data included the total accumulated precipitation from January 1 of each year up to each fly image collection date, the precipitation accumulated only within the 3 wk prior to each fly image collection date, and the proportion of days within the 3 wk prior to each fly image collection date with detectable rainfall. Weather data were collected from the Iowa automated weather observation network using the Mt. Ayr station (Iowa Environmental Mesonet 2014). We report data on temperature, precipitation, and Palmer's Drought Severity Index (PDSI) from 1895 to 2014 to place our data in a larger temporal context in terms of climate extremes (e.g., Debinski et al. 2010).

Statistical Analyses

Analysis of Weather Extreme Effect on Predicted Emergence

To assess the impact of interannual temperature variation on face fly and horn fly emergence, we used thresholds of 70 d of accumulated degree days 12°C or above (Krafsur and Moon 1997) and 10.5 d of accumulated degrees days 25°C or above (Lysyk 1999), respectively, to compare the years of our study (2012 and 2013) to the five-year mean. We conducted a one-tailed t-test of the hypothesis that fly emergence, based on reaching each threshold (70—12°C degree days and 10.5—25°C degree days) in 2012, was not earlier in 2012 than in the other years. The alternative hypothesis was that flies emerged later all other years, i.e., reached the degree day threshold later than 2012, the hottest year of the five years available. We calculated a *P*-value at alpha 0.05 and 95% confidence intervals for number of days to reaching each of the thresholds in 2012 and 2013 (R Core Team 2014).

Analysis of Climatic and Management Influence on Fly Dynamics

To move beyond simple hypothesis testing and build more complex models with greater levels of inference, we used an information-theoretic approach to assess management and climatic influences on seasonal patterns of populations of horn flies and face flies, two of the most injurious fly parasites of cattle. We did not assess stable flies or horse flies in this assessment because both were relatively rare, with only 1% of cow observations having stable flies and only 10% of cow observations having horse flies (Scasta et al. 2015). Because we were primarily interested in the effects of temperature and precipitation, we used potential explanatory variables that we identified *a priori* including the following as described in the Materials and Methods section above: concurrent high temperature, concurrent low temperature, antecedent high temperature 3 wk prior to observation, antecedent low temperature 3 wk prior to observation, total accumulated precipitation, antecedent precipitation 3 wk prior to observation, and days with precipitation in prior 3 wk. We modeled the effects of temperature and precipitation on the seasonal patterns of horn flies and face flies using Akaike's information criterion corrected for small sample sizes (AICc) using AICcmodavg package in R (Mazerolle 2013, R Core Team 2014). The response variable was the mean herd fly load for each pasture across two years and weekly sampling periods, conducted separately for horn flies and face flies. Based on a Shapiro-Wilks test for normality and a constant variance test, we log transformed the fly load variable for both fly species to meet assumptions of our statistical techniques.

We modeled the intraannual dynamics of each species using weekly abundance in three categorical steps (temperature, precipitation, combinations of temperature and precipitation coupled with management) to assist in identifying the most parsimonious model (Burnham and Anderson 2002). Within each step, AICc values were scaled relative to the top model (aka, the model with the lowest AICc set at zero) and differences between models (ΔAICc) were calculated and used to rank models. Models that had $\Delta\text{AICc} \leq 2$ were considered to be in the top set of models. Akaike weights (ω_i), calculated to indicate the relative likelihood of candidate models, were used to determine top models (Burnham and Anderson 2002).

We used a systematic set of modeling steps so each individual step addressed singular weather aspects and led to the construction of more complex models. In Step one, we used the temperature categorical variables only (concurrent high temperature, concurrent low temperature, antecedent high temperature, antecedent low temperature), in Step two we used the precipitation categorical variables only (total accumulated precipitation, antecedent precipitation 3 wk prior, and days with precipitation in prior 3 wk), and at each step compared all models to the null model. In the third and final step, we used the top models for the temperature and precipitation categories based on $\Delta\text{AICc} \leq 2$ and combined these models to build more complex models. In this third step, we also included management (heterogeneity or homogeneity), and compared all additive models (combinations of top candidates from temperature, precipitation, and management steps) to the global model (model that included all variables). Evidence ratios were used to compare top models and importance values (w+) were calculated for the management parameter using "homogeneity" management as the reference to determine the importance of "heterogeneity" management to the given candidate models (Mazerolle 2013). To ensure final models did not include autocorrelated explanatory variables, we calculated Pearson product-moment correlation and considered variables autocorrelated at $r > 0.7$ (Ribic and Sample 2001, Coppedge et al. 2008). To further screen and identify uninformative parameters in final models, we calculated 95% confidence intervals (Burnham and Anderson 2002).

Analysis of Fire Altered Vegetation and Fly Composition

We then conducted an indirect gradient ordination analysis of fly species composition of herds using principal components analysis

(PCA) using all four fly species. Classification envelopes were applied to herds and pastures based on management and year. Class membership is a function of dissimilarity of fly species composition of herds belonging to a class. The distance between symbols approximates the dissimilarity of their species composition as measured by their Euclidean distance. Then we conducted a direct gradient ordination analysis of fly species composition of herds constrained to management (heterogeneity or homogeneity) and vegetation structure variables (woody vegetation, vegetation structure, and litter). The constrained ordination approach utilized redundancy analysis (RDA), a constrained form of the linear ordination method of PCA and included "year" as a covariate to account for the annual climatic differences between years.

Fly species composition data for each herd was the response data and was log-transformed, centered, and standardized by species. Sample diversity was applied as Shannon Wiener's index. Based upon the constrained ordination of herd fly composition data to vegetation structure measures, we compared herd fly composition scores to the measure explaining the first axis in the constrained ordination using ordinary least squares regression and ANOVA ($\alpha = 0.05$). Ordination techniques used CANOCO 5 to account for complex species data and multiple environmental variables (Lepš and Šmilauer 2003, Ter Braak and Šmilauer 2012).

Results

Weather Extreme Effect on Seasonal Initiation of Fly Activity

The study period included two years that varied meteorologically based on NOAA (2015) data. Total precipitation in 2012 was lower than the long-term mean and total precipitation in 2013 was similar to the long-term mean but 2013 was a much wetter summer. According to NOAA records for the state of Iowa, 2012 was the 13th driest year and 2013 was the 81st driest year since 1895 in total precipitation. Furthermore, 2012 was the 5th driest year since 1895 based on PDSI and was the hottest year since 1895 based on the mean annual high temperature and the March to May high temperature. In contrast, 2013 was the 20th coolest year since 1895 for mean annual high temperature and the 4th coolest for March to May high temperature.

The effect of early spring warming in 2012 is reflected in a prediction of horn flies emerging before monitoring began in 2012. Predicted emergence was April 26th 2012, or the 117th day of the year, and field observations began the 140th day of the 2012 (Table 1). This predicted and observed extra early emergence of horn flies was not the case, however, for 2013. Horn flies have a temperature based emergence threshold of 10.5 degrees days more than 25 °C (Lysyk 1999), and the early estimated emergence in 2012 was statistically earlier than the five-year mean of the 141st day of the year ($P < 0.001$; 95% CI 124 d to 158 d; Table 1). Based on accumulated degree days, horn fly emergence in 2013 likely occurred around the 150th day of the year. Similar to horn flies, the rapid spring warming in 2012 also led to first time predicted emergence of face flies based on their F1 generation from overwintering adults on May 8th 2012, or before weekly monitoring began on May 30th (Table 2).

Based on the threshold of 70 degree days more than 12°C, we determined that face fly emergence would have occurred around the 129th day of the year (Table 2). This predicted earlier emergence in 2012 was significantly earlier than the estimated five-year mean of the 163rd day of the year ($P < 0.002$; 95% CI 152 d to 172 d; Table 2). Face fly emergence in 2013 occurred around the 171st day of the year.

Table 1. Predicted emergence dates for horn fly (*H. irritans*) based on the threshold of 10.5 d of accumulated degree days above 25°C from 2010 to 2014 in Mt. Ayr, Iowa, USA

Year	Date	Calendar day
2010	May 26	146
2011	May 24	144
2012	April 26	117[a]
2013	May 30	150
2014	May 28	148
Five-year mean[b]	May 21	141

Field validation based on sampling start dates of May 30th in 2012 and May 20th in 2013.

[a] Significant one-tailed t-test with the alternative hypothesis that all other years reached the face fly emergence threshold later than 2012 ($t = 23.2$, $df = 4$, P-value < 0.001, 95% CI (124–158)).

[b] Based on data from the Iowa Mesonet Mt. Ayr weather station. Data became available starting in 2010 (https://mesonet.agron.iastate.edu/request/coop/obs-fe.phtml).

Table 2. Predicted emergence dates for face fly (*M. autumnalis*) based on the threshold of 70 d of accumulated degree days above 12°C from 2010 to 2014 in Mt. Ayr, Iowa, USA

Year	Date	Calendar day
2010	June 6	157
2011	June 13	164
2012	May 8	129[a]
2013	June 20	171
2014	June 7	158
Five-year mean[b]	June 12	163

Field validation based on sampling start dates of May 30th in 2012 and May 20th in 2013.

[a] Significant one-tailed t-test with the alternative hypothesis that all other years reached the face fly emergence threshold later than 2012 ($t = 10.4$, $df = 4$, P-value < 0.002, 95% CI (152–172)).

[b] Based on data from the Iowa Mesonet weather station at Mt. Ayr. Data became available starting in 2010 (https://mesonet.agron.iastate.edu/request/coop/obs-fe.phtml).

Climatic and Management Influence on Fly Dynamics

Model selection for horn flies revealed that the concurrent high temperature on the day of observation was the weather variable most strongly explaining intraannual horn fly population dynamics and that precipitation was a poor predictor. For the temperature models, the top model was the concurrent high temperature; concurrent low temperature, antecedent high temperature 3 wk prior to observation, and antecedent low temperature 3 wk prior to observation models were not competitive (Table 3).

Akaike weights (ω_i) suggest high temperature was more influential than low temperature, antecedent high temperature 3 wk prior to observation, or antecedent low temperature 3 wk prior to observation with 71% of the model weight. None of the precipitation models were better than the null model (Table 3). Two models were in the top set of predictive candidate models for horn fly intraannual dynamics (Table 3). Both included management and high temperature. The second model, considered the global model, also included accumulated precipitation. Management alone, or any other temperature or precipitation model or combination of models, were not

Table 3. Information-theoretic model selection using Akaike's information criterion corrected for small sample sizes (AICc) for horn fly (*H. irritans*) seasonal patterns as influenced by temperature, precipitation, and management

Categories and models	K	AICc	ΔAICc	ω_i
Temperature				
ConHi	3	−19.95	0.00	0.71
ConLo	3	−17.52	2.43	0.21
Null	2	−14.07	5.88	0.04
AntHi	3	−12.73	7.23	0.02
AntLo	3	−12.58	7.37	0.02
Precipitation				
Null	2	−14.07	0.00	0.46
AccPrec	3	−12.86	1.21	0.25
AntPrec	3	−11.83	2.24	0.15
DwPrec	3	−11.80	2.27	0.15
Final models[a,b]				
Mgmt + ConHi	4	−38.79	0.00	0.63
Global	5	−37.68	1.12	0.36
Mgmt	3	−28.82	9.97	0.00
Mgmt + AccPrec	4	−28.00	10.80	0.00
ConHi	3	−19.95	18.84	0.00
ConHi + AccPrec	4	−18.43	20.36	0.00
Null	2	−14.07	24.73	0.00
AccPrec	3	−12.86	25.93	0.00

K indicates the number of parameters in the model and AICc values were scaled relative to the top model by setting the model with the lowest AICc at zero. Differences between models (ΔAICc) were calculated and used to rank models. Models that had $\Delta\text{AICc} \leq 2$ were considered to be in the top set of models. Akaike weights (ω_i) were calculated as they indicate the relative likelihood of candidate models and are used to determine top models. Evidence ratios were used to compare top models and importance values (w+) were calculated for the management parameter using "homogeneity" management as the reference to determine the importance of "heterogeneity" management to the given candidate models.

[a] Evidence ratio between "Mgmt + HiTemp" and "Global (Mgmt + ConHi + AccPrec)" = 1.75.

[b] Importance values of models with and without "mgmt": w+ (models including parameter) = 1; w- (models excluding parameter) = 0.

[c] Model parameters definitions: ConHi and ConLo (concurrent high and low temperature for each fly observation date), AntHi and AntLo (antecedent high and low temperatures 3 wk prior to each fly observation date), AccPrec (total accumulated precipitation from January 1 up to each fly observation date), AntPrec (antecedent precipitation accumulated the 3 wk prior to each fly observation date), DwPrec (the proportion of antecedent days within the 3 wk prior to each fly observation date with rainfall > 0.001"), and Mgmt (heterogeneity management—patch-burning one-third of a pasture annually, or homogeneity management—burning the entire pasture in 2012 and not burning in 2013).

Table 4. Coefficient estimates and 95% confidence intervals for top climatic variables selected using information-theoretic model selection that influence horn fly (*H. irritans*) seasonal patterns in Mt. Ayr, Iowa, USA, in 2012 and 2013

Model	*P*	Estimate	95% CI
ConHi	0.0054	0.0196	0.0065 to 0.0327
AccPrec	0.3110	0.0004	−0.0003 to 0.0010

competitive (Table 3). The parameter estimate for high temperature was positive, indicating that as the high temperature increased during horn fly observations, horn fly numbers also increased. The parameter estimate for accumulated precipitation was also positive, but the 95% confidence intervals of accumulated precipitation model parameter estimates overlapping zero indicate that accumulated precipitation did not regulate horn fly numbers and was not informative as the other models ($P = 0.31$; Burnham and Anderson 2002; Table 4).

Thus, based on the final model selection and confidence intervals, the top model was management + concurrent high temperature. This top model for horn flies was more influential than any other model with 63% of the total model weight based on Akaike weights (ω_i). The evidence ratio between the top two candidate models was 1.75; an indication of the magnitude of explanatory power of the top model. Furthermore, the importance values of models with and without "management" was 1 for models including "management" as a parameter, indicate that horn flies are sensitive to heterogeneity management with fire.

Model selection for face flies revealed a more complex weather function in determining face fly dynamics as the antecedent low temperature 3 wk prior to observation, concurrent high temperature, and days with precipitation predicted intraannual face fly population dynamics. For the temperature models, the top models were antecedent low temperature 3 wk prior to observation and concurrent high temperature; concurrent low temperature and antecedent high temperature 3 wk prior to observation were not competitive (Table 5).

Akaike weights (ω_i) suggest antecedent low temperature 3 wk prior to observation and concurrent high temperature cumulatively had 92% of the total model weight and were more influential than antecedent high temperature 3 wk prior to observation or low temperature and all of the temperature models were better than the null model. For the precipitation models, the top model was days with precipitation; antecedent precipitation 3 wk prior to observation and accumulated precipitation were not competitive (Table 5). Akaike weights (ω_i) suggest days with precipitation was more influential than the other precipitation models with 100% of the total model weight. One model was in the top set of predictive candidate models for face fly intraannual dynamics (Table 5). This top model included management, antecedent low temperature 3 wk prior to observation and days with precipitation. The next model, considered the global model, also included concurrent high temperature but was not as informative ($\Delta\text{AICc} = 2.22$). No other model or combination of models was competitive (Table 5). The parameter estimates for antecedent low temperature and concurrent high temperature were both positive, indicating that as night-time temperature increased or high temperature during face fly observations increased, face fly numbers also increased. Pearson's product-moment correlation demonstrated low correlation between these variables ($r = 0.23$) and concurrent high temperature was not in the top predictive model (Table 6).

However, the parameter estimate for days with precipitation was negative, indicating that as the proportion of days within the 3 wk prior to an observation with detectable rainfall decreases, face fly numbers increase. None of the 95% confidence intervals for the top climate variables explaining face fly dynamics overlapped zero (Table 6). Thus, based on the final model selection and confidence intervals, the top model was management + antecedent low temperature 3 wk prior to observation + days with precipitation. Akaike weights suggest this top model was more influential than any other model, including the global model with 66% of the model weight. The evidence ratio between the top two candidate models was 3.04, an indication of the magnitude of explanatory power of the top model. Furthermore, the importance values of models with and without "management" was 0.89 for models including

Table 5. Information-theoretic model selection using Akaike's information criterion corrected for small sample sizes (AICc) for face fly (*M. autmunalis*) seasonal patterns as influenced by temperature, precipitation, and management

Categories and models	K	AICc	ΔAICc	ω_i
Temperature				
AntLo	3	85.04	0.00	0.55
ConHi	3	85.82	0.78	0.37
AntHi	3	89.96	4.92	0.05
ConLo	3	91.13	6.09	0.03
Null	2	94.00	8.96	0.01
Precipitation				
DwPrec	3	68.27	0.00	1
AntPrec	3	90.01	21.74	0
AccPrec	3	93.58	25.30	0
Null	2	94.00	25.72	0
Final models[a,b]				
Mgmt + AntLo + DwPrec	5	56.14	0.00	0.66
Global	6	58.37	2.22	0.22
AntLo + DwPrec	4	60.31	4.16	0.08
AntLo + ConHi + DwPrec	5	62.46	6.32	0.03
Mgmt + ConHi + DwPrec	5	66.90	10.75	0.00
DwPrec	3	68.27	12.13	0.00
ConHi + DwPrec	4	69.74	13.60	0.00
Mgmt + AntLo + ConHi	5	77.62	21.48	0.00
AntLo + ConHi	4	79.40	23.26	0.00
AntLo	3	85.04	28.90	0.00
ConHi	3	85.82	29.68	0.00
Null	2	94.00	37.85	0.00

K indicates the number of parameters in the model and AICc values were scaled relative to the top model by setting the model with the lowest AICc at zero. Differences between models (ΔAICc) were calculated and used to rank models. Models that had $\Delta\text{AICc} \leq 2$ were considered to be in the top set of models. Akaike weights (ω_i) were calculated as they indicate the relative likelihood of candidate models and are used to determine top models. Evidence ratios were used to compare top models and importance values (w+) were calculated for the management parameter using "homogeneity" management as the reference to determine the importance of "heterogeneity" management to the given candidate models.

[a] Evidence ratio between "Mgmt + AntLo + DwPrec" and "Global (Mgmt + AntLo + DwPrec + ConHi)" = 3.04.

[b] Importance values of models with and without "mgmt": w+ (models including parameter) = 0.89; w- (models excluding parameter) = 0.11.

[c] Model parameters definitions: ConHi and ConLo (concurrent high and low temperature for each fly observation date), AntHi and AntLo (antecedent high and low temperatures 3 wk prior to each fly observation date), AccPrec (total accumulated precipitation from January 1 up to each fly observation date), AntPrec (antecedent precipitation accumulated the 3 wk prior to each fly observation date), DwPrec (the proportion of antecedent days within the 3 wk prior to each fly observation date with rainfall > 0.001"), Mgmt (heterogeneity management—patch-burning one-third of a pasture annually, or homogeneity management—burning the entire pasture in 2012 and not burning in 2013).

Table 6. Coefficient estimates and 95% confidence intervals for top climatic variables selected using information-theoretic model selection that influence face fly (*M. autumnalis*) seasonal patterns in Mt. Ayr, Iowa, USA in 2012 and 2013

Model	*P*	Estimate	95% CI
AntLo[a]	0.0011	0.0472	0.0207 to 0.0737
ConHi[a]	0.0017	0.0709	0.0295 to 0.1123
DwPrec	< 0.0001	−0.0318	−0.0421 to -0.0216

[a] Pearson's product-moment correlation for AntLo and ConHi ($r = 0.23$).

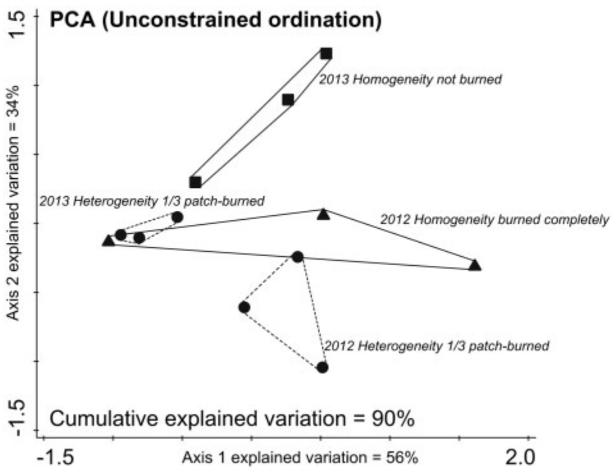

Fig. 1. Unconstrained ordination using principle components analysis (PCA) of herd fly composition scores in 2012 and 2012 for two treatments. The dashed-line classification envelopes represent heterogeneity management using patch-burn grazing where a different third of the pasture was burned in 2012 and 2013. The solid-line classification envelopes represent homogeneity management that either burned the entire pasture in 2012 or did not burn any of the pasture in 2013. Total variation is 8.2 and the first axis explained 56% of the variation, the second axis explained 34% of the variation, and the first two axes explained 90% of the variation cumulatively.

"management" as a parameter indicate that face flies are also sensitive to heterogeneity management with fire.

Fire Altered Vegetation and Fly Composition

Unconstrained ordination using principal components analysis (PCA) of the four fly species suggests that fly composition of herds was different between pastures, treatments, and years (Fig. 1). The first PCA axis had an eigenvalue of 0.556 and explained 56% of the variance of fly species data. The second PCA axis had an eigenvalue of 0.339 and the first two axes combined explained 90% of the variance of fly species data. The first axis appears to be explained primarily by interpasture and interannual differences because the three 2012 burned completely pastures are spaced out along the entire length of the first axis (Fig. 1) The second axis is clearly explained by the application of fire based on the separation of the unburned pastures (Fig. 1). Classification envelopes applied to herds and pastures based on management and year demonstrate that herds in 2013 that were on pastures not burned were compositionally dissimilar than pastures burned with patch burns in 2012 and 2013 or pastures burned completely in 2012. Furthermore, the distance between symbols for the four respective classes indicates that herds and pastures managed with heterogeneous fire were more similar to pastures managed with homogeneous applications of fire than those excluded from fire (Fig. 1).

Redundancy analysis (RDA) of the four fly species constrained to three vegetation structure variables revealed that different fly species have different environmental responses to fire. The first axis explained 61% of the fitted variance of fly species data, which was well correlated with the vegetation structure explanatory data ($r = 0.92$; Fig. 2). The first two axes combined explained 96% of the fitted variance for fly species. The permutation test of significance for all axes under the full model was significant ($F = 3.7$; $P = 0.004$). The first axis is explained by vegetation structure and the second axis is explained by management (heterogeneity or homogeneity) and woody plant cover (Fig. 2). The response of the three measures of vegetation structure were species specific; face flies were

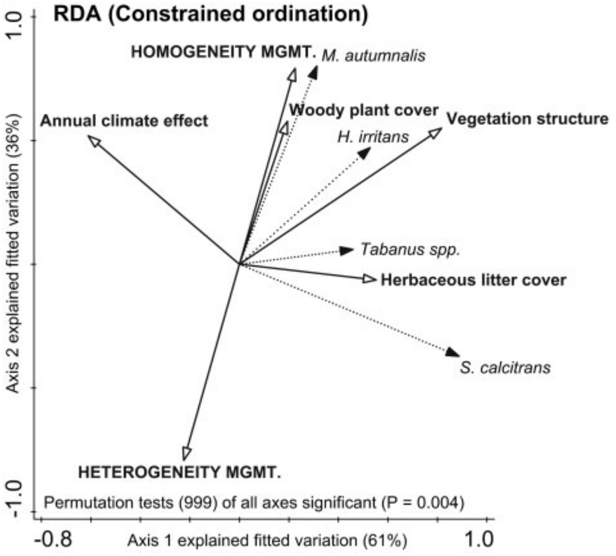

Fig. 2. Constrained ordination of vegetation structure and composition relative to fly species abundance using redundancy analysis (RDA), an indirect gradient form of principle components analysis (PCA). Solid lines indicate treatments or vegetation measurements influenced by treatments and dashed lines represent fly species and the direction of steepest increase. Total variation is 8.2 and explanatory variables alone account for 62%. The permutation test using 999 iterations for all axes is significant (pseudo-$F = 2.8$, $P = 0.014$). The first axis explained 67% of the variation and is described by the increase in vegetation structure and the response of horn flies. The second axis explained 31% of the variation and is described by the differential treatment effects and increase in woody plant cover and face fly response attributed to the homogeneity treatment. The first two axes explain a cumulative fitted variation of 97%.

correlated with woody plant cover, horn flies were correlated with vegetation structure, and stable flies and horse flies were correlated with herbaceous litter cover and climate. Homogeneity management is associated with increasing woody plant cover and vegetation structure. Neither type of management is associated with increasing herbaceous litter cover which is not surprising because both types of management apply a three-year fire return interval (Fig. 2).

The species-specific responses to certain vegetation features demonstrate three results that may influence management. First, as vegetation structure increases so did herd fly composition scores ($P < 0.01$; Fig. 3a). Vegetation structure alone explained 50% of the variation of herd fly composition scores. Based on the linear equation ($y = 5.6x + 1.9$), herd fly composition scores increase 5.6 for every 1 dm increase in vegetation structure, or as the height of the vegetation increases so does the total composition of fly parasites on cattle (Fig. 3a). Second, as vegetation structure increases so did horn fly numbers ($P < 0.01$; Fig. 3b). Vegetation structure alone explained 45% of the variation of herd horn fly numbers. Based on the linear equation ($y = 19x + 6.5$), mean horn flies per cow in the herd increase 19 for every 1 dm increase in vegetation structure (Fig. 3b). Third, as woody plant cover increases so did face fly numbers ($P < 0.01$) (Fig. 3c). Woody plant cover alone explained 60% of the variation of herd face fly numbers. Based on the linear equation ($y = 1.4x + 5.7$), mean face flies per cow in the herd increase 1.4 for every 1% increase in woody plant cover (Fig. 3c).

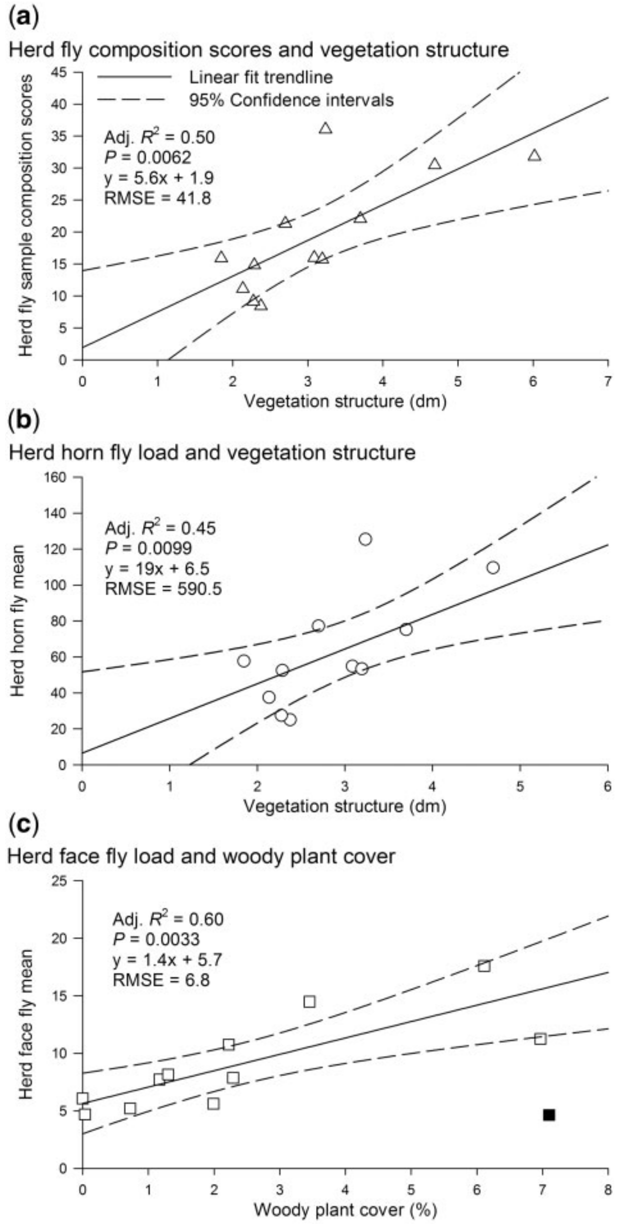

Fig. 3. Influence of vegetation structure as measured by visual obstruction on herd fly composition scores (**a**) and horn flies (**b**), and the influence of woody plant canopy cover on face flies (**c**). Symbols represent the annual mean for individual cattle herds ($n = 12$) in 2012 and 2013 managed with heterogeneity or homogeneity. A single outlier data point in panel c, displayed as the filled box, was not used to fit the trendline, as it was identified as a "fringelier" following Osborne and Overbay (2004) and Wainer (1976). RMSE—residual mean-square error.

Discussion

These results indicate changing climate extremes and vegetation structure may lead to greater parasitism of cattle and that restoration of fire in fire-dependent ecosystems may be a mitigation strategy. Contextually, the timeframe of our study included opposite ends of the temperature gradient relative to the last century with and coupled with spatio-temporally variable applications of fire provided an opportunity to quantify host–parasite ecological implications. It is also critical to point out that the fact that these two fly species emerged 24 to 34 d earlier than expected means livestock had to deal with the stress of their parasitism for an additional month of time in 2012. Furthermore, separating the effects of climate and vegetation change on host-parasite interactions is difficult (Pérez-Rodríguez et al. 2013). Ours is the first study that assesses pasture flies on cattle as the observational unit and as a function of weather conditions and vegetation features in pastures managed extensively with fire as the experimental (treatment) unit. This difference is important because other studies examined fly responses to temperature and precipitation using fly traps independent of livestock hosts or vegetation features, but our study integrated climate, vegetation, and host ecology—important covariates if the future is likely be warmer, drier, and shrubbier. As livestock respond to global change, the dynamics of obligate blood or mucus feeding parasites such as horn flies and face flies may also be influenced interactively, not independently, by temperature, precipitation, and vegetation characteristics. The increased threat of parasitism, coupled with potential nutritional stress (Craine et al. 2010) associated with changing global patterns, will require adaptations to how we manage animal welfare and grazing operations.

The role of temperature and moisture in parasite biology has been long understood because infestations are highly dependent on precipitation and temperature variation (Teskey 1969). The current predictions for increasing temperature and drought frequency in much of the western United States, coupled with our study indicates that grazing livestock may experience greater parasitism, animal welfare may be of greater concern, and parasite-related production losses could increase. These conditions may lead to shorter dormancy periods of parasites, prevention of dormancy altogether, longer periods of animal exposure, greater physical activity of parasites, and greater egg and pupae survival (Wang 1964, Stoffolano and Matthysse 1967, Ragland and Sohal 1975, Caldwell and Wright 1978). Temperature was the most informative covariate for all three fly groups assessed in the Goulson et al. (2005) study that used fly traps. In that case, fly emergence, abundance and activity was positively correlated with the temperature during the preceding 3 wk. However, in our study of flies on cattle, concurrent temperatures at the time of animal or parasite observation were equally or more important than the antecedent temperature 3 wk prior to observation, and this result is supported by the influence of ambient temperature on fly physical activity (Ragland and Sohal 1975). Our finding of a negative correlation between precipitation and face fly activity is also supported by previous studies that indicate low relative humidity was correlated with increased face fly activity (Benson and Wingo 1963). Furthermore, predicted and observed emergence for both face flies and horn flies was significantly earlier in 2012 due to earlier spring warming. Although we did not analyze stable flies in this paper due to low numbers in 2013, higher temperatures during development can also increase adult longevity of stable flies which corresponds to the higher stable fly numbers observed in 2012 (Gilles et al. 2005, Scasta et al. 2015).

Global changes in climate and vegetation structure are neither independent nor mutually exclusive. The change in temperature and precipitation patterns, coupled with carbon dynamics and land use change, may be facilitating an increase in shrub and tree encroachment in grasslands (Archer et al. 1995, Engle et al. 2008, Buitenwerf et al. 2012). A major anthropogenic land cover change in North America over the last two centuries has resulted from suppression of fire and alteration of fire frequency and severity regimes, a potential driver of parasite and infectious disease exposure and risk (Scasta 2015). Our study has demonstrated that heterogeneous fire, applied to restore historical fire-grazing disturbances and ecological patterns and processes, is an important parameter in parasitic fly predictive models and host–parasite dynamics. This is in contrast to Goulson et al. (2005), who concluded fly population changes are primarily driven by weather rather than biotic factors, specifically temperature and rainfall. We suspect that the reason for the difference in conclusions is that Goulson et al. (2005) used traps for flies in structures while we assessed grazing livestock that respond to biotic factors, and subsequently are parasitized by flies that also respond to biotic factors. Similar responses to the biotic influence of vegetation structural changes have also been clearly demonstrated for ticks on cattle and mosquitoes on rangeland (Polito et al. 2013, O'Brien and Reiskind 2013) and similar host–parasite interactions have been altered by climate change for similar blood-obligate parasites of birds (Møller 2010) and gastrointestinal parasites of sheep (Rose et al. 2015). Furthermore, as temperatures escalate and cattle seek thermal refuge, they may be drawn to areas dominated by woody vegetation more frequently (Allred et al. 2013), leading to greater exposure of associated parasites. Thus, it is critical to understand host distribution patterns relative to environmental conditions to better predict future host–parasite interactions (Pickles et al. 2013).

In conclusion, given that our study demonstrated the influence of both climate and vegetation change on fly parasites of cattle, four implications emerge. First, livestock producers should expect parasites such as horn flies and face flies to increase. This increase will require more regular monitoring of cattle for exposure and fly loads relative to economic treatment thresholds. Second, the influence of climate and vegetation change on insect pests may be relevant to situations beyond livestock parasites. Parasites that are problems for humans and seek-hosts independent of anthropogenic structures, such as mosquitoes and ticks, may also become increasingly problematic for the same reasons (Epstein et al. 1998, Léger et al. 2013, O'Brien and Reiskind 2013). Third, vegetation structure may be as important as climate in driving the dynamics of fly parasites of cattle. This is also true for parasites such as ticks (Polito et al. 2013; Léger et al. 2013). Finally, managing vegetation structure, especially reducing woody plants, with either natural processes like fire or contemporary methods such as physical removal may be a proactive livestock parasite management strategy. The influence of global change coupled with the rapid development of resistance by parasites to pesticides suggests that alternative parasite management strategies such as managing vegetation structure will become increasingly important for adapting to climate change (Spratt 1997, Wardhaugh 2005, Sutherst 2001, Oyarzún et al. 2008, Scasta 2015, Scasta et al. 2015). The radical weather during our study period offered a fortuitous opportunity to understand the dynamics of fly parasitism of cattle on extensive pastures managed with different spatio-temporal applications of fire. The serendipitous alignment of these extreme conditions allows for insight to potential climate scenarios, and we speculate that treatment differences would have been apparent had conditions been more neutral. However, the ability to measure responses at both extremes of the climate gradient allows for the conclusion that fire may be as important of a driver as weather extremes, particularly thermal extremes.

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