

Commingled black and white cows (*Bos taurus*; Angus and Charolais) in high-elevation rangeland are differentially parasitised by *Haematobia irritans*

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Abstract. Globally horn flies (*Haematobia irritans*) are one of the most economically damaging parasites of beef cattle. These obligate blood-feeding external parasites take blood meals from cattle leading to blood loss, annoyance avoidance behaviours, and reductions in animal performance. Development of chemical resistance by horn flies suggests that novel management strategies are needed. More in-depth understanding of parasitism relative to hide colour and temperature, especially in a changing climate, may enhance animal production. In peak parasitism periods of 2016 and 2017, we measured horn fly loads on commingled black Angus and white Charolais cows in a cold high-elevation rangeland in Wyoming, USA. We tested how breed, year, and interactions explained horn fly parasitism and economic thresholds. In 2016 we also measured ambient and external cow temperatures to further elucidate thermal ecology mechanisms explaining horn fly hide colour preferences. Mean annual horn fly infestations were always four times greater or more on black cows than white cattle both years, but not all cattle reached economic thresholds all years and the breed by year interaction was not significant. Difference in horn fly preference for black cattle over white cattle in our cold high-elevation environment may be explained by greater absolute and relative external surface temperatures of black hided cows. Host colour and thermal preferences of horn flies could be incorporated into integrated pest management strategies that only treat darker hided cattle and producers in cold high-elevation environments conduct real-time monitoring to determine if treatments are even needed on a year-by-year basis.

Additional keywords: environmental stress, grazing management, integrated pest management, parasitology, rangelands.

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Introduction

Beef producers relying on rangeland and pastureland are challenged by complex environmental, climate/weather, nutrition, and parasite/disease issues that constrain production outcomes such as weight gains and animal performance of increasingly intricate genotype and phenotypes of cattle (Copping *et al.* 2018; Derner *et al.* 2018). For cattle grazing these rangelands and pasturelands, horn flies (i.e. buffalo flies; (Muscidae: Diptera) *Haematobia irritans* (L.)) are one of the most economically damaging external parasites globally, including in Australia, South America, and the United States (Bean *et al.* 1987; Byford *et al.* 1992; Mendes and Linhares 1999; Guglielmo *et al.* 2001). From a United States domestic economic impact perspective, the annual inflation-adjusted estimate of losses to the national cattle industry exceeds \$1.75 billion USD (Swiger and Payne 2017). The negative economic consequences are a result of the direct and indirect effects horn flies have on cattle. The direct effect is attributed to the

feeding on a bovid host by taking many blood meals that leads to blood loss (Cupp *et al.* 2010). Consequently, the indirect effects that follow the repeated biting and blood meal feeding of horn flies includes the physical irritation of the parasites and annoyance avoidance behaviours (i.e. defence behaviours) such as tail switching, hide twitching or panniculus reflex, head throwing, and leg stomping (Mullens *et al.* 2017). Cumulatively, these lead to reduced weight gains, reduced foraging time, and reduced milk production with losses documented in cows and their calves and other classes of cattle such as bulls and yearlings (Byford *et al.* 1992).

Conventional strategies for mitigating horn fly induced losses on cattle include the use of chemical active ingredients in parasticides (Foil and Hogsette 1994). These products can be topically applied to animals (sprayed, rubbed, shot from a gun-like device), fed, injected, or deployed through ear tags. Although these products have been shown in certain situations to be effective, there is a need for novel non-chemical strategies

to manage horn flies due to the rapid development and expression of chemical resistance (Oyarzún *et al.* 2008). Research of non-chemical strategies has included alterations to the rangeland environment with fire (Scasta 2015a; Scasta *et al.* 2014), grazing management that alters the space and timing of use (i.e. rotational grazing, see Steelman *et al.* 2003), grazing management that induces intake of naturally occurring secondary compounds (Parra *et al.* 2016), animal breeding and selection and in particular the use of *Bos indicus* cattle (Tugwell *et al.* 1969; Fordyce *et al.* 1996), phenotypic selection for resistance traits (Pruett *et al.* 2003), and the use of different hide colour or combinations of colour (Schreiber and Campbell 1986).

From the perspective of what we know about animal breeding and selection as an alternative horn fly management strategy, there are multiple host-specific determinants for horn fly densities and parasitism success that help explain inter-herd variation including host odour and volatile semiochemicals (Jensen *et al.* 2004; Oyarzún *et al.* 2009), blood physiology and blood volume yields (Cupp *et al.* 2010), hair density and oily secretions of the sebaceous glands (Stelman *et al.* 1997), and defensive behaviours (Mullens *et al.* 2017). However, it is not simply a function of olfactory cues or physiological features of the animal that stimulate host selection, but is also a function of visual cues. Such host visual stimuli includes both shapes and colour (Gibson and Torr 1999). Hide colour specifically is postulated to be a characteristic that could be strategically manipulated or integrated into management strategies because horn flies have demonstrated preference for darker cattle (Franks 1964; Schreiber and Campbell 1986). However, quantifying the mechanisms underlying the different preferences and associated applications for beef enterprises are lacking. For example, hide colour, or combinations of hide colour, have not always been shown to influence horn fly abundance as shown by black/white (Holstein cows) versus black-only cattle that were commingled (Guglielmone *et al.* 2002). This may be the result of the evolutionary adaptation of some ungulates against the visual orientation that many Diptera fly species use for host location by searching for a large dark animal form, as demonstrated by the striping pattern of zebras (*Equus grevyi*, *E. quagga*, and *E. zebra*) (Waage 1981; Blahó *et al.* 2013). However, assessments of the role of hide colour have also been confounded by the comparison of different bovid species within a commingled group and/or separate groups of *Bos taurus* and *Bos indicus* cattle with hide colour not being a significant explanatory variable for horn fly abundance in either situation in a Queensland, Australia study (Doube 1984). Finally, individual animal resistance traits have also confounded explicit differences between different coloured cows (Pruett *et al.* 2003). The reality for many commercial beef enterprises is that they often have heterogeneous herds of cattle that includes cows or yearlings of different hide colours. In such situations, a more mechanistic understanding could inform integrated pest management strategies for this persistent parasite on rangelands and pasturelands.

Further complicating management of livestock parasites more generally is the contemporary dynamic climate changes we are experiencing globally, especially as it pertains to the

margins of a parasitic species range, and the role of topography and weather as constraints for infestations. For example, horn fly dynamics in cold steppe environments are not as well understood as they are in warm tropical environments (Tugwell *et al.* 1969). In addition, high-elevations may provide a buffer to horn fly infestations especially for rangelands >2400 m above sea level (Kaufman *et al.* 1999). This elevational buffer is hypothesised to be associated with cooler temperatures and livestock raised in such environments may not need to be treated with insecticides every year (Kaufman *et al.* 1999). However, more sampling and information is needed about inter- and intra-annual fluctuations in this cold environment to guide integrated pest management of horn flies (Scasta 2015b).

Given the economic damage caused by horn fly parasitism of cattle, lack of clarity on the role of hide colour and associated parasite preference dynamics for *Bos taurus*, the lack of information about horn fly dynamics in high-elevation and cold environments, and the need for novel strategies that can be integrated with existing management options, we sought to ask the following questions: (1) How is horn fly abundance affected by commingled black and white *Bos taurus* cattle? (2) Do horn fly loads approach or exceed economic thresholds in our cold and high-elevation environment? (3) Do differences in external animal temperatures during infestation periods function as a possible mechanism explaining horn fly distribution across different hide coloured cattle?

Materials and methods

Study area

The general study area is high-elevation rangeland at ~2190 m above sea level near Laramie, WY, USA (41°19'N, 105°35'W) and is within major land resource area 034A 'cool central desertic basins and plateaus'. Annual precipitation is 254–356 mm and typically in a bimodal precipitation pattern and mean average monthly temperature ranges from 0.1°C to 26.7°C. The high-elevation rangeland and cold physiognomy classifies our study area as BSk (B – arid; S – steppe; k – cold) per the Köppen-Geiger climate classification for areas that are temperate, continental, with winter snowfall, and large temperature gradients (Peel *et al.* 2007).

This project was conducted using cattle and land owned by the University of Wyoming (UW). All of the land used was owned by either the UW Agricultural Experiment Station (AES) (AES Beef Unit) west of Laramie, WY, USA or the UW Department of Zoology and Physiology (ZOO Red Buttes) south of Laramie, WY, USA. The AES Beef Unit ranch consists of ~2500 acres of rangeland and sub-irrigated meadows along the Laramie River and includes loamy upland ecological sites, saline upland ecological sites, and saline sub-irrigated ecological sites. The dominant vegetation includes native grasses such as western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve), slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners), blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths), with a minor and sub-dominant component of native shrubs such as sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) and rabbitbrush species (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom

& Baird and *Chrysothamnus viscidiflorus* (Hook.) Nutt.). In addition to the native plant communities there are areas dominated by exotic grasses including crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey), and creeping meadow foxtail (*Alopecurus arundinaceus* Poir.). The ZOO Red Buttes ranch consists of ~350 acres of rangeland and sub-irrigated meadows dominated by the grasses mentioned at the AES Beef Unit, with areas dominated by native riparian vegetation and including species such as arrowgrass (*Triglochin* L.), alkali sacaton (*Sporobolus airoides* (Torr.) Torr.), inland saltgrass (*Distichlis spicata* (L.) Greene), streambank wheatgrass (*Elymus lanceolatus* subsp. *lanceolatus* (Scribn. & J.G.Sm.) Gould), and threadleaf sedge (*Carex filifolia* Nutt.). Vegetation taxonomy and nomenclature follows the USDA Plant Database (USDA NRCS 2018).

Cattle management and sampling procedures

In 2016, 42 black Angus cows (black hided) and 42 Charolais cows (white hided) were acquired and commingled together and placed on the same pasture in early June of 2016. All cows were autumn calving. In 2017, five of the original white cows were retained and were commingled with 35 head of the same black cows. In both years, we sampled horn fly (*Haematobia irritans*) populations on cattle during the peak parasite period of the summer. Each year we conducted weekly sampling for a period of eight total weeks annually beginning in early June (10 June 2016 and 13 June 2017) through early August (3 August 2016 and 11 August 2017) (see Table 1 for specific sampling dates). For each sampling event, we located cows between the hours of 0700 a.m. and 1000 a.m. consistently because morning assessments have been found to be higher than noon or evening counts (Smythe *et al.* 2017). Digital images of as many cattle as possible from both breeds were obtained from a distance of <30 m using a high resolution digital camera equipped with a 250-mm digital zoom lens. Images were comprised of one side of each cow that was illuminated by the morning sun. In the laboratory, a digital grid was overlain on images and digital zoom was used for

counting horn flies (Scasta *et al.* 2017). We used visual ear tags, brands, and if possible other physical characteristics to assign a unique identification for each cow when possible. This was not possible for 49 of the 849 individual cow by sampling combinations, which were believed to be unique animals within each sampling period and a subsequent 'unknown' identification was assigned. All field and laboratory sampling was conducted by the same researcher to avoid any observer bias or confounding factors. Because the preferences of horn flies selection of bovid hosts includes phenotypic traits such as body size (Steelman *et al.* 1996), genotypic traits such as hide colour (Steelman *et al.* 1991; Pruett *et al.* 2003), and feeding success on a specific bovine possibly due to anticoagulation mechanisms of the fly against the coagulation systems of that particular host (Pruett *et al.* 2003; Untalan *et al.* 2006), sampling as many cattle as possible from both breed groups encompassed the gradients of variation possible relative to parasite selection

Table 1. Sampling date and sample size for black Angus and white Charolais cattle in 2016 and 2017 on high-elevation rangeland at ~2190 m above sea level near Laramie, WY, USA (41°19'N, 105°35'W)

Year	Sampling date (day of year)	Black cows (n)	White cows (n)
2016	10 June (162)	27	31
	17 June (169)	41	41
	24 June (176)	32	40
	30 June (182)	39	41
	7 July (189)	41	41
	14 July (196)	36	41
	21 July (203)	41	41
	3 August (216)	35	41
	2017	13 June (164)	19
22 June (173)		18	5
29 June (180)		26	5
5 July (186)		20	5
14 July (195)		21	5
18 July (199)		26	5
4 August (216)		30	5
11 August (223)		40	5

Table 2. Sample dates, sample size, temperature, and solar radiation features of the days sampling of external black Angus and white Charolais cow temperatures. Sampling was conducted during the three summer months in 2016 in a high-elevation rangeland at ~2190 m above sea level near Laramie, WY, USA (41°19'N, 105°35'W) and cows were commingled. Daily shortwave and longwave radiation estimates obtained for sampling dates from the NASA POWER (Prediction of Worldwide Energy Resources) Project Data Sets (<https://power.larc.nasa.gov/>, accessed 9 November 2018) from the following coordinates (latitude 41.2978 and longitude -105.6715)

Sampling data and temperature and solar radiation data	30 June 2016 (182 days)	13 July 2016 (195 days)	3 August 2016 (216 days)
Black Angus (n)	23	14	14
White Charolais (n)	25	14	14
Timing of sampling	7–8 a.m.	1–3 p.m.	11–12 a.m.
Ambient temperature (°C)	16.2	29.7	32.3
Average top-of-atmosphere insolation ^A	41.43	40.69	38.32
Average insolation incident on a horizontal surface ^A	12.88	30.56	18.71
Average downward longwave radiative flux ^A	30.10	25.28	31.14

^AMJ/m².day; derived from <https://power.larc.nasa.gov/>.

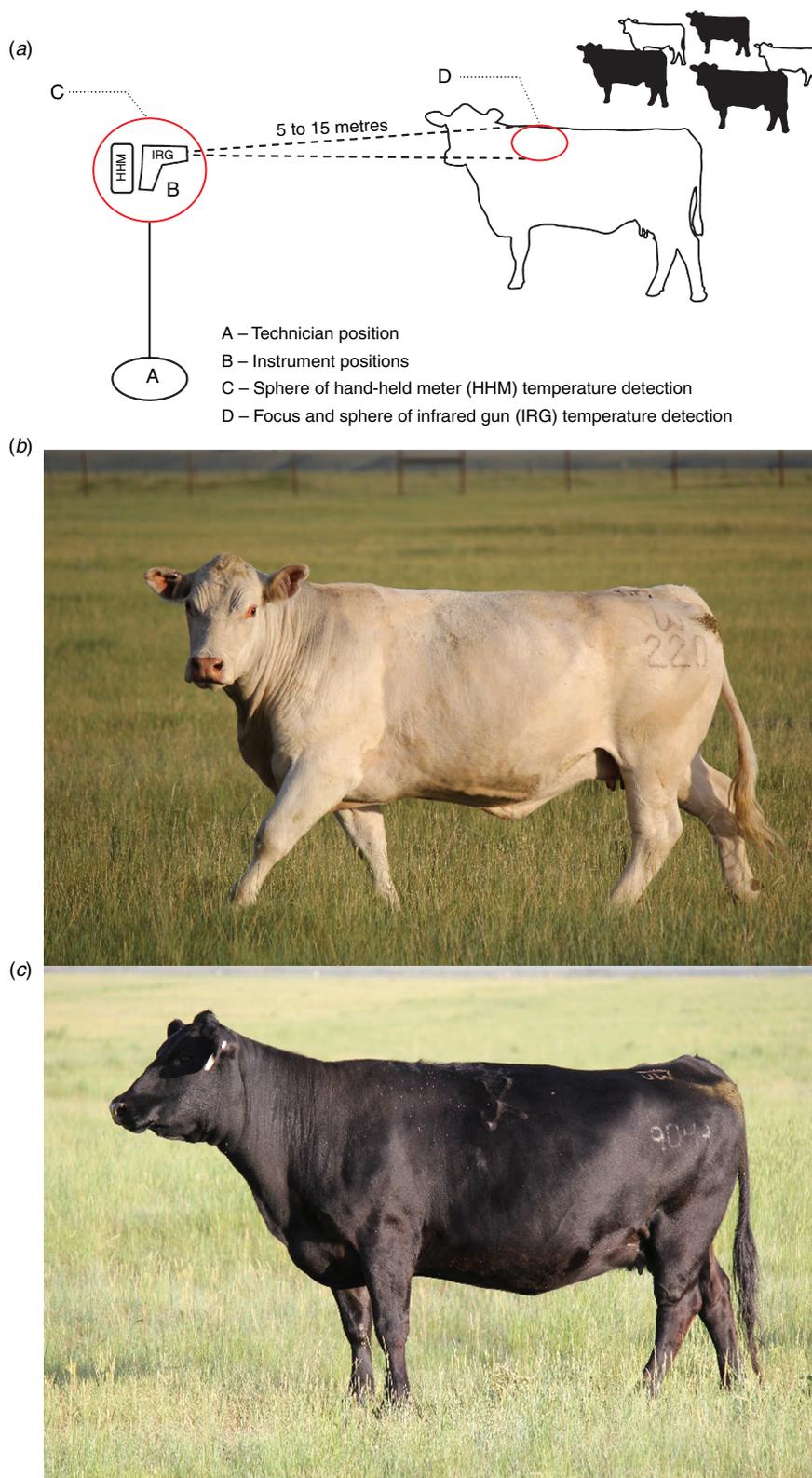


Fig. 1. (a) Thermal measurement procedure for external cow surface temperature and ambient temperature used in June, July, and August 2016, coupled with digital images of (b) Charolais and (c) Angus cows to relate horn fly densities with thermal dynamics. Pictures shown here are from the 30 June 2016 sampling date for both horn flies and thermal metrics.

of hosts. Thus, as complete of a herd sample selection of animals from each breed group would truly encompass the variation extremes of low fly carrier and high fly carrier animals. This is important for the objective of our study to detect herd variation through time as a function of breed and hide colour differences – not individual animal variation *per se*. Sampling dates and sample sizes are summarised in Table 1. Cattle management followed the guidelines stated in the Guide for the Care and Use of Agricultural Animals in Research and Teaching.

Animal temperature data

To understand the potential thermal environment driving the variation of horn fly selection or parasitism relative to different hide colours (i.e. thermoregulation), we also quantified external animal temperatures at three separate intervals in June, July, and August of 2016 at different times of the day (morning, mid-day, early afternoon) (Table 2). This was accomplished by using two temperature measurement devices. The first device was an infrared high temperature thermometer (Extech Instruments® 42 545 made by FLIR Systems®, Nashua, NH, USA) laser gun with a temperature range of -50 to 1000°C and a distance to target ratio of 50:1 that was used to determine the external temperature of cows at the upper shoulder/withers region of the body from a distance of 5–15 m (Fig. 1a) similar to Brown-Brandl *et al.* (2006). For our study specifically, this location of the animal was selected because this was the dominant location of horn fly locations noted during the study (Fig. 1b, c). The second device was a hand-held weather meter (Kestrel® 3000, Boothwyn, PA, USA) that measured the ambient temperature from the same position the infrared laser gun was positioned to measure the external cow body surface temperature (Fig. 1a). The measurement of the external temperatures of cows and the ambient temperature allowed us to then calculate the temperature differential or ΔT as the difference between the two temperature measurements (Porter and Gates 1969).

Environmental temperature data

In order to better understand the solar radiation influencing thermal dynamics on the days of sampling described above, we obtained shortwave and longwave radiation estimates including average top-of-atmosphere insolation, average insolation incident on a horizontal surface, and average downward longwave radiative flux from the NASA POWER (Prediction of Worldwide Energy Resources) Project Data Sets (Chandler *et al.* 2010; NASA 2018).

We acquired daily maximum temperatures from the Parameter-elevation Relationships on Independent Slopes Model interpolation method (PRISM Climate Group 2018). The Parameter-elevation Relationships on Independent Slopes Model extrapolates weather data using digital elevation model grid cells by developing a climate–elevation regression that uses $\sim 10\,000$ existing weather stations that are assigned weights relative to the physiographic similarity of the weather station to the grid cell of interest (Daly *et al.* 2008). Resolution of this data is at 2.5 arcmin (~ 4 -km grid) (PRISM Climate

Group 2018) and we used the cell at latitude 41.2972 and longitude -105.6657 with data from the AN81d dataset.

Statistical analyses

In order to determine how horn fly abundance was affected by breed and hide colour, we used a mixed effects modelling approach to compare breed average horn fly abundance at the annual level. In this approach, we averaged breed horn fly abundance by week and used the 8 weekly sampling dates as replicates for each year. Because we were sampling the same breed groups through time, we assigned breed group as a repeated-measure. Fixed effects in this model were breed, year, and the breed by year interaction. In order to determine if horn fly loads approach or exceed economic thresholds in our cold and high-elevation environment, we graphed weekly means and weekly high individual horn fly load by year, week, and breed. We then conducted a second analysis by week using individual cows as the replicates

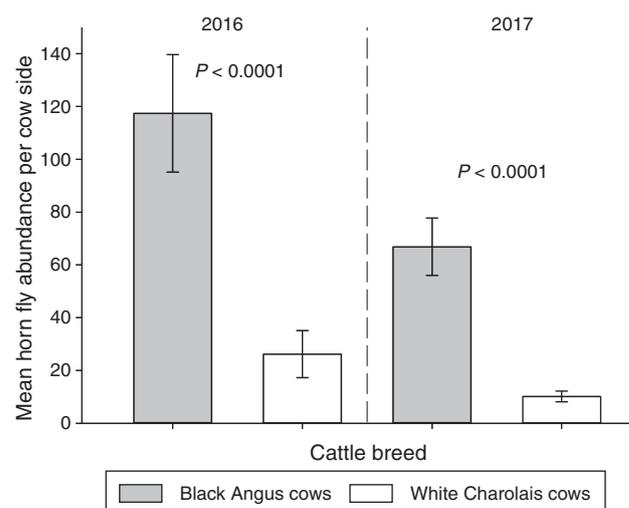


Fig. 2. Annual mean horn fly abundance and standard errors for commingled black Angus and white Charolais cows in 2016 and 2017. Means compared in a mixed effects model using the weekly sampling interval as the replicate (8 weeks annually), breed group as a repeated-measure, and considered significantly different at $\alpha = 0.05$. The response variable was square-root transformed to meet assumptions of normality but here we present raw means. The study site was high-elevation rangeland at ~ 2190 m above sea level near Laramie, WY, USA ($41^{\circ}19'N$, $105^{\circ}35'W$) and all sampling was conducted between the hours of 0700 a.m. and 1000 a.m. Digital images of as many cattle as possible from both breeds were obtained from a distance of <30 m using a 250-mm digital zoom lens.

Table 3. Fixed effects tests using seasonal horn fly means with week as the replicate ($n = 8$) and using breed group as the repeated-measure in a mixed effects modelling approach

Effects	DFNum	DFDen	F Ratio	P-value
Breed	1	21.6	51.7427	<0.0001
Year	1	21.6	8.2429827	0.009
Breed by Year	1	21.6	0.3835872	0.542

within each weekly sampling event and using animal identification as a random effect. Prior to either analyses, we calculated residuals and used a Shapiro-Wilk test for normality and based on a W statistic of 0.82 and P -value <0.0001 we determined that the response variable was non-normally distributed. Because our response variable is count data we then applied a square-root transformation (McDonald 2014). We were also interested in the total accumulated horn fly parasitism and so calculated a mean accumulated horn fly count and plotted each breed by year combination as a function of sampling time. We used an analysis of covariance to determine if the slopes of the accumulation lines differed relative to sampling timing, breed, and their interaction. In order to determine if external animal temperatures were different between black and white cattle, we used three paired sample t -test for commingled animals stratified by breed and analysed by three sampling dates (June, July, August) in 2016 for ambient temperature, cow external temperature, and difference between cow external temperature and ambient temperatures (ΔT) (Porter and Gates 1969; Wang *et al.* 2015). The method of quantifying the difference between skin temperature and surface air temperature have also been used more broadly for estimating all-wave net radiation using remotely sensed data (Wang *et al.* 2015).

When determining effects within and across years, we consider weekly sampling interval as the replicate ($n = 8$) with breed group means as the sampling unit and individual animals as the sub-sample. However, individual cows within each breed group were considered the replication in analyses assessing breed effects within a single sampling event for horn flies or a single sampling event for temperature (see Table 1 for ranges). In other words, in these instances cow breed groups were considered the experimental unit and individual animals

within groups were considered the sampling unit (Adams *et al.* 2000; Iason and Elston 2002). For research of production systems in extensive landscapes such as ours, it is logistically and financially challenging to replicate systems in space and the use of time in place of spatial replication is effective (Hart *et al.* 1988; Adams *et al.* 1989, 1994). The use of breed groups as the experimental unit within the same pasture through time has also been applied in other livestock experiments assessing breed, sire traits, cow age, and milk production (Adams *et al.* 1986; Anderson and Urquhart 1986; Colburn *et al.* 1997; Lathrop *et al.* 1988; Winder *et al.* 1996). Moreover, grazing distribution studies assessing phenotypic traits have also used an analogous experimental approach where sub-groups within a single larger group were commingled (Bailey *et al.* 2001).

Results

Horn fly abundance by commingled black and white Bos taurus cattle

Mean horn fly abundance was significantly affected by breed ($P < 0.0001$) with black cattle having higher seasonal means of horn flies than white cattle in both 2016 and 2017 (Fig. 2; Table 3). Black cows had a mean (\pm s.e.) horn fly abundance per cow side of 117 ± 22 in 2016 and 67 ± 11 in 2017 and white cows had a mean of 26 ± 9 in 2016 and 10 ± 21 in 2017 (Fig. 2). Mean horn fly abundance was also significantly affected by year ($P < 0.009$) with lower mean horn fly abundance in 2017 (Fig. 2; Table 3). Mean horn fly abundance was not affected by the interaction of breed by year ($P = 0.54$) suggesting that both breeds responded to the inter-annual fluctuations similarly (Table 3). A potential explanation for this can be attributed to the temporal trend observed in both years. It seemed to take a bit longer for spring warming to be

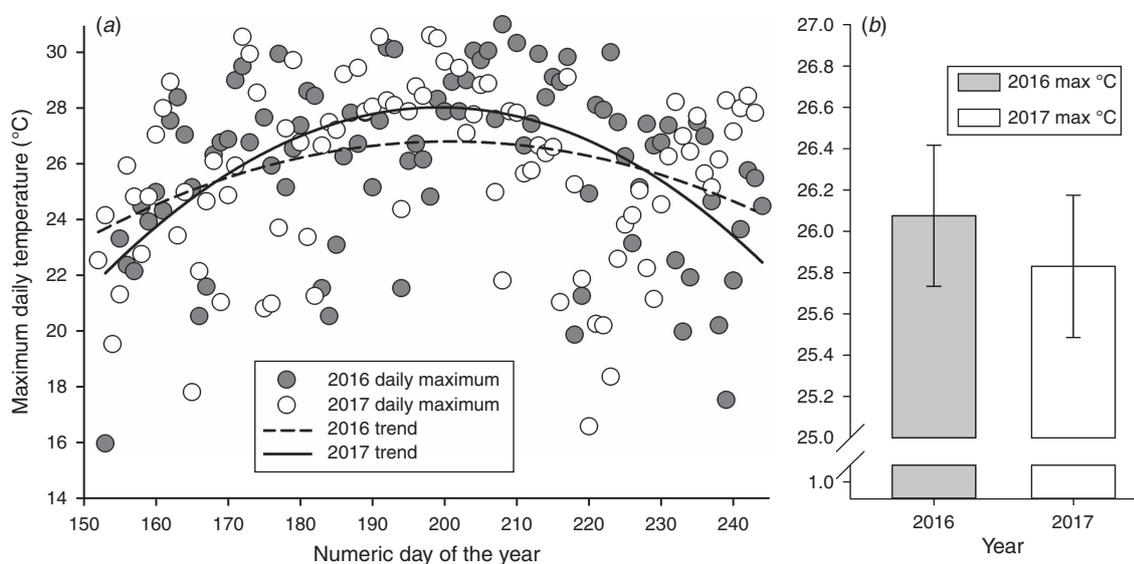


Fig. 3. (a) Maximum daily temperatures and (b) seasonal means for 2016 and 2017 from a high-elevation rangeland study site at ~ 2190 m above sea level near Laramie, WY, USA ($41^{\circ}19'N$, $105^{\circ}35'W$). (a) Maximum daily temperatures are displayed for the period of study each year and include a quadrate trendline indicating the seasonal warming and cooling patterns. Data acquired from the Parameter-elevation Relationships on Independent Slopes Model interpolation method at a resolution of 2.5 arcmin (~ 4 -km grid) using the cell at latitude 41.2972 and longitude -105.6657 and the AN81d dataset.

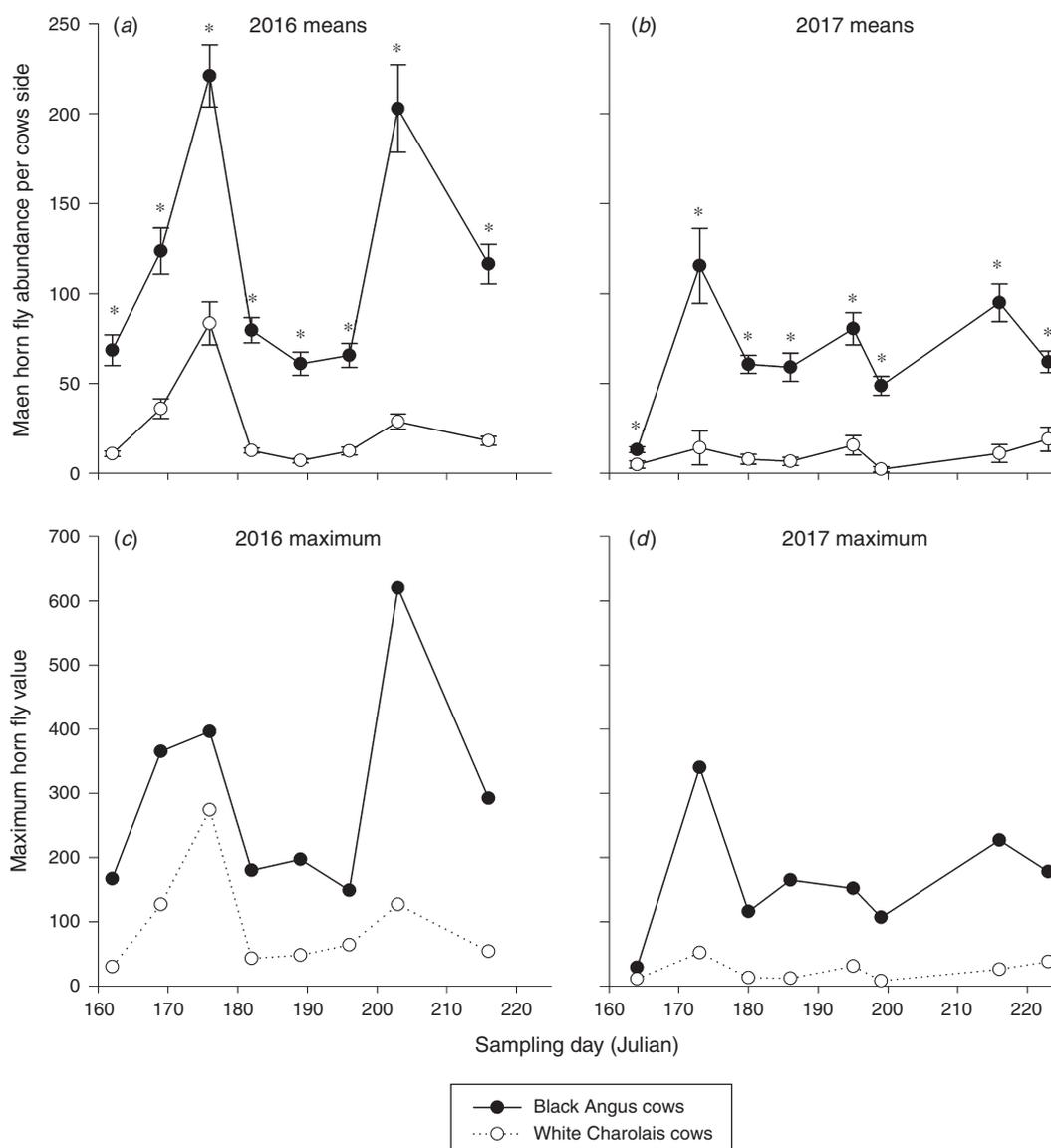


Fig. 4. Weekly mean horn fly abundance and standard errors for commingled black Angus and white Charolais cows in (a) 2016 and (b) 2017 and weekly high individual horn fly load in (c) 2016 and (d) 2017. Weekly means compared in a mixed effects model (a and b) using the individual animal as the replicate (variable n from 5 to 41; see Table 1), animal identification as a random effect, and considered significantly different at $\alpha = 0.05$. The response variable was square-root transformed to meet assumptions of normality but here we present raw means. The study site was high-elevation rangeland at ~2190 m above sea level near Laramie, WY, USA (41°19'N, 105°35'W) and all sampling was conducted between the hours of 0700 a.m. and 1000 a.m. Digital images of as many cattle as possible from both breeds were obtained from a distance of <30 m using a 250-mm digital zoom lens.

expressed in 2017 than in 2016 and cooler weather occurred earlier in 2017 than in 2016 (i.e. a narrower optimal thermal window for parasite development in 2017) (Fig. 3).

When we compared the means using animals as the replication for each week, black cattle always had higher mean horn fly abundance than white cattle for all 16 weeks of sampling across years (Fig. 4a, b). The individual black cow with the highest horn fly load was also always higher than the individual white cow with the highest horn fly load for all 16 weeks of sampling across years (Fig. 4c, d). When

assessing both mean horn fly abundance and maximum individual infestations by breeds, intra-annual patterns were similar between breeds, but white cattle were always lower (Figs 4a–d). The mean cumulative counts of horn flies was significantly explained by time of sampling ($P < 0.0001$), breed-year combination ($P < 0.0001$), and the interaction of time of sampling and breed-year combination ($P < 0.0001$) (Fig. 5). The slopes (m) for each breed-year combination were always greater for black cattle ($m_{2016} = 16.0$ and $m_{2017} = 8.6$) than for white cattle ($m_{2016} = 3.5$ and $m_{2017} = 1.2$) (Fig. 5).

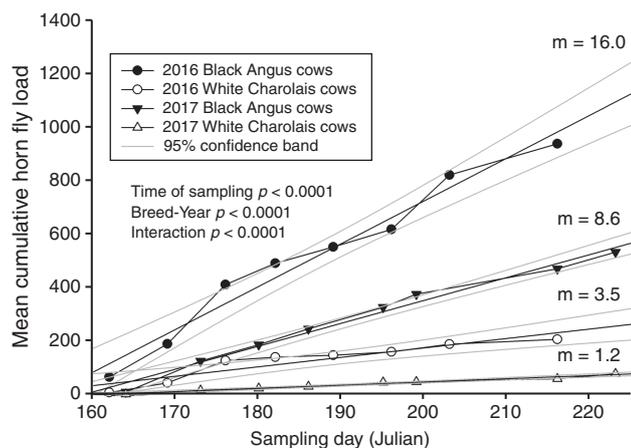


Fig. 5. Mean accumulated horn fly count for commingled black Angus and white Charolais cows plotted by breed and year combination as a function of sampling time. Slopes (m) of the accumulation lines analysed with analysis of covariance relative to sampling timing, breed, and the sampling timing by breed interaction. The study site was high-elevation rangeland at ~ 2190 m above sea level near Laramie, WY, USA ($41^{\circ}19'N$, $105^{\circ}35'W$).

Horn fly economic thresholds in our cold and high-elevation environment

Based on the commonly used economic threshold for treatment of >200 flies per cow (or >100 flies per cow side) (Kunz *et al.* 1984; Oyarzún *et al.* 2008), we can evaluate the breed-year combinations in terms of the need for treatment and production. On average, black cattle were above the threshold in 2016 with 118 per side (times 2 for 236 per cow) but not in 2017 with 67 per side (times 2 for 134 per cow) (Fig. 2). However, white cattle on average were never above the threshold with 26 per side in 2016 (times 2 for 52 per cow) and 10 per side in 2017 (times 2 for 20 per cow) (Fig. 2), and at only $\sim 25\%$ of the threshold in our study would not have warranted treatment any years. When assessing the inter-annual variation, black cattle on average were above the economic threshold 4 out of 8 weeks in 2016 but only 1 out of 8 weeks in 2017 (Fig. 4*a, b*). In contrast, white cattle only exceeded the economic threshold 1 week out of the 16 weeks of sampling across years (Fig. 4*a, b*). Individuals within each breed provide further insight to economic thresholds and treatment decisions, as the most infested individual black cow exceeded the economic threshold 8 out of 8 weeks in 2016 and 7 out of 8 weeks in 2017 or more than 94% of the combined total sampling period (Fig. 4*c, d*). However, the most infested white cow only exceeded the economic threshold 3 out of 8 weeks in 2016 and 0 out of 8 weeks in 2017 or less than 20% of the combined total sampling period (Fig. 4*c, d*).

External animal temperatures during infestation periods

At our three sampling periods in June, July, and August of 2016, mean ambient temperatures were the same for commingled cattle in June and August ($P > 0.05$) but not July ($P < 0.05$) (Fig. 6*a*; black cattle sampled at slightly warmer ($\sim 1^{\circ}C$) micro-climates). Regardless, cow external temperature and the difference between cow external temperature and

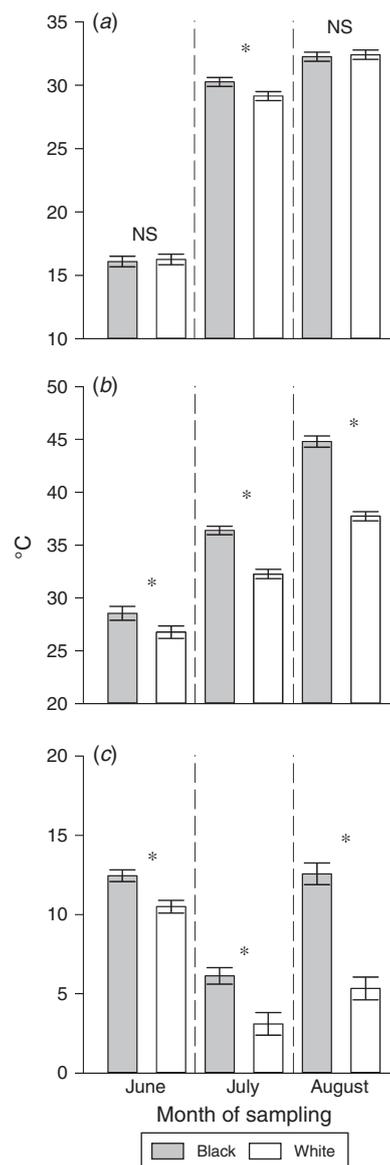


Fig. 6. (a) Ambient temperature, (b) cow external surface temperature, and (c) difference between cow external temperature and ambient temperatures (ΔT) in a high-elevation rangeland study site at ~ 2190 m above sea level near Laramie, WY, USA ($41^{\circ}19'N$, $105^{\circ}35'W$). Ambient temperature was acquired using a Kestrel 3000 weather station and cow external surface temperature was acquired using an infrared gun from the same position the ambient temperature was measured with the infrared beam positioned at the shoulder of the cow. Sampling was conducted in 2016 on 30 June, 13 July, and 3 August on sunny days, at different times of the day, and under varying solar radiation conditions (see Table 3 for additional details).

ambient temperatures (ΔT) were always higher for black cows than white cows ($P < 0.05$) (Fig. 6*b, c*).

Discussion

In our study we quantified a difference in horn fly parasitism between *Bos taurus* breeds and this difference was explained by hide colour and potentially the thermal ecology of the bovid host. Other potential breed differences that could be additional

mechanisms explaining our breed results include host odors, hemostasis, and defensive behaviours that deserve additional study in the future. The black cattle always had higher average and maximum individual horn fly loads and black cattle were the only breeds that had a herd average exceeding economic thresholds in our study and environment. Our isolation of hide colour within the *Bos taurus* species is important because some studies reported that hide colour did not influence numbers of flies on individuals within a herd but these assessments were likely confounded by *Bos indicus* and *Bos taurus* species influences (Doubé 1984). In 2016 and 2017, black cattle had horn fly loads >4x higher and >6x higher respectively than white cattle. The accumulation of total horn flies through time also occurred at a more rapid rate for black cows than for white cows. This has implications for animal production, and specifically beef sire and dam selection, because Angus and Charolais are among the most popular beef breeds in the US and Australia (Keel *et al.* 2017; Copping *et al.* 2018). Moreover, the low horn fly densities on white cows in our study (less than 100 flies per cow at many of the sampling intervals) are predicted to translate to lower defensive behaviour rates and subsequent performance losses (Mullens *et al.* 2017).

The mechanism explaining the differences measured between breeds is potentially attributed to differences in external cow temperatures and fly thermoregulation which our additional sampling addressed. We hypothesised that the greater horn fly preference displayed for black cattle was in part a function of the thermal ecology of cattle and horn fly thermoregulation. Specifically, the external temperatures of the black cows were always greater than the external temperatures of the white cows, which has also been shown in assessments of the same breeds/hide colours in a confined feeding scenario using similar methods that we used (Brown-Brandl *et al.* 2006). However, to date we have found no research available quantifying how horn flies thermoregulate relative to host external temperatures but other Diptera fly species such as robber flies (Diptera: Asilidae) and reindeer warble flies (*Hypoderma tarandi* L. (Diptera: Oestridae)) have been shown to display such behaviour (Anderson *et al.* 1994; Morgan *et al.* 1985). The relative differences of external cow temperatures between breeds was variable in terms of magnitude with a range of absolute cow external surface temperature differences between breeds from 2°C to 7°C, which encompasses the range reported by Brown-Brandl *et al.* (2006) of 4.6–6.6°C depending on the time of day. The ΔT range, which is important for thermodynamic equilibria of animals with their environment (Porter and Gates 1969), was 6.13–12.56°C for black cows and 3.10–10.49°C for white cows depending on the day of sampling. The absolute differences are an indication of the different albedo (the fraction of downward radiation that is reflected) values for different hide colours with white cattle expected to have greater albedo values than black cattle. The variation in the magnitude of absolute values and the magnitude of ΔT is also influenced by other factors at the time of sampling such as cloudiness, humidity, and atmospheric conditions (Wang *et al.* 2015). The actual external cow temperature for both breeds appears to be inversely explained by the average top-of-atmosphere insolation (short-wave) and the ΔT of black cows appears to be explained by the daily downward longwave radiative flux,

which was lower at the July sampling date than the June or August sampling dates (Table 2).

Our findings suggest that in commingled herds with black and white *Bos taurus* cattle, the host-parasite relationship is driven by breed differences and inter-annual variation. From the breed effect perspective, commingled herds with black and white *Bos taurus* cattle, different horn fly abundance can be expected with black cattle having higher infestations. This could be integrated with other horn fly management strategies that use a chemical active ingredient by treating only the subset of the whole herd that is likely to have horn fly infestations exceeding economic thresholds, and in our case this was black cattle only at certain times (Schreiber and Campbell 1986). This is important for major cattle production regions of the Australia, South America, and the US where horn fly resistance to synthetic pyrethroids and organophosphate is common (Elzen and Hardee 2003; Oyarzún *et al.* 2008; Heath and Levot 2015).

Finally, our results suggest that horn fly ecology and management in our cold high-elevation environment may function differently than in warmer sub-tropical and tropical environments. This different function has a strong management application because horn fly infestations were not a problem relative to economic thresholds every year. This suggests that conventional treatment every year with chemical active ingredients (Foil and Hogsette 1994) may not be necessary in high-elevation and cold environments similar to ours. This type of adaptive approach may be well suited for integrated pest management approaches to horn fly management and reduce over use of chemicals – an alternative strategy that may help avoid development of chemical resistance (Oyarzún *et al.* 2008).

Conclusions

Quantitative assessments of host-parasite ecology for livestock using extensive rangeland environments is necessary to develop new mitigation strategies and optimise animal production (Scasta and Koepke 2016). This is especially important as predictions for future climate may alter thermal drivers of parasitism as has been projected for our study area, which is in the northern mixed grass prairie generally (Derner *et al.* 2018). In other words, continued quantitative assessments at the margins of the range of parasites, such as cold and high-elevation regions such as our study site, are necessary to detect how current assumptions apply and if changes are occurring. For example and specific to our study, questions that must be addressed are: Are economic thresholds being reached more frequently? Are flies emerging earlier? and What is the season length of parasitism through time? Adoption of integrated pest management strategies that consider cattle hide colour can be employed for commercial cattle operations that have heterogeneous groups of cattle in terms of hide colours (Schreiber and Campbell 1986). The integration of our findings into commercial cattle operations could affect profit margins because any reduction of horn fly infestations are anticipated to improve weight gains, foraging, and milk production (Bean *et al.* 1987; Byford *et al.* 1992). The combination of lighter hided cattle with cattle with

denser hair coats could also integrate multiple host-specific determinants determining horn fly densities as demonstrated by infestation differences between Charolais and Chianina cattle, both of which are white-coloured breeds (Steelman *et al.* 1991). Future research should address if other biting Diptera flies that are known parasites of cattle, such as *Musca autumnalis*, *M. domestica*, *Musca vetustissima*, *Stomoxys calcitrans*, and *Tabanus* species, have a dark host preference (Gibson and Torr 1999; Scasta *et al.* 2017; Godwin *et al.* 2018). Additional inquiry should also further quantify specific fly locations on different zones of the bovid host's body coupled with zone specific temperature measurements to better understand how flies are thermoregulating on different cattle breeds in dynamic thermal environments.

Conflict of interest

The authors declare no conflicts of interest.

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